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UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

EFFET DES PERTURBATIONS D'ORIGINE ANTHROPIQUE SUR DEUX
ESPÈCES VÉGÉTALES D'IMPORTANCE CULTURELLE

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

MAXIME THOMAS

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AVANT-PROPOS

Cette thèse par articles, réalisée dans le cadre du doctorat en sciences de l'environnement de l'Université du Québec en Abitibi-Témiscamingue, présente le résultat de mes recherches sur l'effet des perturbations anthropiques sur deux espèces végétales d'intérêt autochtone, *Rhododendron groenlandicum* et *Vaccinium angustifolium*. Elle se compose d'un chapitre d'introduction (Chapitre I), de trois chapitres en anglais sous forme d'articles scientifiques (Chapitres II, III et IV), et d'un chapitre de conclusion (Chapitre V).

Le chapitre II, « *How will climate change and forest harvesting influence the distribution of two culturally salient species?* », traite de l'effet des changements climatiques et de la récolte forestière sur l'habitat et l'aire de répartition de *Rhododendron groenlandicum* et *Vaccinium angustifolium*. L'article correspondant a été publié dans la revue *Science of the Total Environment* en avril 2024.

Le chapitre III, « *Effect of industrial disturbances on the flavonoid concentration of Rhododendron groenlandicum* », traite de l'effet des perturbations liées aux sites miniers et aux lignes de transport d'hydroélectricité sur la composition en flavonoïdes des feuilles de *R. groenlandicum*. L'article correspondant a été publié dans la revue *Botany* en mai 2023.

Le chapitre IV, « *Unraveling the interplay of the soil microbiome and (poly)phenol content in blueberry in response to disturbances* », étudie les interactions entre les perturbations liées aux sites miniers et aux lignes de transport d'hydroélectricité, les propriétés physico-chimiques du sol, le microbiome du sol, et la composition en composés phénoliques des fruits de *V. angustifolium*. L'article correspondant est en préparation pour soumission à une revue scientifique.

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

ADN	Acide désoxyribonucléique
AGEORI	Âge et origine du peuplement forestier
ArcGIS	Aeronautical reconnaissance coverage geographic information system. Logiciel d'information géographique
ANOVA	Analysis of variance (analyse de la variance)
ASV	Amplicon sequence variant
AUC	Area under curve. Métrique d'évaluation de la performance d'un modèle
CanESM2	Canadian earth system model version 2
CEC	Cation exchange capacity (capacité d'échange de cations)
CMIP5	Climate model intercomparison project phase 5
CO ₂	Dioxyde de carbone
CSS	Culturally salient species (espèce d'importance culturelle)
dbRDA	Distance-based redundancy analysis (analyse de redondance basée sur la distance)
DNA	Deoxyribonucleic acid (acide désoxyribonucléique)
e.g.	<i>exempli gratia</i> (par exemple)
FORCOV	Forest cover (couvert forestier)
GAM	Generalized additive model (modèle additif généralisé)
GBM	Generalized boosted model (modèle boosté généralisé)
GLM	Generalized linear model (modèle linéaire généralisé)

HCl	Chlorure d'hydrogène
HFR	Homogeneous fire regime
HSS	High strength silica
ICP	Inductively coupled plasma
INAF	Institut sur la nutrition et les aliments fonctionnels
<i>in situ</i>	Dans son milieu naturel
LC	Liquid chromatography
LDA	Linear discriminant analysis
LEfSe	Linear discriminant analysis effect size. Analyse identifiant la différence d'abondance de plusieurs variables entre des groupes sur la base du score de LDA.
MANOVA	Multivariate analysis of variance (analyse de variance multidimensionnelle)
MAXENT	Maximum entropy (modèle d'entropie maximale)
MFFP	Ministère des forêts de la faune et des parcs du Québec
MS/MS	Spectrométrie de masse en tandem
NAD	North american datum. Système de référence géodésique pour l'Amérique du Nord
NMDS	Non-metric multidimensional scaling. Technique d'ordination non contrainte
NSERC	Natural sciences and engineering research council of Canada
PACs	Proanthocyanidines
PC	Principal component (composante principale)
PCA	Principal component analysis (analyse en composantes principales)

PDA	Photo diode-array
p. ex.	Par exemple
PERMANOVA	Permutational analysis of variance (analyse de variance par permutations)
RCP	Representative concentration pathway. Scénario de forçage radiatif permettant de modéliser l'influence des changements climatiques sur le climat futur
RDA	Redundancy analysis (analyse de redondance)
RF	Random forest (forêt aléatoire)
ROS	Reactive oxygen species (espèces réactives de l'oxygène)
SDM	Species distribution model (modèle de distribution d'espèce)
SRES	Special report on emission scenarios
TSS	True skill statistic. Métrique d'évaluation de la performance d'un modèle
UPLC	Ultra performance liquid chromatography
UQAT	Université du Québec en Abitibi-Témiscamingue
UV	Ultraviolet

LISTE DES SYMBOLES ET DES UNITÉS

*	Significatif au seuil $P \leq 0.05$
**	Significatif au seuil $P \leq 0.01$
***	Significatif au seuil $P \leq 0.001$
<	Inférieur à
>	Supérieur à
\leq	Inférieur ou égal à
%	Pourcent
°C	Degré celsius
°N	Degré de latitude nord
ω^2	Omega carré
μm	Micromètre
cm	Centimètre
g/L	Gramme par litre
m	Mètre
mg	Milligramme
mg/g	Milligramme par gramme

min	Minute
mL	Millilitre
mm	Millimètre
mmol/L	Millimole par litre
nm	nanomètre
km	Kilomètre
km ²	Kilomètre carré
kv	Kilovolt
<i>r</i>	Coefficient de corrélation
R ²	R carré. Coefficient de détermination. Mesure de l'ajustement d'un modèle
rpm	Révolution par minute
P	Valeur de p. Mesure de la significativité d'une différence, en % de probabilité d'observer la différence par hasard

RÉSUMÉ

La forêt boréale est soumise à de nombreuses perturbations, anthropiques comme naturelles, qui affectent non seulement le paysage, mais également les espèces végétales et animales. Ces perturbations peuvent altérer les écosystèmes et affecter la culture de certaines populations. C'est notamment le cas des communautés autochtones, dont le mode de vie dépend d'espèces d'importance culturelle pour la pratique de diverses activités traditionnelles. Il est donc nécessaire d'évaluer le devenir des espèces d'importance culturelle face aux perturbations actuelles et futures pour comprendre les répercussions environnementales et culturelles qui en découlent.

L'objectif de cette thèse était donc d'étudier l'effet de différentes perturbations en forêt boréale sur les espèces d'importance culturelle. Plus particulièrement, deux espèces d'importance culturelle ont servi de cas d'étude : *Rhododendron groenlandicum* (thé du Labrador) et *Vaccinium angustifolium* (bleuet à feuilles étroites). Ces deux espèces sont importantes dans les cultures autochtones pour leur consommation à des fins nutritionnelles et médicinales. Les feuilles de *R. groenlandicum* servent à soigner de nombreux maux (p. ex. tonique ou traitement du rhume). Les fruits de *V. angustifolium* occupent une place d'importance dans la diète autochtone, et contribuent au lien des autochtones avec leur territoire via les activités de cueillette. Ces deux espèces ont également un rôle important dans l'environnement, car elles influencent la succession forestière en limitant la colonisation et la croissance des arbres.

Les communautés autochtones ont une conscience aigüe de l'effet des perturbations sur leur territoire. Ainsi, cette thèse a été réalisée en collaboration avec trois communautés autochtones dans l'est du Québec : la communauté d'Abitibiwinni (Anicinapek), celle de Mistissini (Eeyouch) et celle de Nemaska (Eeyouch). Les territoires traditionnels de ces communautés représentent l'aire d'étude de la thèse. Ces communautés ont également choisi les espèces étudiées ainsi que certaines des perturbations à étudier.

Dans le chapitre II, l'effet des changements climatiques et des coupes forestières sur la répartition des deux espèces dans le futur a été évalué. Les changements climatiques, surtout s'ils sont importants, entraîneront une diminution de la présence des deux espèces dans le paysage boréal. Cette diminution sera due à une augmentation de la proportion de feuillus dans le paysage, défavorables à la présence des deux espèces étudiées, à cause d'une forte augmentation de fréquence et sévérité des feux. L'effet des coupes forestières s'additionnera à celui des changements climatiques, accentuant davantage la proportion de feuillus dans le paysage. En conséquence, pour maintenir les deux espèces étudiées dans le paysage, il est nécessaire de limiter l'augmentation

de la proportion de feuillus. Pour ce faire, il faudrait prendre en compte les zones forestières susceptibles de brûler lors de la planification des coupes, et planter des conifères plus adaptés à des feux fréquents, comme le pin gris, pour maintenir la proportion de conifères dans le paysage.

Dans le chapitre III, l'effet de la présence d'une mine ou d'une ligne hydroélectrique sur les composés d'intérêt médicinal de *R. groenlandicum* a été étudié. La présence de différentes mines (or, cuivre et lithium) entraîne une diminution de la concentration en (poly)phénols, des composés d'intérêt pour la santé humaine, dans les feuilles de l'espèce. À l'inverse, la présence d'une ligne hydroélectrique entraîne une augmentation des (poly)phénols. Cela implique que le potentiel médicinal de l'espèce serait diminué par les mines, et augmenté par les lignes hydroélectriques. Cependant, d'autres facteurs sont à considérer avant de conclure quant aux propriétés médicinales de *R. groenlandicum*. En effet, les perturbations peuvent être associées avec la présence de polluants néfastes pour la santé humaine. Cet aspect a donc besoin d'être évalué avant d'émettre de potentielles recommandations pour la santé humaine.

Dans le chapitre IV, l'effet de ces deux mêmes perturbations sur les composés d'intérêt nutritionnel de *V. angustifolium* a été étudié. D'autres éléments ont également été considérés pour obtenir un portrait plus complet de l'effet des perturbations sur cette espèce, à savoir les propriétés du sol et le microbiome du sol. La présence d'une mine ou d'une ligne hydroélectrique n'entraîne pas d'effet notable sur les composés d'intérêt nutritionnel de *V. angustifolium*. Cela peut s'expliquer par la production de composés différents d'une espèce à l'autre pour répondre aux perturbations. De plus, il est possible que les fruits soient exposés de façon différente aux perturbations que les feuilles. En revanche, les mines et les lignes hydroélectriques influencent les propriétés du sol et le microbiome du sol. Le sol à proximité des mines est plus concentré en métaux, notamment en cuivre et fer, résultant en une abondance plus élevée de microorganismes tolérants aux métaux tels que le genre de champignon *Oidiodendron*. Le sol sous les lignes hydroélectriques est pauvre en carbone, et contient divers débris ligneux, ce qui peut expliquer l'abondance plus élevée de microorganismes saprotrophes tels que la classe de bactérie Ktedonobacteria. Enfin, deux taxons bactériens se sont montrés prometteurs pour améliorer le potentiel nutritif et médicinal de *V. angustifolium*. Les classes Bacilli et Desulfotobacteriia, bien que n'étant pas affectées par les mines et lignes hydroélectriques, étaient liées à des concentrations plus élevées de (poly)phénols dans les fruits de *V. angustifolium*. En trouvant les conditions environnementales favorables à ces deux classes bactériennes, il serait possible d'optimiser leur abondance, et ainsi les concentrations en (poly)phénols des bleuets.

Cette thèse permet de mettre en lumière les effets complexes des perturbations sur les espèces d'importance culturelle, et la nécessité d'utiliser différentes approches pour les étudier adéquatement. En effet, les effets des perturbations sont multiples, peuvent interagir, et ne sont pas toujours facilement visibles au premier abord. De plus, les

perturbations peuvent avoir des conséquences environnementales, mais également socio-culturelles, lorsqu'elles touchent des espèces utilisées par les autochtones par exemple. Il est donc important d'évaluer l'effet des perturbations sur les espèces végétales de façon complète afin de mieux comprendre les conséquences qui en découlent et de prendre les décisions adaptées pour limiter ces conséquences.

Mots clés : thé du Labrador, bleuet, mines, lignes hydroélectriques, changements climatiques, coupe forestière, perturbations, (poly)phénols, microbiome, sol, modélisation.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 La forêt boréale

Le terme « forêt boréale » désigne une forêt de la zone circumpolaire, où les températures peuvent passer sous le point de congélation 6 à 8 mois par année (Burton et al. 2010). Par conséquent, ce type de forêt se caractérise par une dominance d'arbres tolérants au froid, principalement des genres *Abies*, *Larix*, *Picea*, *Pinus*, *Populus* et *Betula* (Brandt 2009). La forêt boréale est très vaste; elle représentait environ 30% des 3,9 milliards d'hectares de forêts sur la planète en 2013 (Burton et al. 2010; Brandt et al. 2013; Gauthier et al. 2015). Rien qu'au Canada, elle couvrait 270 millions d'hectares, soit environ 7% de la superficie forestière mondiale en 2013 (Brandt et al. 2013).

L'importance de la forêt boréale ne s'arrête pas à sa superficie. Elle comporte l'un des plus grands stocks de carbone de la planète, notamment dans ses tourbières, à hauteur d'environ un tiers du carbone terrestre (Pan et al. 2011; Bradshaw et Warkentin 2015; Gauthier et al. 2015). Elle contient également une grande partie des réserves d'eau douce mondiales dans ses lacs, rivières et milieux humides (Gauthier et al. 2015), et approvisionne de nombreuses industries en ressources naturelles, notamment en bois (Burton et al. 2010; Brandt et al. 2013). De plus, la forêt boréale abrite une biodiversité faunique emblématique, avec des espèces telles que le bison (*Bison bison* Linnaeus) ou le caribou (*Rangifer tarandus* Gmelin), et sert de refuge à des milliers d'oiseaux

migrateurs (Kayes et Mallik 2020). La forêt boréale comporte également une biodiversité végétale d'importance, avec certaines espèces rares comme le pin à écorce blanche (*Pinus albicaulis* Engelmann) (Mahalovich et Stritch 2013), et des communautés de sous-bois qui remplissent des rôles cruciaux dans l'écosystème, notamment en lien avec le cycle des nutriments et la succession forestière (Nilsson et Wardle 2005). Enfin, la forêt boréale possède également une valeur culturelle, car en plus d'être une source de loisirs et de spiritualité, elle fait partie intégrante du mode de vie traditionnel des communautés autochtones, pour lesquelles elle est, entre autres, un lieu d'héritage et de transmission de savoir, un garde-manger et une pharmacie naturelle (Parlee et al. 2005; Saint-Arnaud et al. 2009; Basile et al. 2017).

La forêt boréale est un milieu riche en ressources naturelles, exploitées par différentes industries (p. ex. : minière, forestière, énergétique). À ces perturbations anthropiques s'ajoutent des perturbations naturelles variées (p. ex. : feux, épidémies d'insectes). Ainsi, les perturbations anthropiques et naturelles façonnent les paysages boréaux en constante évolution (Venier et al. 2014; Gauthier et al. 2015; Bélisle et Asselin 2021). Les perturbations naturelles, comme les feux, affectent la forêt boréale depuis des siècles et sont nécessaires au maintien de son équilibre dynamique (Gromtsev 2002; Bergeron et al. 2006; Burton et al. 2010; Kayes et Mallik 2020). Cependant, avec les changements climatiques, il est possible que les perturbations naturelles atteignent des fréquences et des sévérités dépassant la capacité de la forêt boréale à persister dans son équilibre dynamique. Par exemple, les feux augmenteront en fréquence et sévérité à mesure que le climat deviendra plus chaud et sec (Wang et al. 2017; Boulanger et al. 2018b), et la demande croissante en énergie et en matières premières laisse présager un maintien ou un accroissement des perturbations liées aux industries extractives (Kreutzweiser et al. 2013; Venier et al. 2014; Webster et al. 2015; Trojahn et Teuber 2021; Mauleón 2022). Dans ce contexte, la forêt boréale et les espèces qu'elle abrite font face à un avenir incertain face aux perturbations grandissantes. Dans le cadre de cette thèse, nous nous concentrerons sur le devenir d'espèces végétales face aux

perturbations s'accroissant en forêt boréale. De par leur caractère sessile, les espèces végétales ne peuvent éviter les perturbations au cours de leur vie, et y sont donc exposées de façon constante (Vitt et al. 2010; Winder et al. 2011, 2021).

1.2 Perturbations

Les perturbations affectant la forêt boréale sont nombreuses, et cette thèse ne prétend pas les traiter de façon exhaustive. Quatre perturbations d'importance seront traitées ici : les changements climatiques, la coupe forestière, les activités minières et le transport d'hydroélectricité. Ces perturbations peuvent être divisées en deux catégories. D'une part, les perturbations ayant un effet à large échelle, provoquant le remplacement ou la modification de peuplements entiers : les changements climatiques et l'aménagement forestier. Ces perturbations affectent les espèces boréales notamment par la modification du couvert forestier, donc de leur habitat. D'autre part, les perturbations ayant un effet plus localisé, qui occupent une plus faible superficie : les activités minières et le transport d'hydroélectricité. Ces perturbations affectent les espèces boréales directement, en les forçant à s'adapter à un stress local (Aitken et al. 2008; Sharma et al. 2020) ou en fragmentant leur habitat (Li et Lin 2019).

1.2.1 Changements climatiques

La forêt boréale est parmi les écosystèmes dans lesquels les changements climatiques projetés sont les plus importants (Intergovernmental Panel on Climate Change 2014; Gauthier et al. 2015). En effet, tandis que l'augmentation de la température moyenne projetée d'ici 2050 à l'échelle de la planète est de 1 à 2°C, l'augmentation projetée pour les écosystèmes boréaux est de 2 à 5°C durant le même laps de temps (Price et al. 2013;

Intergovernmental Panel on Climate Change 2014). Au Canada, cette augmentation des températures pourrait être accompagnée d'augmentations locales des précipitations, mais qui ne suffiraient pas à compenser les besoins en eau accrus des plantes (Intergovernmental Panel on Climate Change 2014; Chaste et al. 2019). L'augmentation des températures générera donc des conditions plus sèches, qui, couplées à une augmentation des événements climatiques extrêmes liés aux changements climatiques (p. ex. sécheresses et gels tardifs), entraîneront une diminution de la croissance des arbres et une augmentation de leur mortalité (Peng et al. 2011; Chaste et al. 2019; Marquis et al. 2022). Les espèces forestières de début de succession, notamment les feuillus, devraient bénéficier de l'augmentation des températures et du CO₂ atmosphérique, au détriment des espèces de fin de succession, principalement des conifères (Goldblum et Rigg 2005; Searle et Chen 2017; Boulanger et al. 2022). Ces conditions climatiques pourraient également faire basculer certaines parties de la forêt boréale vers d'autres états stables moins arborés tels que des landes (Jasinski et Payette 2005; Girard et al. 2008).

En plus de leur effet direct sur la végétation, les changements climatiques affectent également la forêt boréale en modifiant les régimes de feux. Un climat plus chaud et sec augmenterait les probabilités d'ignition (et par conséquent la fréquence) et la sévérité des feux (Wang et al. 2017; Boulanger et al. 2018b). Des feux plus fréquents auront pour effet de rajeunir l'âge moyen des peuplements à l'échelle du paysage, en les empêchant d'atteindre les stades plus avancés de la succession avant le feu suivant (Weir et al. 2000; Bergeron et al. 2017). Des feux plus fréquents et sévères pourraient aussi, à l'échelle du site, causer des « accidents de régénération » puisque les arbres n'auraient pas le temps d'atteindre la maturité sexuelle entre deux incendies, les peuplements forestiers étant alors remplacés par des zones non forestières (Marchais et al. 2020, 2022; Baltzer et al. 2021).

De tels changements dans la composition forestière pourraient avoir des conséquences sur la flore de sous-bois et la faune de la forêt boréale. Certaines de ces espèces sont associées avec des peuplements de fin de succession composés de conifères comme l'épinette noire (*Picea mariana* (Miller) Britton, Stern & Poggenburgh), et sont donc menacées par la diminution de ces peuplements. C'est le cas, par exemple, de différentes espèces d'oiseaux, dont le pic à dos noir (*Picoides arcticus* Swainson) (Boulanger et al. 2023), ou de certaines communautés de bryophytes (Barbé et al. 2020).

1.2.2 Aménagement forestier

L'industrie forestière contribue de façon importante à l'économie du Canada, employant plus de 200 000 personnes et ayant généré 35 milliards de dollars canadiens en 2021, soit 1,5% du produit intérieur brut (Ressources Naturelles Canada 2022). Le Canada produit plus de 80 millions de mètres cubes de bois chaque année et est le premier pays exportateur de produits du bois au monde (Burton et al. 2010). Une bonne partie du volume de bois récolté provient de la forêt boréale, qui est soumise à des coupes forestières sur environ 35% de son étendue (Bogdanski 2008). Au Canada, la majorité du bois est récolté par coupe totale (Gauthier et al. 2008; Cyr et al. 2009). L'une des principales conséquences des coupes en forêt boréale est le remplacement de vieilles forêts de conifères par des peuplements plus jeunes, notamment feuillus (Cyr et al. 2009; Kuuluvainen et Gauthier 2018; Boulanger et Pascual Puigdevall 2021). De plus, contrairement aux feux, les coupes ne sont pas aléatoires, ce qui contribue à homogénéiser le paysage, et donc diminue la diversité d'habitats disponibles pour les espèces boréales (Cyr et al. 2009). Les coupes forestières ciblent notamment davantage certains types de vieux peuplements à haute valeur commerciale, ce qui diminue la diversité des vieilles forêts (Martin et al. 2020). L'effet des coupes se cumule également avec celui des feux, ce qui accentue le basculement de la forêt vers des zones

moins ou non arborées (Girard et al. 2008; Boulanger et Pascual Puigdevall 2021). En effet, lorsqu'un feu suit de près une coupe, cela élimine les arbres avant qu'ils ne soient matures, donnant lieu à ce qu'on appelle un échec de régénération : les arbres ne peuvent se régénérer à nouveau faute de graines et la zone bascule vers un état non forestier (Splawinski et al. 2019).

Les modifications du paysage forestier entraînées par l'aménagement forestier accentuent la diminution des espèces boréales associées aux peuplements de conifères de fin de succession (Boulanger et al. 2023). L'aménagement forestier menace donc également les espèces d'oiseaux ou les communautés de bryophytes mentionnées dans la section précédente (Barbé et al. 2020; Boulanger et al. 2023). Certaines espèces sont même plus fortement affectées par l'aménagement forestier que par les changements climatiques; c'est le cas de l'ours grizzli (*Ursus arctos* Linnaeus) (Venier et al. 2014), ou encore du caribou forestier (*Rangifer tarandus* Gmelin), qui est déjà mis en péril par la diminution des vieilles forêts (St-Laurent et al. 2022; Leblond et al. 2022).

1.2.3 Activités minières

La forêt boréale du Canada est riche en minéraux; l'industrie minière y représente un secteur d'activité important (Bogdanski 2008; Burton et al. 2010). En 2021, l'industrie minière du Canada a généré 55,5 milliards de dollars canadiens, principalement en produisant des minéraux comme de l'or, du fer, du cuivre et du nickel (Gouvernement du Canada 2023). Lorsqu'on inclut les activités de transformation des matières extraites et les industries de la métallurgie qui en découlent, le secteur minier a généré 91 milliards de dollars canadiens en 2021, soit 4% du produit intérieur brut, et employait 403 000 personnes (Gouvernement du Canada 2023).

Le revers de la médaille, c'est que la génération de cette richesse a des conséquences sur l'environnement. Il y a plus de 200 sites miniers actifs au Canada, et plus de 10 000 anciens sites non restaurés, sans compter les conséquences des activités annexes comme l'exploration minière (Tremblay et Hogan 2006; Gouvernement du Canada 2023). La création d'un site minier entraîne le défrichage de peuplements forestiers, et donc la dégradation de l'habitat des espèces qu'ils abritent, pour faire place aux différentes infrastructures (Sonter et al. 2018; Haddaway et al. 2019). En plus de cette perturbation initiale, le site minier, une fois en exploitation, génère des résidus pouvant contenir des éléments toxiques, notamment des métaux lourds (Yu et Zahidi 2023). Ces métaux lourds peuvent se retrouver en suspension dans l'air sous forme de poussière, et ainsi sortir du site minier pour contaminer l'environnement (Yin et al. 2023b, 2023a; Yu et Zahidi 2023). Les métaux pénètrent ensuite dans les espèces végétales, soit directement par dépôt de particules contaminées, soit en pénétrant dans l'eau ou le sol pour ensuite être absorbés (Bordeleau et al. 2016; Karaca et al. 2018).

La présence de métaux lourds dans une plante peut avoir des conséquences néfastes sur son fonctionnement. En effet, les métaux lourds peuvent réagir avec l'oxygène présent dans les cellules de la plante, produisant des espèces réactives de l'oxygène (ROS, Reactive Oxygen Species) en quantités excessives : on parle alors de stress oxydatif (Feki et al. 2021; Noor et al. 2022). En quantités contrôlées, les ROS contribuent à la signalisation cellulaire (Apel et Hirt 2004; Choudhury et al. 2017). La quantité de ROS dans une plante est contrôlée par l'effet détoxifiant de réactions enzymatiques et non enzymatiques (Gill et Tuteja 2010; Huang et al. 2019). Lorsque ces réactions ne suffisent plus à maintenir l'équilibre et que les ROS sont présentes en excès, elles deviennent toxiques car elles dégradent les protéines et les lipides dans les cellules, et ultimement perturbent les fonctions cellulaires et endommagent l'ADN de la plante (Ali et al. 2019; Noor et al. 2022). Ces effets des ROS au niveau cellulaire peuvent se répercuter au niveau de la plante entière lorsque de nombreuses cellules sont touchées, entraînant des conséquences sur son métabolisme, sa germination ou sa reproduction

par exemple (Adeel et al. 2019; Yin et al. 2021). Des dommages importants à l'ADN peuvent même entraîner la mort des cellules, donc des nécroses, qui peuvent finalement conduire à la mort de la plante (Anjum et al. 2015; Sharma et al. 2020; Feki et al. 2021). Pour combattre les stress oxydatifs, la plante dispose de son métabolisme secondaire, une batterie de composés chimiques qui lui permettent de s'adapter à son environnement (Schützendübel et Polle 2002; Sytar et al. 2013; Thakur et al. 2019). Parmi les composés chimiques impliqués dans la réponse des plantes aux stress oxydatifs, les composés phénoliques, tels que les flavonoïdes, sont particulièrement importants (Agati et Tattini 2010; Sytar et al. 2013; Kumar et Pandey 2013; Thakur et al. 2019). En effet, les composés phénoliques peuvent détoxifier les ROS en les réduisant avant qu'elles ne causent des dommages à la plante (Figure 1.1) (Agati et Tattini 2010; Kumar et Pandey 2013). De plus, les composés phénoliques peuvent chélater les métaux lourds (Keilig et Ludwig-Müller 2009; Sytar et al. 2013), ce qui contribue à diminuer le stress oxydatif généré par les activités minières. La production de ces composés permet donc à la plante de survivre aux stress oxydatifs mais elle a un coût pour la plante, ce qui peut réduire sa croissance (Herms et Mattson 1992; Huot et al. 2014; Fiorucci 2020).

Les mines peuvent également affecter les plantes de façon indirecte, en modifiant le sol sur lequel elles poussent. L'exploitation minière acidifie souvent l'environnement alentour et cause donc une diminution du pH du sol en l'absence de restauration (Dudka et Adriano 1997; Johnson et Hallberg 2005). Lorsque des mesures de restauration sont prises, l'effet inverse peut se produire : l'acidification du sol générée par la mine est surcompensée, donnant lieu à un sol plus basique que la normale (Dimitriu et al. 2010). La modification du pH du sol par les activités minières peut avoir des conséquences néfastes sur la croissance des plantes, notamment en modifiant la disponibilité des nutriments et des oligo-éléments (Comerford 2005; Calvo-Polanco et al. 2017).

De plus, des changements dans les conditions du sol entraînent également des conséquences sur un autre acteur important pour les plantes : le microbiome, c'est-à-dire les bactéries et champignons du sol. Les plantes, via leur système racinaire, sont étroitement liées au microbiome du sol, qui peut les influencer de façon positive comme négative (Ali et al. 2017; Trivedi et al. 2020). La grande majorité des plantes forme des symbioses avec des champignons mycorhiziens du sol pour capter plus efficacement les nutriments dont elles ont besoin (Jeffries et al. 2003; Brundrett 2009; Trivedi et al. 2020). Certaines bactéries promeuvent également la croissance des plantes, notamment en les aidant à capter des nutriments (Richardson 2001; Franche et al. 2009; Ali et al. 2017; Rahman et al. 2018). Le microbiome du sol contient aussi divers pathogènes qui peuvent infecter les plantes et générer des ROS (avec les conséquences mentionnées plus haut) (Mendes et al. 2013; Schlaeppli and Bulgarelli 2015; Ali et al. 2017; Huchzermeyer et al. 2022). Par exemple, les champignons du genre *Fusarium* causent le flétrissement ou le pourrissement de nombreuses plantes d'intérêt agronomique telles que le blé, les pommes de terre ou les piments (Bentley et al. 2006; Wharton et al. 2006; Fernández et al. 2021). Les champignons du genre *Phytophthora*, quant à eux, infectent et causent le pourrissement des racines de différentes espèces d'arbres telles que le chêne vert (*Quercus ilex* Linnaeus) ou l'aulne glutineux (*Alnus glutinosa* (Linnaeus) Gaertner) (Ruiz-Gómez et al. 2019; Fuller et al. 2023). Le microbiome est sensible aux caractéristiques physico-chimiques du sol, notamment le pH (Fierer et Jackson 2006; Ali et al. 2017); qui peuvent être modifiées par l'activité minière (Dimitriu et al. 2010; Pershina et al. 2020; Kirillovna Kimeklis et al. 2022). En fonction des caractéristiques physico-chimiques affectées et des micro-organismes présents dans le sol avant perturbation, l'abondance relative des pathogènes peut augmenter ou diminuer, de même que l'abondance relative des micro-organismes bénéfiques. Ces changements dans le microbiome du sol peuvent se répercuter sur les plantes, affectant leur croissance et leur nutrition (Ali et al. 2017; Trivedi et al. 2020), ou encore leur

métabolisme secondaire (p. ex. la production des composés phénoliques qui sont impliqués dans la réponse aux pathogènes) (Treutter 2006; Kumar and Pandey 2013).

1.2.4 Transport d'hydroélectricité

Au Canada, notamment au Québec, la majorité de l'électricité est produite par des barrages hydroélectriques (Hydro-Québec 2023a). Pour acheminer l'électricité produite par ces barrages, souvent situés dans des zones reculées au nord, jusqu'aux différentes villes, de nombreuses lignes de transport d'électricité sont nécessaires. Plus de 34 000 km de lignes de transport d'électricité à haute tension sont présentes rien qu'au Québec, dont un tiers à très haute tension (735 000 volts) (Hydro-Québec 2023b). Ces nombreuses lignes de transport affectent les espèces boréales de différentes manières. Les lignes de transport créent des ouvertures linéaires dans la forêt, ce qui fragmente le paysage forestier (Li et Lin 2019) et peut affecter le mouvement d'espèces animales, qui évitent les zones exposées pour réduire le risque de prédation (Richardson et al. 2017; Biasotto et Kindel 2018). Les oiseaux sont également soumis à un risque de collision avec les infrastructures de transport; le nombre de décès annuel d'oiseaux par ce genre d'incident a été estimé à 10 000 000 d'individus au Canada (Calvert et al. 2013). La présence d'une ligne de transport électrique affecte également les espèces végétales, notamment en modifiant l'habitat des plantes de sous-bois à la suite du retrait des arbres (Richardson et al. 2017; Biasotto et Kindel 2018). L'ouverture du couvert forestier augmente l'exposition des plantes de sous-bois au soleil, ce qui peut entraîner des changements dans la composition des communautés végétales en faveur d'espèces plus tolérantes à un ensoleillement accru (Richardson et al. 2017). L'exposition accrue des plantes de sous-bois au soleil peut également affecter leur métabolisme. En effet, le soleil émet des rayons ultraviolets qui, comme les métaux lourds, sont une source de stress oxydatif, c'est-à-dire qui provoquent l'apparition de

ROS dans les cellules de la plante (Bergamini et al. 2004). La plante répond à ce genre de stress grâce à son métabolisme secondaire, notamment en produisant des composés phénoliques, ce qui lui permet de détoxifier les ROS pour limiter les dommages dans les cellules (Figure 1.1) (Agati et Tattini 2010; Kumar et Pandey 2013).

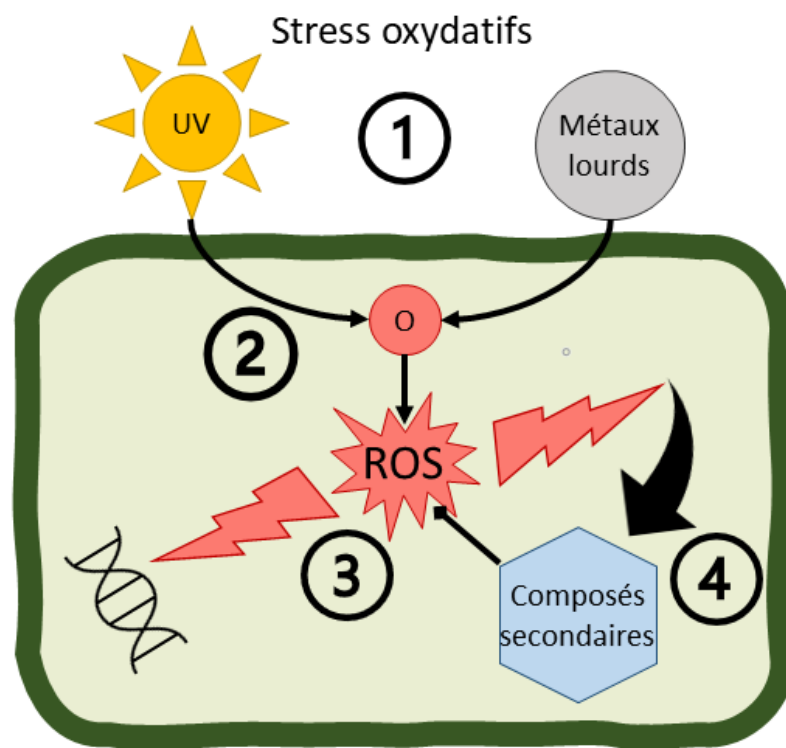


Figure 1.1 Représentation de l'effet des stress oxydatifs sur la plante au niveau cellulaire. 1 : Les stress oxydatifs, tels que l'exposition aux UV ou aux métaux lourds, atteignent la plante. 2 : Les stress oxydatifs affectent l'oxygène (O) présent dans les cellules de la plante, créant des espèces réactives de l'oxygène (ROS) (Bergamini et al. 2004; Feki et al. 2021). 3 : Les ROS engendrent des dommages aux lipides, aux protéines et à l'ADN (Ali et al. 2019; Noor et al. 2022). 4 : La cellule répond à ce stress en produisant des composés secondaires, notamment des composés phénoliques, qui détoxifient les ROS (Agati et Tattini 2010; Kumar et Pandey 2013).

1.3 Conséquences culturelles des perturbations : les espèces d'importance culturelle

En affectant les espèces boréales, les perturbations entraînent des conséquences sur l'environnement, mais également sur les pratiques culturelles de certaines populations humaines. En effet, certaines espèces occupent une place prépondérante dans la culture de certaines populations : on parle alors d'espèce d'importance culturelle ou d'espèce culturelle clé (Garibaldi et Turner 2004). Les espèces d'importance culturelle sont particulièrement présentes dans le mode de vie des communautés autochtones, qui en dépendent pour la pratique d'activités traditionnelles (Parlee et al. 2005; Boulanger-Lapointe et al. 2019).

Lorsque des espèces d'importance culturelle sont perturbées, cela peut entraîner des répercussions sur la culture des populations qui en dépendent. Par exemple, pour la communauté anicinape de Kitcisakik à l'ouest du Québec, le pin blanc (*Pinus strobus* Linnaeus) sert de repère pour s'orienter sur le territoire, fait partie de mythes et légendes, et possède différents usages en médecine traditionnelle (Uprety et al. 2013). Cependant, les coupes forestières, notamment les coupes totales, mettent en péril la pérennité du pin blanc, et donc la pérennité des pratiques culturelles qui dépendent des services écosystémiques que cette espèce fournit (Uprety et al. 2017). Le bleuet fausse-myrtille (*Vaccinium myrtilloides* Michaux) est un autre exemple d'espèce d'importance culturelle pour les communautés cries, dénées et métisses dans la région de Fort McKay en Alberta (Nielsen et al. 2020) et pour les communautés atikamekw au Québec (Pelletier 2022). Cette espèce occupe une place importante dans la diète traditionnelle, est utilisée en médecine traditionnelle, et sert à faire des teintures (Garibaldi 2009; Nielsen et al. 2020). Or, les propriétés nutritionnelles et médicinales d'une plante dépendent fortement de sa teneur en composés du métabolisme secondaire tels que les composés phénoliques (Agati et Tattini 2010; Del Rio et al. 2013; Kumar et Pandey 2013; Durazzo et al. 2019). Une perturbation, par exemple une mine, pourrait affecter

le métabolisme secondaire de la plante, et donc ses propriétés nutritionnelles et médicinales, et les usages culturels qui en dépendent. Étudier les espèces d'importance culturelle est donc un bon moyen d'évaluer l'effet écologique, mais également l'effet socio-culturel des perturbations (p. ex. Uprety et al. 2017).

Les communautés autochtones ont une conscience aigüe de l'effet des perturbations sur leurs territoires traditionnels (Bissonnette et al. 2018; Fuentes et al. 2020). Les projets en collaboration avec les communautés autochtones sont donc le moyen le plus efficace de comprendre l'effet des perturbations sur leurs territoires (McCarter et al. 2018; Bélisle et Asselin 2021). Ainsi, cette thèse a été réalisée en collaboration avec trois communautés autochtones au Québec, dans l'est du Canada : Abitibiwinni (Anicinapek), Mistissini (Eeyouch) et Nemaska (Eeyouch). Ces communautés ont été impliquées à plusieurs niveaux dans les études constituant cette thèse. Des membres de chaque communauté ont été consultés au cours de discussions informelles. Ces discussions ont permis aux communautés de déterminer les perturbations à étudier à l'échelle locale, c'est-à-dire les mines et les lignes hydroélectriques, ainsi que les espèces à étudier. Les membres des communautés ont également été consultés concernant les lieux d'échantillonnage, et les résultats des études leurs ont été communiqué lors d'événements dédiés.

1.4 Présentation des espèces étudiées

1.4.1 *Rhododendron groenlandicum*

Le thé du Labrador (*Rhododendron groenlandicum* (Oeder) Kron et Judd) est une plante de sous-bois de la famille des éricacées, qui se trouve à travers le Canada et dans certaines parties des États-Unis (Hébert et Thiffault 2011). Cette espèce pousse

principalement sur des sols plus ou moins saturés en eau, tels que dans des tourbières ou dans des pessières à mousses (Jobidon 1995; Gucker 2006). Elle est capable de croître sur des sols acides et pauvres en nutriments, mais est peu tolérante à l'ombre (Jobidon 1995; Hébert et Thiffault 2011). Un plant de *R. groenlandicum* mesure 30 à 120 cm de hauteur en moyenne, et possède des feuilles avec une face inférieure tomenteuse caractéristique, de couleur blanche sur les jeunes feuilles et rousse sur les feuilles matures (Figure 1.2) (Jobidon 1995). *Rhododendron groenlandicum* est anémochore, mais se reproduit également végétativement par marcottage, grâce à un réseau de tiges et de racines qui se trouve dans la couche organique du sol (Karlin et Bliss 1983; Hébert et Thiffault 2011). Cette caractéristique permet à l'espèce de proliférer après des perturbations ouvrant la canopée sans affecter le sol, telles que des feux de faible sévérité ou des coupes avec protection du sol (Lecomte et al. 2005; Hébert et Thiffault 2011).



Figure 1.2 *Rhododendron groenlandicum* en forêt boréale. Source : Maxime Thomas.

L'intérêt culturel de *R. groenlandicum* repose sur son usage dans la médecine traditionnelle autochtone. Ses feuilles sont préparées sous forme d'infusion

consommée à diverses fins médicinales, telles que diurétique, tonique, ou pour traiter le rhume ou l'arthrose (Uprety et al. 2012). Cette plante possède également des vertus antidiabétiques associées aux composés phénoliques présents dans ses feuilles (Saleem et al. 2010; Uprety et al. 2012; Eid et al. 2016).

1.4.2 *Vaccinium angustifolium*

Le bleuët à feuilles étroites (*Vaccinium angustifolium* Aiton) est également une plante de sous-bois de la famille des éricacées, mais sa répartition se cantonne à la moitié est du Canada et au nord-est des États-Unis (Tirmenstein 1991; Desmet et Brouilet 2013). Cette espèce peut croître sur des sols relativement humides, mais particulièrement sur des sols secs comme des affleurements rocheux (Hunt 2009; Marozau et Gordej 2019). *Vaccinium angustifolium* est acidophile et peu tolérante à l'ombre; elle a notamment besoin d'un milieu ensoleillé pour produire des fruits en quantité (Marozau et Gordej 2019; Gouvernement du Québec 2021). Les plants de *V. angustifolium* mesurent 15 à 60 cm en moyenne, et possèdent des tiges et des feuilles glabres (Figure 1.3) (Marie Victorin et al. 1975; Tirmenstein 1991). Les graines de cette espèce sont dispersées par les animaux qui consomment ses fruits, principalement des oiseaux et des mammifères (Marozau et Gordej 2019; Gouvernement du Québec 2021). Tout comme *R. groenlandicum*, *V. angustifolium* peut se reproduire végétativement par marcottage grâce à un réseau de tiges et racines dans le sol organique (Ahlgren 1960; Sheppard 1991). Cela permet également à *V. angustifolium* de coloniser rapidement le milieu après des perturbations ouvrant le couvert forestier sans affecter le sol (Sheppard 1991; Marozau et Gordej 2019).



Figure 1.3 Plant de *Vaccinium angustifolium* portant des fruits sous une ligne hydroélectrique. Source : Maxime Thomas.

Vaccinium angustifolium occupe une place importante dans la culture autochtone, notamment dans la diète traditionnelle, dont les bleuets font partie intégrante (Arnason et al. 1981; Batal et al. 2021). Les bleuets sont riches en antioxydants et possèdent des propriétés antidiabétiques, ce qui contribue à leur importance dans la diète autochtone (Smith et al. 2000; Uprety et al. 2012; Weber 2022). En outre, les sorties sur le territoire lors des cueillettes et la préparation de mets traditionnels, comme la pâte de bleuet, contribuent à renforcer le lien des autochtones avec leur territoire et leurs traditions (Boulangier-Lapointe et al. 2019; Basile et al. 2022; Pelletier 2022).

1.5 Objectifs et structure de la thèse

L'objectif général de cette thèse est d'étudier les différents effets des perturbations d'origine anthropique sur deux espèces d'importance culturelle. À notre connaissance, cette thèse est la première étude de cette ampleur sur l'effet des perturbations

anthropiques sur des espèces d'importance culturelle. Afin de faire un portrait le plus complet possible de l'effet des perturbations, cette étude s'organise en 3 chapitres, dont les objectifs spécifiques sont les suivants :

Dans le chapitre II, l'objectif est d'évaluer l'effet des perturbations à large échelle, c'est-à-dire les changements climatiques et l'aménagement forestier, sur la répartition des deux espèces étudiées. Pour ce faire, les données des Points d'Observation Écologique du Ministère des Ressources Naturelles et des Forêts du Québec, ainsi que des données de télédétection et d'inventaires forestiers sont utilisées. Ces données servent à alimenter deux types de modèles utilisés en combinaison : un modèle simulant l'évolution du paysage forestier en fonction de différents scénarios de changements climatiques et d'aménagement forestier (LANDIS-II), et des modèles de répartition des espèces étudiées dans le paysage futur simulé (*species distribution models*). Peu d'études ont entrepris de projeter l'effet des perturbations anthropiques sur la répartition d'espèces d'importance culturelle. Cette étude utilise donc une nouvelle approche en combinant deux modèles pour compléter les connaissances à ce sujet.

Dans les chapitres III et IV, l'objectif est de caractériser l'effet des perturbations locales, c'est-à-dire les mines et les lignes de transport hydroélectrique, sur le métabolisme de *R. groenlandicum* (Chapitre III) et de *V. angustifolium* (Chapitre IV). Pour répondre à cet objectif, des échantillons des parties consommées de la plante ont été collectés, c'est-à-dire les feuilles pour *R. groenlandicum* (Chapitre III) et les fruits pour *V. angustifolium* (Chapitre IV) à proximité de mines, sous des lignes hydroélectriques, et en forêt non perturbée. Les concentrations en composés phénoliques ont ensuite été mesurées dans les échantillons afin de les comparer en fonction des perturbations (Chapitres III et IV), et ainsi de déterminer l'effet des perturbations sur le potentiel médicinal et nutritionnel de ces deux plantes. Peu d'études ont évalué l'effet des

perturbations sur le profil phénolique de plantes sauvages *in situ*, alors que ce sont ces plantes qui sont consommées par les usagers du territoire en forêt boréale, notamment les peuples autochtones. Ces deux chapitres visent donc à combler cette lacune.

Le chapitre IV a également pour objectif d'étudier les interactions entre perturbations, propriétés du sol, microbiome du sol, et production de composés phénoliques par *V. angustifolium*. En plus des analyses décrites ci-dessus, des échantillons de sol ont été prélevés aux mêmes endroits que les échantillons de fruits. Différentes propriétés physico-chimiques de ces échantillons de sols ont été analysées, et l'ADN microbien (bactérien et fongique) a été extrait. En séquençant cet ADN, il est possible d'identifier les bactéries et champignons présents dans les échantillons de sol ainsi que leur abondance. Les microbiomes des différents échantillons ont alors pu être comparés pour déterminer leurs effets et celui des propriétés du sol sur les composés phénoliques produits par *V. angustifolium*. L'effet des perturbations anthropiques (mines et lignes de transport hydroélectrique) a également été considéré. Les perturbations, les propriétés du sol, le microbiome du sol, et le profil phénolique des plantes interagissent de façon étroite et complexe, et il reste encore beaucoup à apprendre sur le sujet. Cette étude contribue donc à étoffer les connaissances sur certaines de ces relations.

Enfin, le Chapitre V met en relation les résultats des chapitres précédents et discute les connaissances développées dans cette thèse. Les limites de la thèse et les perspectives qui en ressortent sont également présentées.

CHAPITRE II

COMMENT LES CHANGEMENTS CLIMATIQUES ET LES COUPES
FORESTIÈRES INFLUENCERONT-ILS LA DISTRIBUTION DE DEUX
ESPÈCES D'IMPORTANCE CULTURELLE ?

HOW WILL CLIMATE CHANGE AND FOREST HARVESTING INFLUENCE
THE DISTRIBUTION OF TWO CULTURALLY SALIENT SPECIES?

Maxime Thomas¹, Yan Boulanger², Hugo Asselin³, Mebarek Lamara¹,
Nicole J. Fenton¹

¹Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

²Service Canadien des Forêts, Québec, Québec, Canada

³École d'études autochtones, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

Corresponding author: Maxime Thomas (maxime.thomas@uqat.ca)

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Le chapitre suivant a été amélioré par diverses suggestions et diffère donc légèrement
de l'article publié.

2.1 Résumé

Les paysages boréaux font face à des perturbations grandissantes qui peuvent affecter des espèces culturelles clé, c'est-à-dire des espèces d'importance culturelle qui façonnent de façon majeure l'identité culturelle d'un peuple. Étant donné leur importance, l'effet des perturbations sur de telles espèces devrait être étudié pour être capable d'assurer leur pérennité. Nous avons évalué comment les changements climatiques et la récolte forestière peuvent affecter la qualité de l'habitat de *Rhododendron groenlandicum* et *Vaccinium angustifolium*, deux espèces culturelles clé pour de nombreux peuples autochtones dans l'est du Canada. Nous avons utilisé le modèle de paysage forestier LANDIS-II en combinaison avec des modèles de distribution de ces deux espèces pour simuler la qualité de leurs habitats sur les territoires de trois communautés autochtones en fonction de différents scénarios de changements climatiques et de récolte forestière. Les paramètres sensibles au climat incluaient les régimes de feux ainsi que la croissance des arbres. Les scénarios de changements climatiques modérés étaient associés avec une augmentation de la proportion de *R. groenlandicum* et *V. angustifolium* dans le paysage, cette dernière espèce répondant également positivement aux scénarios de changements climatiques importants. La récolte avait un effet minimal, mais diminuait légèrement la probabilité de présence des deux espèces là où elle prenait place. D'après les résultats de modélisation, aucune des deux espèces n'est à risque sous des scénarios de changements climatiques modérés. Cependant, sous des changements climatiques importants, *R. groenlandicum* pourrait décliner alors que la proportion d'arbres décidus augmenterait dans le paysage. Des stratégies de mitigation des changements climatiques, telles que des feux dirigés, pourraient être nécessaires pour limiter cette augmentation. Cela empêcherait la diminution de *R. groenlandicum*, et contribuerait à préserver la biodiversité et les volumes récoltables.

Mots-clés : Peuples autochtones, réchauffement climatique, modélisation forestière, feu, coupe, bleuet, thé du Labrador.

2.2 Abstract

Boreal landscapes face increasing disturbances that can affect cultural keystone species, i.e. culturally salient species that represent the cultural identity of Indigenous people. Given their importance, the effect of disturbances on such species should be assessed to be able to act to ensure their perennity. We assessed how climate change and forest harvesting will affect the habitat quality of *Rhododendron groenlandicum* and *Vaccinium angustifolium*, two cultural keystone species for many Indigenous peoples in eastern Canada. We used the forest landscape model LANDIS-II in combination with species distribution models to simulate the habitat quality of these two species on the territories of three Indigenous communities according to different climate change and forest harvesting scenarios. Climate-sensitive parameters included wildfire regimes as well as tree growth. Moderate climate change scenarios were associated with an increased proportion of *R. groenlandicum* and *V. angustifolium* in the landscape, the latter species also responding positively to severe climate change scenarios. Harvesting had a minimal effect, but slightly decreased the probability of presence of both species where it occurred. According to the modeling results, neither species is at risk under moderate climate change scenarios. However, under severe climate change, *R. groenlandicum* could decline as the proportion of deciduous trees would increase in the landscape. Climate change mitigation strategies, such as prescribed fires, may be necessary to limit this increase. This would prevent the decrease of *R. groenlandicum*, as well as contribute to preserve biodiversity and harvestable volumes.

Keywords: Indigenous peoples, climate warming, forest modeling, fire, logging, blueberry, Labrador tea.

Highlights

- Culturally salient species (CSS) face increasing disturbances in boreal landscapes.
- We modeled how climate change and forest harvesting will affect two CSS.
- Species habitat quality was projected as a function of future landscape features.
- Severe climate change could cause a decline of *R. groenlandicum*.
- Limiting the expansion of deciduous trees will help maintain the studied species.

2.3 Introduction

With increased anthropogenic climate forcing, boreal landscapes will be highly affected in the future. For example, in Canada, warming temperatures and decreasing precipitation are expected to decrease tree growth rates and increase their mortality (Aubin et al. 2018; Boisvert-Marsh et al. 2019), and also to increase wildfire risk and severity (Wang et al. 2017; Boulanger et al. 2018b). These changes will favor pioneer species as well as those adapted to warmer climates, such as deciduous trees (Goldblum and Rigg 2005; Searle and Chen 2017). Increased disturbance rates will favor younger landscapes by preventing stands from reaching old ages (Weir et al. 2000; Bergeron et al. 2017). The effects of forest harvesting will cumulate with those of climate, also contributing to an increase in younger stands, as harvesting removes older trees (Langen and Bouman 1997; Cyr et al. 2009; Bouchard and Pothier 2011). The cumulative and interacting effects of climate change and forest harvesting could affect the resilience of the boreal forest, leading to durable changes in the landscapes (Boucher et al. 2017b). For example, several studies predict the replacement of old-growth coniferous stands by young deciduous stands, sparsely-treed woodlands or even non-forested areas due to increasing frequency and severity of disturbances (Girard et al. 2008; Boulanger and Pascual Puigdevall 2021; Boulanger et al. 2022; Augustin et al. 2022).

Large scale changes in boreal landscapes affect boreal wildlife species as their habitats are altered. For example, boreal caribou (*Rangifer tarandus* Gmelin) populations are currently dwindling because of a decrease in old-growth forests due to forest harvesting in the past century, an on-going threat that will be exacerbated in the future with climate-induced increases in fire frequency and severity (St-Laurent et al. 2022; Leblond et al. 2022). As disturbances affecting boreal landscapes continue to increase,

more boreal species associated with old-growth coniferous forests could become at risk, in the future (Cadieux et al. 2019; Bouderbala et al. 2022, 2023; Labadie et al. 2023).

When a species is affected by disturbances, consequences can be felt beyond the ecosystem, especially for so-called cultural keystone species, which bear high cultural importance for certain human populations (Garibaldi and Turner 2004). An example of cultural keystone species is the eastern white pine (*Pinus strobus* Linnaeus) which marks sites of high spiritual value, has medicinal uses, and supports animal species important to traditional practices for the Kitcisakik Algonquin community (Uprety et al. 2013). Another example is mountain cranberry (*Vaccinium vitis-idaea* Linnaeus), which is valued for its importance in traditional diet and medicine by various communities, including the Cree, Dene and Metis community of Fort McKay (Garibaldi 2009). Because of their cultural importance, the loss of cultural keystone species can greatly affect the human populations that depend on them (Uprety et al. 2013; McCarthy et al. 2014; Philip 2021). The response of these species to increasing modifications of the landscape must then be assessed to ensure their persistence in the future.

One way to assess the survival of cultural keystone species is to model their probability of presence under various disturbance and climate change scenarios. Species Distribution Models (SDMs) can be used to predict the probability of presence of a species based on climate and environmental variables (Song et al. 2004; Araújo et al. 2006; Korznikov et al. 2023; Zhang and Wang 2023). However, this approach has well-known shortcomings, notably as it does not account for dynamic processes governing climate- and human-caused changes to landscapes. To date, few studies have modeled the cumulative and interactive effects of climate change as well as natural and anthropogenic disturbances on the probability of presence of cultural keystone species (e.g., Johnson et al. 2015; Nielsen et al. 2020; Chengere et al. 2022). Our study responds to this need by modeling the probability of presence of two cultural keystone

species under future disturbances on the traditional territories of three Indigenous communities in eastern Canada.

This study aimed to assess how the evolution of the landscape under different climate change and forest harvesting scenarios affects the probability of presence of two cultural keystone species, common Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) and early lowbush blueberry (*Vaccinium angustifolium* Aiton). These two cultural keystone species are understory plants valued for their importance in medicine and in the diet of Indigenous communities in Canada (Uprety et al. 2012). *Rhododendron groenlandicum*'s cultural importance lies in the many traditional uses of its leaves, which are prepared in medicinal teas to treat various ailments such as cold, headache and diabetes (Dufour et al. 2007; Uprety et al. 2012; Rapinski et al. 2015). The cultural importance of *Vaccinium angustifolium* rest on its fruits, which are an important part of the traditional diet, thus result in harvesting and food preparation activities (Uprety et al. 2012; Pelletier 2022). These two species are also important in the ecosystem, as they affect succession patterns by limiting the colonization and growth of trees (Mallik 2003; Hébert and Thiffault 2011). *Rhododendron groenlandicum* and *V. angustifolium* were prioritized for the modeling approach by three Indigenous communities in eastern Canada participating in this study. Our research questions were the following: i) What are the effects of climate change on the landscape, and how will this affect the probability of presence of each species? ii) What are the effects of forest harvesting on the landscape, and how will this affect the probability of presence of each species? We will also discuss possible interactive effects of climate change and forest harvesting. Our results will help determine if future disturbance regimes could put cultural keystone species at risk, as well as the best strategy of action to ensure their perennity.

2.4 Methods

2.4.1 Studied species

Rhododendron groenlandicum is a shrub in the Ericaceae family, measuring 30 to 120 cm in height, that is found across Canada and in parts of the United States (Hébert and Thiffault 2011). This species can be recognized by its leaves with a white tomentose underside that turn brown when mature (Hébert and Thiffault 2011). It is preferentially found in humid to wet habitats, is shade intolerant, and can tolerate nutrient-poor and acidic environments (Jobidon 1995). This species is anemochorous, but reproduces mainly vegetatively via a network of roots protected under the organic soil layer (Karlin and Bliss 1983; Hébert and Thiffault 2011). This network allows the species to proliferate by suckering following disturbances that open the canopy without disrupting the organic soil layer, such as some forest harvesting practices (e.g., careful logging) or low severity fires (Lecomte et al. 2005; Hébert and Thiffault 2011). The leaves of *R. groenlandicum* are used in traditional medicine as a tonic or to treat various ailments, such as headaches, colds, or kidney problems (Uprety et al. 2012).

Vaccinium angustifolium is also a species in the Ericaceae family. It averages 15-60 cm in height and is found in the eastern half of Canada as well as in the northeastern United States (Tirmenstein 1991; Desmet and Brouilet 2013). It is acidophilic, prefers full-sun environments and is most productive on dry soils, although it is capable of growing on wetter soils (Hunt 2009; Marozau and Gordej 2019; Gouvernement du Québec 2021). This species is dispersed by animals (mostly birds and mammals) that consume its fruit but can also reproduce vegetatively (Ahlgren 1960; Tirmenstein 1991; Marozau and Gordej 2019; Gouvernement du Québec 2021). As for *R. groenlandicum*, *V. angustifolium* can use its network of roots to proliferate by suckering after low-severity disturbances (Sheppard 1991; Marozau and Gordej 2019). Blueberries have

high cultural value for Indigenous communities (Boulanger-Lapointe et al. 2019; Basile et al. 2022; Pelletier 2022). Notably, they are an important component of the Indigenous diet (Arnason et al. 1981; Batal et al. 2021) and have anti-diabetic and antioxidant properties (Smith et al. 2000; Uprety et al. 2012; Weber 2022).

2.4.2 Study area

The study area is located in the western part of the province of Quebec, Canada, between the 48th and 52nd northern parallels. It corresponds to parts of the traditional territories of the Mistissini and Nemaska First Nations (Cree), and the Abitibiwinni First Nation (Anishnaabe). Only the southern part (51%) of the Mistissini territory is included in the study due to the lack of detailed ecoforestry data for the northern part.

The study area is almost entirely located within the spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh)-moss bioclimatic domain, with a portion in the balsam fir (*Abies balsamea* (Linnaeus) Miller)-paper birch (*Betula papyrifera* Marshall) bioclimatic domain in the southern part of the Abitibiwinni territory, and a portion in the spruce (*Picea mariana*)-lichen woodland bioclimatic domain in the northern part of the Mistissini territory (Figure 2.1). The climate of the study area is continental-subarctic, with a mean daily annual temperature of 0°C, 644 mm of rain and 265 cm of snow annually in the Abitibiwinni territory, whereas the southern portion of the Mistissini territory has a mean daily annual temperature of 0.2°C, while precipitation averages 685 mm of rain and 313 cm of snow annually (Environment and Climate Change Canada 2022). Estimates are less precise for the Nemaska territory, as there is no weather station nearby. According to the two closest stations (approximately 260 km to the north and 220 km to the south-east), the mean daily annual temperature is between -2.9 and 0.2°C, with 454 to 685 mm of rain and 261 cm to 313 cm of snow (Environment and Climate Change Canada 2022).

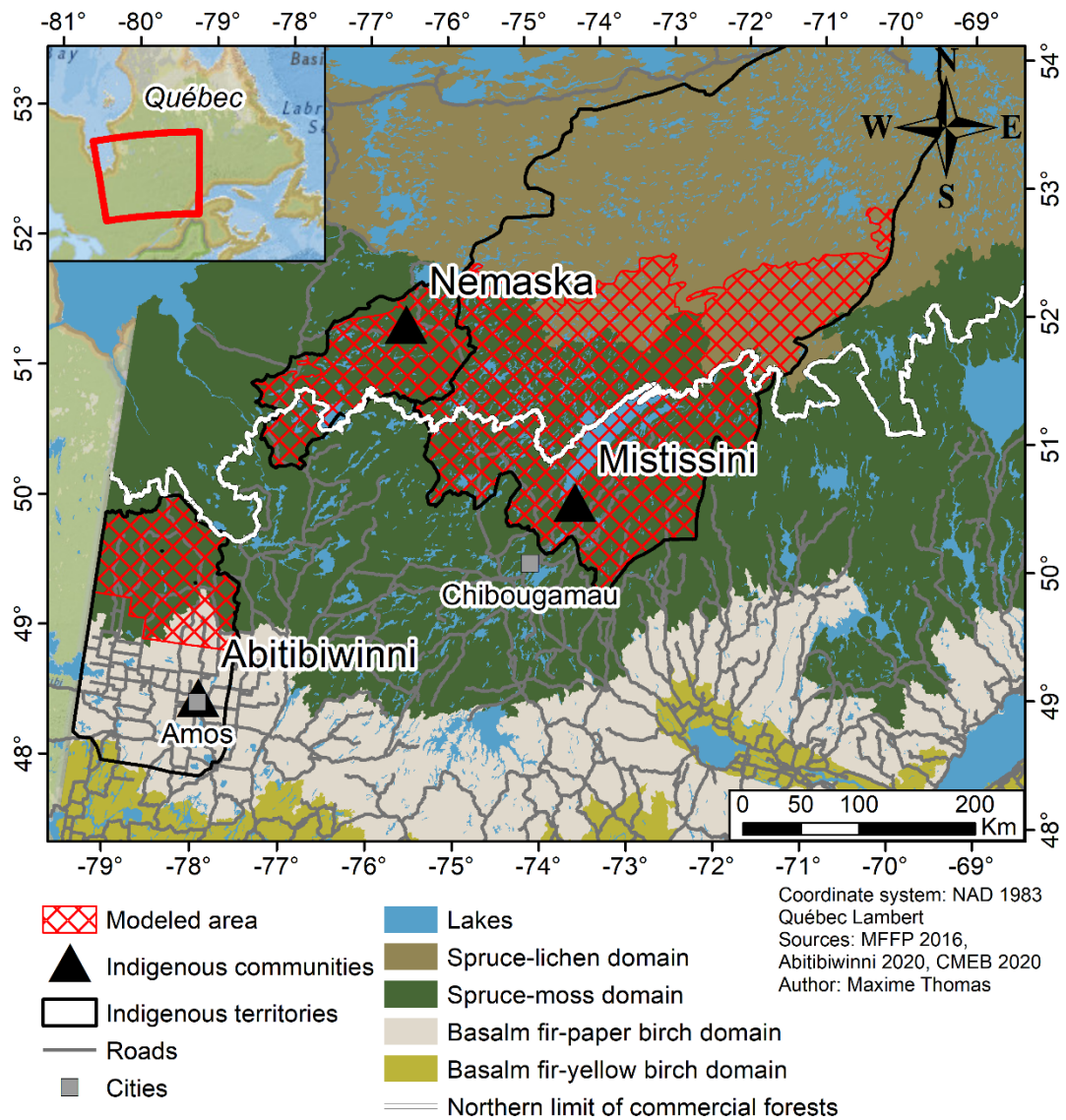


Figure 2.1 Location of the study area in Quebec (eastern Canada). The modeled area is indicated by a red grid.

2.4.3 Modeling approach

The changes in the probability of presence of the studied species were simulated as a function of anthropogenic and climatic disturbances between the years 2000 and 2150. LANDIS-II v7 was used to project the development of the forest landscape under different climatic and forest harvesting scenarios (Scheller et al. 2007). The model was initialized using a combination of remote sensing estimates for above-ground biomass (Beaudoin et al. 2014) and forest inventory data for tree species and age. In parallel, a species distribution model (SDM) was built for each species to project habitat quality based on landscape features. SDMs were built based on government inventory data from the Ministère des Ressources Naturelles et des Forêts using the presence/absence of each species (Ministère des Ressources Naturelles et des Forêts 2023a). Finally, SDMs were used to project the habitat quality in the future for both studied species using future forest landscapes as projected by LANDIS-II under the different climatic and forest harvesting scenarios considered.

2.4.4 LANDIS-II

2.4.4.1 Model description and initialization

LANDIS-II is a spatially-explicit model based on rasters that models the changes in forest composition at different spatial and temporal scales by simulating growth, succession, and different anthropogenic and natural disturbance processes (Scheller et al. 2007). The model is composed of interacting cells in which ecosystem processes at various scales (competition, mortality, disturbance, dispersal, etc.) are simulated over time. In this study, the resolution of the modeled cells was set to 250 m. Cells that were similar in terms of soil and climate characteristics were grouped into ecoregions (Figure

S2.13, Figure S2.14 and Figure S2.15). Initial cell composition and structure were defined using a combination of remote sensing estimates for above-ground biomass (Beaudoin et al. 2014) and forest inventory data for tree species and age (Forest Inventory Plots, Ministère des Ressources Naturelles et des Forêts 2023a).

2.4.4.2 Model projections

The changes in the forest landscapes were projected using LANDIS-II for the period 2000-2150, to encompass at least one full forest rotation, as harvest intervals could vary from 60 years to more than 100 years depending on available stands at a given timestep. The Biomass Succession extension v3.1 of LANDIS-II was used to simulate forest succession (Scheller and Mladenoff 2004; Scheller 2013). This extension simulates the interactions between different tree species within a stand. By taking into account species traits, seed availability, and disturbance history, the extension simulates succession, i.e., growth, reproduction and mortality. Some parameters were set to be dynamic to account for the effect of climate and soil on the growth and reproduction of each species. These dynamic parameters were obtained using PICUS, a spatially explicit model that simulates tree dynamics at the individual level in 100 m² cells interacting within a one-hectare stand (Lexer and Hönninger 2001). A three-dimensional light module was used to simulate the interactions between trees and between cells. PICUS considers climatic (temperature, precipitation, etc.) and soil (pH, composition, etc.) variables. Thus, for each tree species, it was possible to obtain the establishment probability, maximum above-ground biomass, and maximum above-ground net primary productivity for each ecoregion and for each of the different climatic scenarios considered. LANDIS-II and PICUS parameters are available in the supplementary material (Table S2.3 and Table S2.4).

2.4.4.3 Fire and forest harvesting

Fire regimes were simulated with the Base Fire extension v3.0 of LANDIS-II (Scheller and Domingo 2012). This extension simulates fires randomly based on region-specific ignition probabilities, in which fire initiation and spread probabilities are also dependent on time since last fire. The study area was intersected with the Canadian homogeneous fire regime (HFR) zones (Boulanger et al. 2014). The Abitibiwinni territory intersected the Hudson Plains and Eastern James Bay HFR zone, the Mistissini territory intersected the Eastern James Bay and the Eastern Subarctic HFR zones, whereas the Nemaska territory was entirely lying within the Eastern James Bay HFR zone. Fire regime parameters for each zone intersection were calibrated based on models predicting future number of fires and annual area burned developed by Boulanger et al. (2014). As fire projections in Boulanger et al. (2014) were first produced for the special report on emissions scenarios (SRES A2) climate scenarios, fire parameters for each HFR zone were adjusted according to the different Representative Concentration Pathway (RCP) scenarios considered. Moreover, further corrections were made to burn rates by considering the potential negative feedback between changes in landscape age structure and fire activity, as proposed by Boulanger et al. (2017a). When considering all these corrections, the annual area burned for Mistissini and Nemaska was 0.5% at the beginning of the simulations, increasing to 2%, 3.2%, and 3.5% by 2100 under RCP scenarios 2.6, 4.5, and 8.5, respectively. For Abitibiwinni, the annual area burned was 0.25% at the beginning of the simulations, increasing to 0.5%, 0.6% and 0.9% by 2100, under RCP scenarios 2.6, 4.5, and 8.5, respectively.

Forest harvesting was simulated with the Biomass Harvest extension v3.0 of LANDIS-II (Gustafson et al. 2000). To parameterize the forest harvesting rate in the study area, we used historical forest harvesting rates from Quebec records for the period 1980-

2000. All harvests were clearcuts, as this is the forest harvesting method classically used in the study area (Boucher et al. 2017b). Clearcuts were simulated as 150 ha patches within which all cohorts were removed, except for the 0-10 year cohort to account for protection of regeneration during careful logging. It should be noted that a large portion of the study area is north of the northern limit of commercial forests, more specifically, 56% of the modeled territory of Mistissini and 84% of the modeled territory of Nemaska. This portion was therefore not subject to forest harvesting; thus, the effect of forest harvesting could only be evaluated on the Abitibiwinni territory. Forest harvesting parameters were kept constant throughout the simulations. If, at a given time step, there were insufficient harvestable stands left, harvest was conducted until no harvestable stands were available.

2.4.4.4 Simulation parameters

The model was initialized at the year 2000, and the forest landscape was simulated over the period 2000-2150 using 10-year time steps. The results were reported every 50 years, i.e., for the years 2050, 2100, and 2150. The changes in the forest landscape were simulated according to 4 climate scenarios and 4 forest harvesting scenarios. The climate scenarios considered were a reference scenario with no climate change (climate set to 1981-2010 normals), as well as 3 scenarios of low, moderate, and high global warming based on the Intergovernmental Panel on Climate Change (IPCC) RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively (van Vuuren et al. 2011). Climate change affected stand growth and regeneration as well as fire ignition and spread. Climate projections for the years 2011-2100 were obtained from the Climate Model Intercomparison Project phase 5 (CMIP5) archive based on Canadian Earth System Model version 2 (CanESM2) simulated data (Arora and Boer 2010). Climate-dependent variables, i.e., growth and regeneration parameters as well as fire, for the

years 2100-2150 were obtained by extending the projections for the years 2070-2100, as RCP projections stop in 2100 (Boulanger et al. 2019). This allowed to better assess the effect of forest harvesting, as rotation periods can sometimes exceed 100 years.

Forest harvesting scenarios were simulated according to an intensity gradient, with a scenario with no forest harvesting, and 3 scenarios of low (0.5 times the current harvesting rate), moderate (current harvesting rate = 0.7% per year), and high (2 times the current harvesting rate) forest harvesting. Simulations were run according to a two-way factorial design, leading to a total of 16 scenario combinations. For each of these combinations, 5 replicates were run, notably to account for the stochasticity of fire events.

2.4.5 Species distribution models

A species distribution model (SDM) was built to predict the habitat quality for each studied species using data collected between 1986 and 2000 within the network of forest inventory plots of the Ministère des Ressources Naturelles et des Forêts (MRNF). These data included the presence and abundance (expressed as a percentage of the plot covered by the species) of the studied species. The 21,642 plots that corresponded to the bioclimatic domains of the study area were used to calibrate and validate the models (Figure S2.1). An equal weight was given to presence and absence, as the data contained real absences rather than pseudo absences. Presences associated with very low species coverage (less than 10% coverage) were converted to absence, as we were more interested in locations where the species were abundant, which is relevant from a cultural perspective.

The SDMs explaining the observed probability of presence of each species were built based on 5 environmental variables from the governmental forest inventory database:

forest cover (FORCOV), a combination of age and origin of the forest stand (AGEORI), soil drainage class, percent slope, and elevation. These variables were chosen based on environmental features of importance to the studied species according to the literature (see section “Studied species”) and their availability in raster format over the extent of the study area for the year 2000 for compatibility with LANDIS-II. The forest cover variable consisted of 14 classes: the 10 most common forest covers across the province of Quebec, and 4 general classes grouping all other covers (Table 2.1). Forest stand age and origin were combined into a single variable (AGEORI), as the disturbance at the origin of a stand affects its early successional characteristics (Brassard and Chen 2006; Taylor et al. 2013). The database divided stands into 7 age classes: 0-10 years, 10-30 years, 30-50 years, 50-70 years, 70-90 years, 90-120 years, and 120+ years. An origin was only attributed to early succession stands, i.e., classes younger than 70 years, while only the age class was used for older stands. To avoid creating low frequency classes, only clearcut and fire origin were considered, as these are the two most frequent stand-replacing disturbances in the study area. Thus, early succession stands of origin other than fire or clearcut, or with unknown origin, were grouped based only on age class. The soil drainage variable had 7 classes, ranging from xeric to hydric. Finally, slope and elevation were numeric variables expressed in percent and meters, respectively. The drainage class, slope, and elevation of a cell were fixed and did not change during the simulations.

Table 2.1 Explanatory variables retained for the construction of the SDMs with their different classes, their codes, and their meanings.

Variable	Classes
Forest cover (FORCOV)	C: Coniferous species
	BS: Black spruce
	BS-F: Black spruce with fir or black spruce with white spruce
	F-BS: Fir-black spruce JP-BS: Jack pine with spruce
	F: Fir
	JP-BS: Jack pine with spruce
	JP: Jack pine
	M: Mixed forests, i.e. both deciduous and coniferous
	S-PB: Paper birch with fir or white spruce (coniferous dominance)
	PB-S: Paper birch with fir or white spruce (deciduous dominance)
	PB: Paper birch
	A: Aspen
	D: Deciduous species
	N: Non-forested (no trees or trees too young/sparse)
Age-origin of the forest stand (AGEORI)	0 FI: 0-10 years fire origin
	0 CC: 0-10 years clearcut origin
	0: 0-10 years other origin or origin unknown
	10 FI: 10-30 years fire origin
	10 CC: 10-30 years clearcut origin
	10-30 years other origin or origin unknown
	30 FI: 30-50 years fire origin
	30 CC: 30-50 years clearcut origin

Table 2.1 (continued)

Variable	Classes
Age-origin of the forest stand (AGEORI)	30-50 years other origin or origin unknown
	50 FI: 50-70 years fire origin
	50 CC: 50-70 years clearcut origin
	50-70 years other origin or origin unknown
	70: 70-90 years
	90: 90-120 years
	120: 120 years and more
Soil drainage	Xeric
	Xeric-hydric
	Mesic-xeric
	Mesic
	Mesic-hydric
	Subhydric
	Hydric
Slope	Numerical, in percent
Elevation	Numerical, in meters

The SDMs were built and the statistical analyses were conducted with R software version 4.1.2 (R Development Core Team 2021). The R package biomod2 was used for SDM construction, which allows to build ensemble models with a choice of 10 of the most commonly used model algorithms (Thuiller et al. 2021). Among these algorithms, the following 5 were chosen for the construction of the ensemble model: 1) Generalized Boosted Model (GBM, (Ridgeway 1999)), 2) Random Forest (RF, (Breiman 2001)), 3) Generalized Additive Model (GAM, (Hastie and Tibshirani 1986)), 4) Generalized Linear Model (GLM, (McCullagh and Nelder 1989)) and 5) Maximum

Entropy (MAXENT, (Phillips et al. 2006)). The data were randomly divided into a calibration block (75% of the data) and a validation block (25% of the data) (Figure S2.2). The performance of the SDMs was evaluated on the validation block using the TSS (True Skill Statistic) metrics (Allouche et al. 2006). Each algorithm was run in triplicates to account for random variations from run to run, and the ensemble model was constructed with all replicates weighted according to their TSS scores.

2.4.6 Projecting species probability of presence in future forest landscapes

The SDMs were applied to the landscape simulated by LANDIS-II to project the probability of presence of each studied species. For each cell, time step and scenario, the tree species biomass data produced by the LANDIS-II simulations were converted to one of the forest covers presented in Table 2.1. Data on forest stand age and origin were obtained for each cell in the same manner. Other variables (drainage, slope and elevation) were acquired for the study area from Quebec ecoforestry maps (Ministère des Ressources Naturelles et des Forêts 2023b, 2023c) and digital elevation models, and rasterized at the same resolution as the one used in LANDIS-II simulations. The latter variables were kept constant all along the simulation. Using LANDIS-II-derived and static variables along with SDMs, the probability of presence of each of the studied species was projected as a function of the changes in the forest landscape in the different territories, at each time step, and according to the different scenarios considered. The results were reported as the differences in the probability of presence between each climate change scenario and the corresponding baseline climate scenario (no climate change). The difference in probability of presence between scenarios was reported to correct for potential idiosyncrasy of the models, as the influence of scenarios is more relevant to this study than the absolute variation of the probability of presence of the species.

2.4.7 Model output interpretation

To study the most influential landscape features determining the probability of presence of the studied species, the predictions of the SDMs were examined. Graphs of the predicted responses were produced for each value of each variable using the `response.plot2` function of `biomod2` package in R. This function allowed us to obtain the value predicted by the model for a value of a given variable while keeping the other variables at fixed values (in our case, the mean for numerical variables and the most represented class for categorical variables).

A 2-way ANOVA was used to determine the relative effect of forest harvesting scenarios, climate scenarios and their interaction on species probability of presence (species probability of presence \sim forest harvesting scenario * climate scenario). The omega-squared (ω^2) associated with each of the two factors (climate change and harvest), as well as their interaction, was calculated from the ANOVA results, as this type of approach is more accurate than the ϵ^2 approach used by default by the ANOVA (Troncoso Skidmore and Thompson 2013). Using a frequentist approach to analyze simulation results induces a bias of over-representing significant differences (White et al. 2014). Thus, the ω^2 was only used here to quantify the effect size of each variable, and p-values were not reported.

2.5 Results

2.5.1 Landscape features predicting species habitat quality

The Species Distribution Models (SDMs) built for both species performed well, with high sensitivity (>80% for both models) and specificity (>75% for both models) (Table

2.2). While both SDMs had acceptable evaluation scores, the SDM built for *R. groenlandicum* had a higher evaluation score than the SDM for *V. angustifolium*. Thus, while the probability of presence of both species can be predicted based on environmental variables, this method seems particularly appropriate for *R. groenlandicum*.

Table 2.2 Ensemble model scores for *R. groenlandicum* and *V. angustifolium*, calculated using the True Skill Statistics (TSS) and Area Under Curve (AUC) metrics. Scores of the individual models used for building the ensemble model are available in Table S2.1 and Table S2.2. The cutoff represents the probability of presence above which the model considers the species to be present, and is set to maximize model performance (TSS).

		Calibration	Evaluation	Cutoff	Sensitivity (%)	Specificity (%)
TSS	<i>R. groenlandicum</i>	0.668	0.623	0.411	86.87	79.95
	<i>V. angustifolium</i>	0.588	0.385	0.337	82.42	76.44
AUC	<i>R. groenlandicum</i>	0.92	0.885	0.414	86.87	80.47
	<i>V. angustifolium</i>	0.884	0.745	0.334	82.42	76.95

The probability of presence of the two species was primarily explained by forest cover in the models (Figure S2.3 and Figure S2.5). *R. groenlandicum* was mostly found in spruce stands, jack pine stands and non-forested areas, and less present in fir, mixed, and deciduous stands (Figure S2.4). *V. angustifolium* was mostly present in jack pine stands, spruce stands, and non-forest areas and less present in fir and deciduous stands (Figure S2.6). The probability of presence of *V. angustifolium* was also partly explained by the age and origin of stands, with this species being more found in younger stands originating from fire and clear-cuts (Figure S2.6). Other variables had no notable effect on the probability of presence of both species.

2.5.2 Effect of climate change and forest harvesting on forest cover

With increasing anthropogenic climate forcing, pure spruce stands declined in favor of non-forested areas and aspen stands (Figure S2.7, Figure S2.8 and Figure S2.9). A similar trend was observed with increasing forest harvesting rates, although the trend was less marked in the territories of Mistissini and Nemaska as they are not subject to forest harvesting over most of their area. Changes from the 2000 forest cover were more important under the RCP 8.5 and, to a lesser extent, under a 2 x harvest scenarios.

On the Abitibiwinni territory, pure spruce stands were replaced by other coniferous stands under low disturbance scenarios (Baseline-No harvest, RCP 2.6-No harvest, RCP 4.5 No harvest and Baseline-Half harvest; spruce -76% to -86%, coniferous +181% to 466%). In higher disturbance scenarios, pure spruce stands were replaced by aspen stands (+117% to +453%) and non-forest areas (+201% to +771%), to the point that pure spruce stands almost disappeared by 2150 under the most extreme climate and harvest scenarios (-99%) (Figure S2.7). The proportion of non-forest areas increased with increasing forest harvesting (+60% to +98%). At the same time, the proportion of mixedwood stands decreased (+11% to -22%) as the proportion of aspen stands increased (-1% to +263%) in response to increased anthropogenic climate forcing.

Forest harvesting scenarios had a relatively limited effect on the changes in the forest landscape in the territory of Mistissini, because a large part of the modeled territory is located north of the northern limit of commercial forests and is therefore not subject to forest harvesting. The changes in the forest landscape were, therefore, more influenced by the different climate change scenarios (Figure S2.8). The proportion of non-forest areas (+158% to +255%) and aspen stands (+1409% to 2251%) increased as the proportion of pure spruce stands (-84% to -99%) and other coniferous stands (-62% to -92%) decreased in relation to the intensity of climate scenarios.

The effect of the forest harvesting scenarios is practically null on the Nemaska territory, as it is located almost entirely north of the northern limit of commercial forests. As in the Mistissini territory, the proportion of non-forest areas (-49% to +31%) and aspen stands (+457% to +1821%) increases as the proportion of pure spruce (-71% to -98%) and coniferous stands (+55% to -88%) decreases in response to increased fire activity under increased anthropogenic climate forcing (Figure S2.9).

2.5.3 Effect of climate change and forest harvesting on culturally salient species probability of presence

Our projections showed a slight increase in the probability of presence of both species across all territories under most scenarios relative to the baseline climate scenarios (Figure 2.2 and Figure 2.4). Moderate (RCP 4.5) and high (RCP 8.5) climate change scenarios resulted in the largest relative increase in probability of presence for *R. groenlandicum* and *V. angustifolium* respectively. The effect of forest harvesting was generally less important than that of climate change on the probability of presence of both species, although the ratio of importance between forest harvesting and climate change varied between territories along the simulated period (Figure 2.3 and Figure 2.5).

2.5.3.1 *Rhododendron groenlandicum* presence

The probability of presence of *R. groenlandicum* changed relatively little with climate and forest harvesting scenarios (Figure 2.2). Indeed, the deviation from the baseline climate scenario never exceeded 15%. RCP 4.5 was the scenario under which changes

in the forest would most benefit *R. groenlandicum*, and RCP 8.5 the scenario under which changes in the forest would be worst for the species.

Forest harvesting scenarios also had an influence on the presence of *R. groenlandicum*, although mostly restricted to the Abitibiwinni territory, as the other two territories are largely untouched by forest harvesting. The probability of presence of *R. groenlandicum* decreased with increasing forest harvesting, especially under high climate change scenarios.

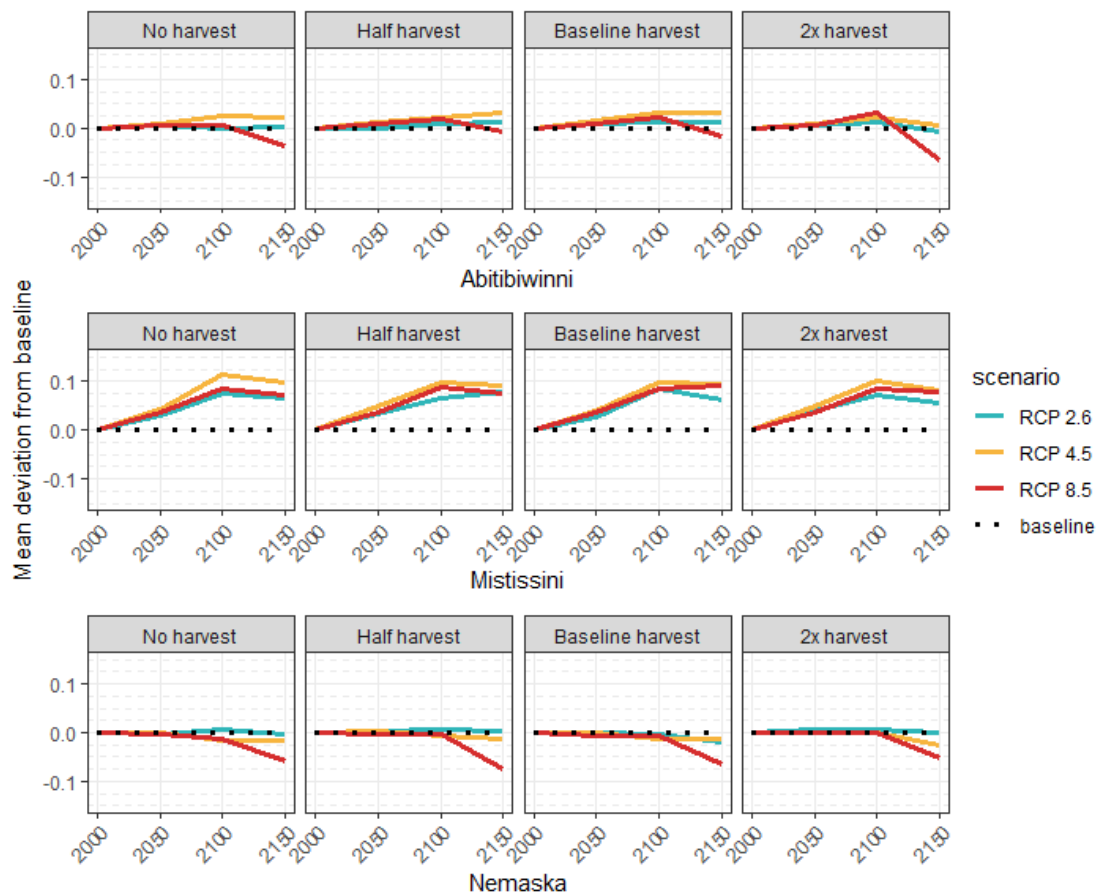


Figure 2.2 Evolution of the average probability of presence of *R. groenlandicum* in the territories of Abitibiwinni, Mistissini, and Nemaska under different climate and forest harvesting scenarios. The evolution of the probability of presence is expressed relative to the baseline scenario (no climate change) for each territory and each harvest scenario.

In the Abitibiwinni territory, the effect of forest harvesting scenarios on the probability of presence of *R. groenlandicum* was more important than the effect of climate change scenarios over the entire duration of the simulation (Figure 2.3). However, the relative importance of climate change versus forest harvesting varied from one time step to another, with a progressive increase in the effect of climate change while the effect of forest harvesting remained relatively stable. In Mistissini, the probability of presence of *R. groenlandicum* was mostly explained by the climate change scenarios throughout the simulation. Finally, the different scenarios explained relatively little of the probability of presence in Nemaska. The analysis attributed around 70% of the variation in 2050 to forest harvesting scenarios, but this is likely a modeling artefact, as forest harvesting barely affects the Nemaska territory. The Nemaska territory is relatively small, highly influenced by fires, and the analysis was based on only 5 replicates. As fire ignition probability was low in 2050, replicates either had a fire with an important effect on the territory, or no fire, thus no effect on the territory. This high variability in fire events prevented the analysis from disentangling the effects of climate scenarios. In addition, the variability in the probability of presence of *R. groenlandicum* was very low in 2050 in Nemaska. The analysis thus falsely attributed the little variation in *R. groenlandicum* probability of presence to random variations between forest harvesting scenarios, which created this artefact. In general, for all territories, the relative importance of the climate change scenarios increased as the simulations progress through time.

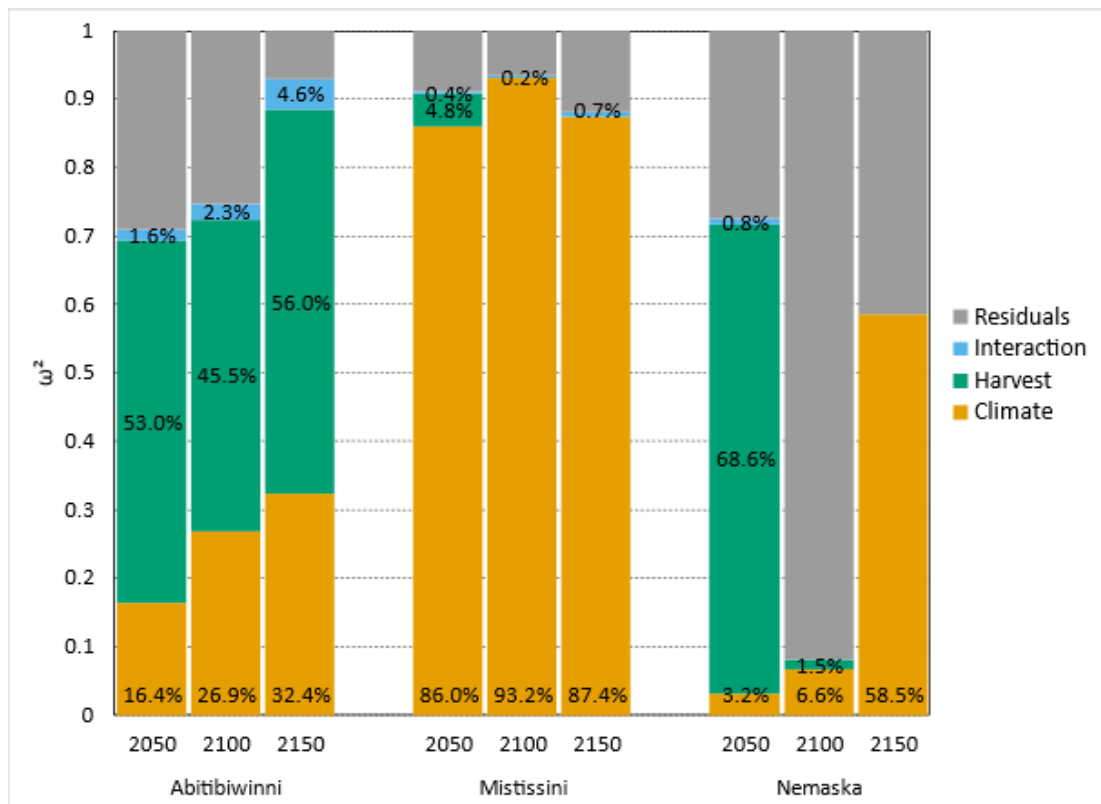


Figure 2.3 Relative importance of climate change scenarios, forest harvesting scenarios, and their interaction in explaining the variation of the probability of presence of *R. groenlandicum*. Relative importance was calculated using ω^2 after a 2-factor ANOVA.

2.5.3.2 *Vaccinium angustifolium* presence

For *V. angustifolium*, there was relatively little variation in the probability of presence among the different scenarios (Figure 2.4). The deviation in probability of presence under the climate change scenarios relative to the baseline climate scenarios was always positive. The probability of presence of *V. angustifolium* increased along with anthropogenic climate forcing. As was the case for *R. groenlandicum*, the probability of presence of *V. angustifolium* decreased with increasing forest harvesting in the Abitibiwinini territory.

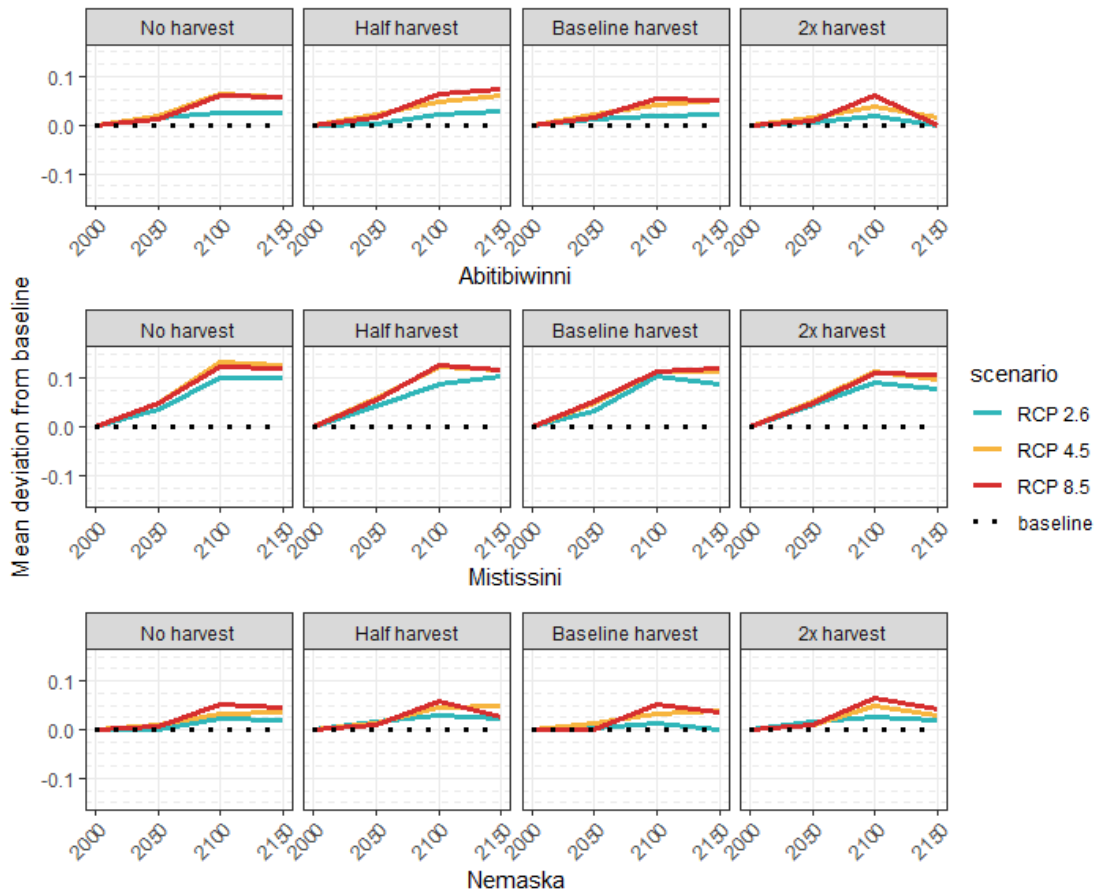


Figure 2.4 Evolution of the average probability of presence of *V. angustifolium* in the territories of Abitibiwinni, Mistissini and Nemaska under different climate and forest harvesting scenarios. The evolution of the probability of presence is expressed relative to the baseline scenario for each territory and each harvest scenario.

In the Abitibiwinni territory, the evolution of the probability of presence of *V. angustifolium* was mostly explained by forest harvesting scenarios (Figure 2.5). However, there was a slight effect of climate change scenarios, especially in 2100. For the other two territories, the effect of forest harvesting scenarios was almost null. Climate change scenarios explained almost all of the variation in the probability of presence of *V. angustifolium* in the Mistissini territory, while variation in the Nemaska territory was less well explained by the scenarios under study.

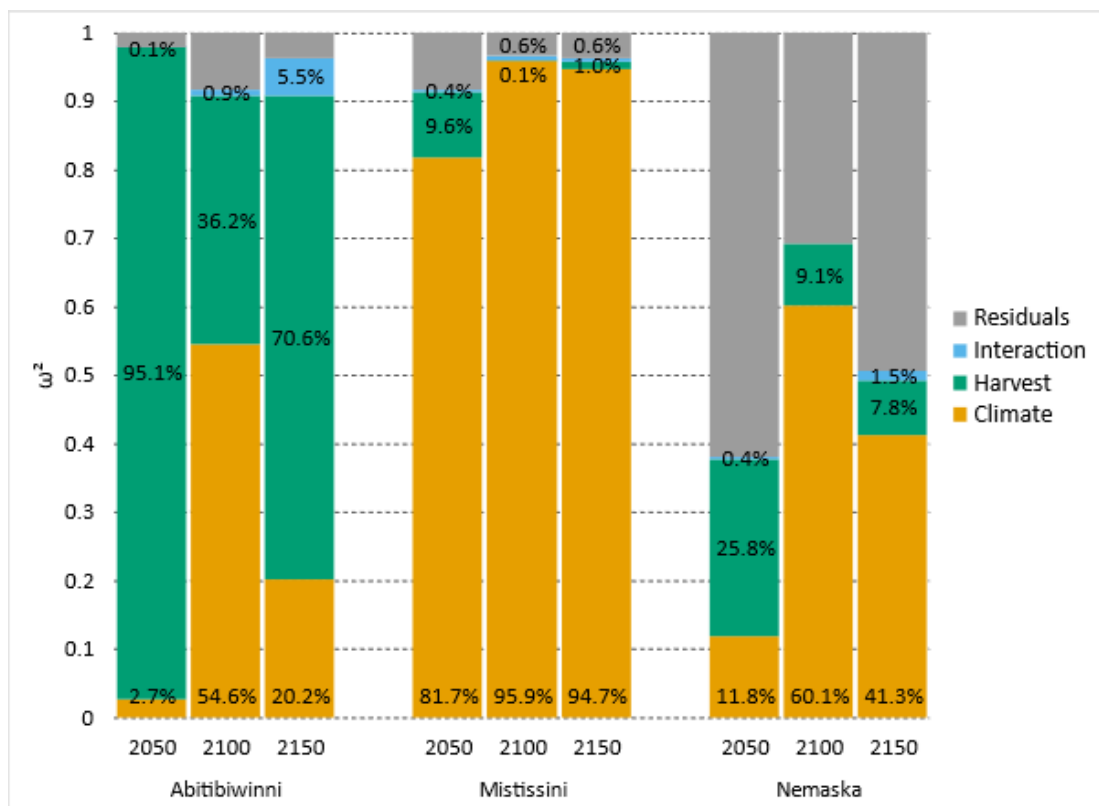


Figure 2.5 Relative importance of climate change scenarios, forest harvesting scenarios, and their interaction in explaining the variation of the probability of presence of *V. angustifolium*. Relative importance was calculated by ω^2 after a 2-factor ANOVA.

2.6 Discussion

Forest cover change was the main driver to predict the probability of presence for both species. Age and origin of stands also had an effect for *V. angustifolium*, while the other variables in our models had little influence on both species. Both studied species had an increased probability of presence under climate change scenarios, due to the increase in non-forested areas in the landscape, which are good-quality habitats for both species. However, this trend reversed in 2150 for *R. groenlandicum* under RCP 8.5 scenario, as the increase in non-forested areas was accompanied by a sharp increase

in aspen stands, which are poor-quality habitats. The added effect of forest harvesting in the Abitibiwinni territory further increased the proportion of aspen to the detriment of *R. groenlandicum*.

2.6.1 Effect of climate change on the landscape and on the studied species

We showed that an increase in the proportion of aspen in the landscape would be detrimental to *R. groenlandicum* and *V. angustifolium*, as these species are not associated with deciduous stands (Laberge Pelletier 2007; Humbert et al. 2007; Hébert and Thiffault 2011; Thiffault et al. 2015). Fire activity is projected to increase in western Quebec under climate change (Boulanger et al. 2017b, 2022; Boulanger and Pascual Puigdevall 2021; Augustin et al. 2022) which will lead to more frequent fires, preventing many stands from reaching late-successional stages, which are mostly coniferous (Bergeron 2000; Shenoy et al. 2011; Boucher et al. 2017a). Late-successional spruce stands could be replaced by early-successional species such as aspen and white birch (Bergeron 2000; Paudel et al. 2015), especially under the worst-case climate change scenarios (RCP 8.5). Indeed, the increase in proportion of aspen stands is further enhanced by substantial increases in temperatures which are also known to promote aspen growth in northern latitudes, at the expense of most coniferous species (Paudel et al. 2015).

However, the climate-induced increase in fires could also have positive impacts on the habitat of both studied species under certain circumstances, notably because of the increase in non-forested areas. Non-forested area can either occur for a short period after stand-replacing disturbances (e.g., severe fires) or more permanently in the absence of post-disturbance regeneration (Jasinski and Payette 2005; Splawinski et al. 2019; Schab et al. 2021). Such climate-induced increases in non-forested areas is beneficial to both studied species, as they can take advantage of canopy openings

following disturbances, notably through their ability to reproduce vegetatively (Laberge Pelletier 2007; Hébert and Thiffault 2011; Marozau and Gordej 2019). They are also known to persist for a long time after disturbances, especially under high light conditions, making them more likely to subsist in stands that experience regeneration failure (Laberge Pelletier 2007; Hébert and Thiffault 2011).

2.6.2 Effect of forest harvesting on the landscape and on the studied species

Forest harvesting has an additive effect with climate change, as it contributes to increase the proportion of aspen stands on the landscape (Laquerre et al. 2011; Marchais et al. 2022), because aspen can sucker after forest harvest and quickly dominate stands (Laquerre et al. 2011; Marchais et al. 2022). The proportion of aspen increased the most in the Abitibiwinni territory, where the additive effect of forest harvesting and climate change was most pronounced. Harvest-induced increases in the proportion of aspen stands, which are poor quality habitats for studied species, explains why forest harvesting tends to decrease the probability of presence of both species (Laberge Pelletier 2007; Humbert et al. 2007; Hébert and Thiffault 2011; Thiffault et al. 2015).

2.6.3 Limitations

Simulation of complex ecological processes necessitated a few choices and assumptions in our models, which bring some limitations. First, while we predicted the probability of presence of the two studied species, we could not predict the fruiting of *V. angustifolium*, which would be necessary for an accurate assessment of its value, because berries are an important part of this species' interest to First Nations

(Boulanger-Lapointe et al. 2019; Basile et al. 2022). Second, we could not account for the effect of the studied species on the regeneration and growth of tree species. Ericaceous plants are known to limit tree regeneration after disturbances, through nutrient use and the production of allelopathic phenolic compounds (Mallik 2003; Laberge Pelletier 2007; Hébert et al. 2010; Hébert and Thiffault 2011; Ménard et al. 2019). Thus, our models may have overestimated the rate of forest succession in some cases.

We also used some simplifications regarding disturbances. First, even if clearcuts are the dominant forest harvesting method in our study area, partial cuts are increasingly used. Partial cuts could be less favorable to the studied species, as they do not open the canopy as much as clearcuts (Hébert et al. 2010; Bose et al. 2014). In addition, we did not simulate the use of site preparation after harvest, as this practice is still relatively uncommon in the study area. Site preparation has the objective to limit the reproduction and growth of so-called competing vegetation (including ericaceous shrubs), which would decrease the probability of presence of both studied species under forest harvesting scenarios (Lorente et al. 2012; Thiffault et al. 2013; Thiffault and Hébert 2017). Third, we did not change the northern limit of commercial forests during the simulations. While it could be argued that increased productivity in the north could lead to a northward repositioning of the limit, this is unlikely, as fire susceptibility would be too high for harvest to be sustainable (Oris et al. 2014; Pau et al. 2023). Last, although fire regimes responded to stand age, they did not respond to changes in forest composition, although deciduous trees are known to be less flammable than conifers (Krawchuk et al. 2006; Boulanger et al. 2018a; Marchal et al. 2020). Since our simulations predict an increase of the deciduous proportion in the study area, fire occurrence in the future could be lower than that predicted by our models.

2.6.4 Implications for species long term persistence and forest management

Based on our results, low to moderate climate change should not be a threat to the long-term persistence of *R. groenlandicum* and *V. angustifolium* in the study area. Such scenarios could even contribute to their persistence in a changing boreal landscape, notably through the increase in non-forested areas. However, more severe climate change could increase the proportion of deciduous tree species in the landscape, which would decrease the habitat quality of both studied species.

As previously shown, the long-term persistence of both species might depend on harvesting strategies. North of the northern limit of commercial forests, even without the impact of forest harvesting, it is likely that the landscape will open up in response to increased fire activity due to climate change (Mansuy et al. 2012; Oris et al. 2014; Augustin et al. 2022). The probability of presence of both studied species would thus either remain the same, or increase, as they would benefit from increased light availability in a more open landscape (Hébert and Thiffault 2011; Ministère des Ressources Naturelles 2013). However, in the commercial forest, business-as-usual or intensified forest harvesting rates could aggravate climate change consequences (Brice et al. 2019; Splawinski et al. 2019; Bouchard et al. 2019; Määttänen et al. 2023). As such, adaptation strategies may be necessary to maintain these species in the landscape, notably for *R. groenlandicum*, which could suffer most from the cumulative impacts of harvesting and climate change.

The most effective strategy to maintain the probability of presence of *V. angustifolium* and *R. groenlandicum* is to limit the increase of deciduous (aspen) stands in the landscape due to climate change and forest harvesting, as deciduous stands are poor-quality habitats for both studied species. Within the commercial forest, lowering harvesting rates, for example by considering areas that could burn in the calculation of the annual harvestable volumes, could help mitigate the increase in deciduous stands

at the landscape level. Including fire risk in forest planning could also help maintain a greater stability in harvested volumes from year to year and limit the additive effects of harvesting and climate change (Acuna et al. 2010; Leduc et al. 2015; Daniel et al. 2017). Furthermore, although it was not simulated within the current study, limiting post-fire salvaged logging could help maintain studied species' habitats as this strategy is known to favor deciduous rather than coniferous regeneration (Boucher et al. 2014). Favoring coniferous species that are more resilient to high fire frequency, such as jack pine through post-fire plantation, could also help maintain good habitat quality under increasing anthropogenic climate forcing (Cyr et al. 2022). Likewise, retention harvesting, through the preservation of seedtrees, could enhance the regeneration of black spruce and jack pine after fire and improve the long term persistence of coniferous species within the landscapes (Cyr et al. 2022). Within both the commercial and northern forests, prescribed burns, a method used historically by Indigenous communities to control fire severity (Lewis et al. 2018; Hoffman et al. 2022), could create sufficient open areas while limiting the occurrence of large fires and hence extensive aspen regeneration under increased anthropogenic climate forcing (Le Goff et al. 2005; Gauthier et al. 2014; Beverly et al. 2020). In addition, these strategies aiming at mitigating the proportion of the deciduous component within the landscape would be beneficial not only to the studied species, but to other boreal species, e.g., birds (Cadieux et al. 2020), caribou (St-Laurent et al. 2022; Leblond et al. 2022) and bryophytes (Barbé et al. 2020). Yet, no single strategy should be used to preserve culturally salient species under a changing climate. The uncertainty associated with climate change demands flexible management strategies adapted to the context and objectives of each region (Boulanger et al. 2023).

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CHAPITRE III

EFFET DES PERTURBATIONS INDUSTRIELLES SUR LA CONCENTRATION
EN FLAVONOÏDES DE *RHODODENDRON GROENLANDICUM*

EFFECT OF INDUSTRIAL DISTURBANCES ON THE FLAVONOID
CONCENTRATION OF *RHODODENDRON GROENLANDICUM*

Maxime Thomas¹, Mebarek Lamara¹, Hugo Asselin², Nicole J. Fenton¹

¹Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

²École d'études autochtones, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

Corresponding author: Maxime Thomas (maxime.thomas@uqat.ca)

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Le chapitre suivant a été amélioré par diverses suggestions et diffère donc légèrement
de l'article publié.

3.1 Résumé

La forêt boréale est sujette à des perturbations anthropiques variées, incluant la coupe forestière, les activités minières, et la production et le transport d'hydroélectricité. Ces perturbations affectent les communautés autochtones et les espèces d'importance culturelle dont elles dépendent pour la pratique d'activités traditionnelles et de subsistance. *Rhododendron groenlandicum* est l'une de ces espèces dont les feuilles sont utilisées pour traiter des maux variés, dû à leur concentration en composés chimiques à activité biologique tels que les flavonoïdes. Notre objectif était d'évaluer l'effet de perturbations anthropiques sur les propriétés chimiques de *R. groenlandicum* sur les territoires de trois communautés autochtones. Les échantillons de feuilles ont été collectés à proximité de mines, sous des lignes hydroélectriques, et dans des sites non perturbés. Nos résultats ont montré que les variations de concentrations en flavonoïdes étaient principalement reliées au territoire ($R^2 = 0.43$, $P = 0.0005$), tandis que le type de perturbation avait un effet faible ($R^2 = 0.18$, $P = 0.02$). Les échantillons de Nemaska, le territoire le plus au nord avec les peuplements forestiers les plus ouverts, avaient des concentrations plus élevées en épicatechine (+23%, $P = 0.03$). Les concentrations en quercétine-3-glucoside étaient plus faibles à proximité des mines (-19%, $P = 0.01$). Les effets des perturbations sur la signature chimique de *R. groenlandicum* sont complexes, et une évaluation complète des conséquences des activités industrielles sur la valeur des territoires autochtones doit prendre en compte d'autres espèces d'importance culturelle.

Mots-clés : Thé du Labrador, peuples autochtones, perturbation anthropique, composés phénoliques, espèce d'importance culturelle.

3.2 Abstract

The boreal forest is subject to various anthropogenic disturbances, including logging, mining, and hydroelectricity production and transport. These disturbances affect Indigenous communities and the culturally salient species they depend on for the practice of traditional and subsistence activities. *Rhododendron groenlandicum* is one such species whose leaves are used to treat various ailments, due to their concentration in biologically active chemicals such as flavonoids. Our objective was to assess the effect of anthropogenic disturbances on the chemical properties of *R. groenlandicum* on the territories of three Indigenous communities. Leaf samples were collected near mines, under hydroelectric power lines, and in non-disturbed sites. Our results showed that variations in flavonoid concentration were mainly related to territory ($R^2 = 0.43$, $P = 0.0005$), while disturbance type had a smaller effect ($R^2 = 0.18$, $P = 0.02$). Samples from Nemaska, the northernmost territory with the most open forest stands, had higher concentrations of epicatechin (+23%, $P = 0.03$). Quercetin-3-glucoside concentrations were lower near mines (-19%, $P = 0.01$). The effects of disturbances on the chemical signature of *R. groenlandicum* are complex, and a complete assessment of the consequence of industrial activity on Indigenous landscape value must take into account other culturally salient species.

Keywords: Labrador tea, Indigenous people, anthropogenic disturbance, phenolic compounds, culturally salient species.

3.3 Introduction

The boreal forest is disturbed by various anthropogenic activities, which alter species composition, homogenize landscapes, and decrease biodiversity (Venier et al. 2014; Gauthier et al. 2015). In Canada, mining and hydroelectric development are two of the main anthropogenic disturbances affecting the boreal forest (Venier et al. 2014; Bélisle and Asselin 2021). Mining waste contaminates the soil and the water resources with heavy metals, which are then absorbed by plants and animals (Bordeleau et al. 2016; Karaca et al. 2018). Chronic exposure to this heavy metal pollution has harmful consequences on animal and human health, as well as on plant germination, reproduction, and metabolism (Adeel et al. 2019; Yin et al. 2021). Power transportation lines create linear openings in the forest that fragment the landscape (Li and Lin 2019).

Disturbances can also have less visible effects, as a species may persist in a disturbed environment by adapting to it (Aitken et al. 2008; Sharma et al. 2020). Plants can notably adapt by modulating their secondary metabolite profiles in response to different biotic and abiotic stresses (Thakur et al. 2019). For stresses related to climate and anthropogenic disturbances, flavonoids are particularly important in plant response (Jaakola and Hohtola 2010). For example, cold stress can trigger flavonoid biosynthesis (Treutter 2006; Sharma et al. 2019). Flavonoids also represent an important response mechanism in plants facing oxidative stress, such as heavy metal pollution or UV radiation exposure due to forest canopy opening (Agati and Tattini 2010; Kumar and Pandey 2013). As antioxidants, flavonoids reduce the reactive oxygen species generated by oxidative stress, thus decreasing oxidative damages to the plant (Agati and Tattini 2010; Kumar and Pandey 2013). Flavonoids can also reduce UV stress by absorbing parts of UV radiation (Agati and Tattini 2010; Laoué et al. 2022). In addition, heavy metal stress is further reduced by flavonoids as they can chelate heavy metals (Keilig and Ludwig-Müller 2009; Sytar et al. 2013). It should be noted that the

chelation of heavy metals and the reduction of oxidative damage can deplete flavonoids, thus inducing a decrease in flavonoid concentration (Michalak 2006; Dutta and Maharia 2012; Sleptsov et al. 2021).

When stresses are long-lasting or recurring, plant adaptations can result in distinct secondary metabolite profiles due to genetic or genetic expression differences (Polatoglu 2013). Changes in the quantity or composition of secondary metabolites can affect plant morphology, growth, or medicinal and nutritional properties (Agati et al. 2012; Del Rio et al. 2013; Kumar and Pandey 2013; Durazzo et al. 2019).

The effect of flavonoid concentration on the medicinal and nutritional properties of plants is complex. The benefits associated with plant consumption are the result of a mixture of metabolites rather than the effect of a single compound (Egert and Rimbach 2011). In the case of flavonoids, their absorption and bioavailability can vary greatly depending on source, food preparation technique, or regimen (Khan et al. 2021). Additionally, while the health benefits associated with flavonoid consumption have been widely studied, there is still relatively little research on their potential toxicity at higher concentrations (Khan et al. 2021). For example, they can cause noxious interactions with medication or induction of iron deficiency (Corcoran et al. 2012). Therefore, higher concentrations of flavonoids do not necessarily result in increased medicinal and nutritional benefits.

Changes in plant properties affect Indigenous communities who occupy and steward boreal landscapes, as they depend on certain species to carry out traditional activities (Parlee et al. 2005; Boulanger-Lapointe et al. 2019). For example, blueberry (*Vaccinium myrtilloides* Michaux) is a source of traditional food and medicine and is used as a dye by Indigenous communities across Canada (Nielsen et al. 2020). Species of great importance in Indigenous cultures are considered culturally salient species (Hunn 1999; Garibaldi and Turner 2004; Ladle et al. 2019). Culturally salient species

are particularly useful to assess the effects of disturbances on both social and ecological systems (e.g., Uprety et al. 2017).

Following our project development discussions with three Indigenous communities in western Quebec (Canada), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron and Judd) was identified as a culturally salient species to be studied to determine the effects of anthropogenic disturbances. The leaves of this ericaceous shrub are widely used to treat many ailments, such as colds, open wounds, osteoarthritis, migraines, and diabetes (Uprety et al. 2012). Most of these properties are likely due to the presence of phenolic compounds, such as flavonoids in leaves extracts (Saleem et al. 2010). For example, *R. groenlandicum*'s anti-diabetic properties are due to the adipogenic activity of catechin and epicatechin, flavonoids of the flavan-3-ols class, which contributes to lowering blood glucose levels (Eid et al. 2016). *Rhododendron groenlandicum* also contains high concentrations of proanthocyanidins (Saleem et al. 2010), flavonoids with many known medicinal properties, such as antioxidant, anticarcinogenic, anti-inflammatory, and kidney-protective effects (Ivey et al. 2013; Li et al. 2016; Yokota et al. 2016; Dasiman et al. 2022).

The objective of this study was to assess the effects of anthropogenic disturbances on the flavonoid concentration of *R. groenlandicum* on the territories of three Indigenous communities in western Quebec. Two industrial anthropogenic disturbances of concern to Indigenous communities in the study area were considered: mining sites and hydroelectric power lines. Our hypotheses were that (i) *R. groenlandicum* individuals near mining sites have higher flavonoid concentrations due to pollution stress, notably the oxidative stress induced by heavy metal pollution; and (ii) *R. groenlandicum* individuals in disturbed areas, especially under hydroelectric power lines, have higher flavonoid concentrations because of the UV-related oxidative stress due to higher sun exposure resulting from forest canopy opening. Our results will help determine the

extent to which anthropogenic disturbances can affect the medicinal and nutritional properties of a culturally salient species of the eastern Canadian boreal forest.

3.4 Material and methods

3.4.1 Study area

This study took place in western Quebec (Canada), between 49°N and 52°N, on the traditional territories of three Indigenous communities: Abitibiwinni (Anishnaabe), Nemaska, and Mistissini (Cree) (Figure 3.1). The Abitibiwinni First Nation's territory is located northwest of the community, near the border with Ontario. It covers an area of 11,430 km², mostly in the black spruce – feathermoss bioclimatic domain, but with the southernmost part in the balsam fir – paper birch bioclimatic domain (Bélisle and Asselin 2021). The territory of the Nemaska Cree Nation covers 14,929 km² and is located at the northern limit of the black spruce – feathermoss bioclimatic domain (Cree Mineral Exploration Board 2020). This territory has been affected by large forest fires in recent decades, resulting in an over-representation of early-successional forests in the landscape (Eeyou Planning Commission 2017). The territory of the Mistissini Cree Nation has its southern part in the black spruce – feathermoss bioclimatic domain and its northern part in the spruce lichen woodland bioclimatic domain. It is much larger than the territories of the other two communities, covering 121,939 km² (Cree Mineral Exploration Board 2020).

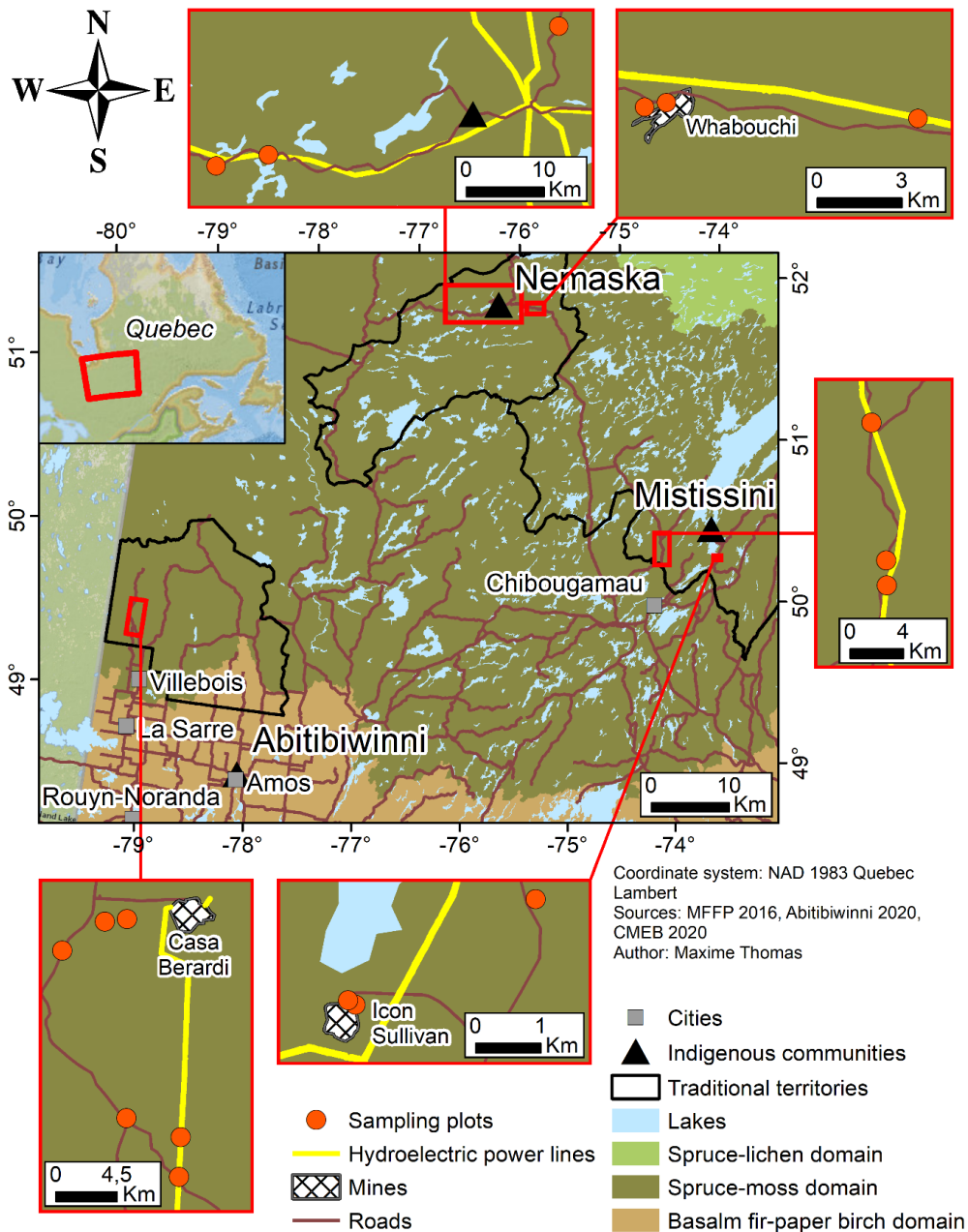


Figure 3.1 Location of the study area in Quebec (eastern Canada). The red insets around the main map are zoom-ins showing the locations of the sampling sites, with locations of hydroelectric power lines, roads, and mines. Map produced with data from the Ministère des Forêts de la Faune et des Parcs du Québec, the First Nation of Abitibiwinni, and the Cree Mineral Exploration Board using the ArcGIS software (NAD 1983 Québec Lambert projection).

3.4.2 Sampling

All the sampling sites were located in the black spruce – feathermoss bioclimatic domain (Figure 3.1). For each Indigenous territory, potential sites were selected using ArcGIS, based on the conditions favorable for the growth of *R. groenlandicum* retrieved from a governmental database (Ministère des Forêts, de la Faune et des Parcs du Québec, MFFP) (Table S3.1) (Blouin and Berger 2004). This database contains information about vegetation (e.g., forest stand age) and characteristics of the physical environment (e.g., soil type). We pre-selected sites with similar characteristics in terms of forest stand and soil type to limit the effect of variables other than those studied. Sampling sites under hydroelectric lines were pre-selected with regards to the surrounding forest stands, as hydroelectric lines are clear of trees. Discussions were then held with members of each community to ensure that the pre-selected sites were likely to contain *R. groenlandicum*, and that they were actively used by community members for plant collection. A total of 18 sites were sampled, six per territory: two sites within 200 m of a mine, two sites under a hydroelectric line, and two controls at least 500 m away from these anthropogenic disturbances. The distance to mining sites was chosen based on previous studies that found that the impact of mines on vegetation extended to 200 m on average (Boisvert et al. 2021; Yin et al. 2022, 2023a). Each site was located at least 100 m from roads to avoid edge effects, such as disturbance from dust deposits raised by passing vehicles, and to limit trampling (Figure 3.1). Sampling sites were in spruce stands and had a mesic to subhydic soil (full information regarding the characteristics of the sampling sites can be found in Table S3.1 and Table S3.2).

In the Abitibiwinni territory, the Casa Berardi gold mine was built in the late 1980s and has been in continuous operation since 2007. An electricity transportation line (161 kV) delivers electricity to the mine site. In the Nemaska territory, the Whabouchi lithium mine has been in development since the mid 2010s. The extraction has not started yet

due to economic challenges, but the mining infrastructure has been constructed and some preliminary operations were undertaken (e.g., soil removal and rock blasting), which resulted in a certain amount of pollution. The Nemaska territory is crossed by very high-voltage electricity transportation lines (735 kV) that were built in the 1970s and 1990s as part of major hydroelectric projects in northern Quebec (Hydro-Québec 2022). In the Mistissini territory, the Icon-Sullivan copper mine was in operation in the 1960s-1970s and has been closed since 1976. However, as the site has not yet been restored, remaining tailings and infrastructures still affect the surrounding landscape. Lower voltage electricity transportation lines (161 kV) are present on the territory. We collected the samples under hydroelectric lines near the center of the rights-of-way to minimize the differences in terms of sun exposure between sites, as hydroelectric lines of different voltages have rights-of-way of different widths (30-80 m).

Sampling took place between 7:00 a.m. and 5:00 p.m. on August 4, 24, and 27 in the territories of the Abitibiwinni, Mistissini, and Nemaska First Nations, respectively. The collection in the Abitibiwinni territory was carried out at an earlier date to account for the phenological advance related to the difference in latitude with the other two territories. For the same reason, the collection in the Mistissini territory took place a few days before the collection in the Nemaska territory. Within each site, 5 samples of approximately 10 grams of *R. groenlandicum* mature leaves from the current year were collected and preserved immediately on dry ice. Each sample was collected on stems from a single individual, and different samples were collected at least a few meters apart to avoid sampling the same individual twice, as the species is clonal. After each day of sampling, samples were transferred to a -80 °C freezer where they were stored until the extraction of flavonoids.

3.4.3 Extraction of phenolic compounds

The collected samples were sent to Institute of Nutrition and Functional Foods, Laval University, Quebec, Canada, for extraction and analysis of flavonoids. Frozen leaves were freeze-dried and then ground into powder. A 500 mg aliquot of ground leaves was extracted twice in 20 mL of methanol 80% by sonication for 20 min. Extracts were centrifuged 4 min at 4000 rpm at room temperature, then supernatants were combined and filtrated on a 0.22 μm nylon filter.

3.4.4 Analysis of total phenolic content

Total phenolic content was determined in the phenolic extracts by Folin-Ciocalteu colorimetric method according to Dudonné et al. (2015). Briefly, 100 μL of 10 fold diluted Folin-Ciocalteu reagent and 80 μL of sodium carbonate solution at 75g/L were added to plant extracts. The mix was allowed to incubate 1h at room temperature, then the absorbance was measured at 765 nm and converted to a concentration by comparison to a gallic acid standard.

3.4.5 Analysis of flavan-3-ols and flavonols by UHPLC with ultraviolet-visible

Flavan-3-ols and flavonols were analyzed on an Acquity H-Class Ultra Performance LC system (Waters) coupled to an Acquity PDA detector and triple quadrupole TQD mass spectrometer equipped with a Z-spray electrospray interface. Compounds were separated on an Acquity UPLC HSS T3 1.8 μm 2.1 x 100mm column. Flavan-3-ols were quantified as catechin equivalents using 280 nm chromatogram and a 6-points calibration curve. Flavonols were quantified as quercetin equivalents using 360 nm

chromatogram and a 6-points calibration curve. Mass spectrometry in multiple reaction monitoring modes was used to confirm compound identifications.

3.4.6 Acid-catalysis of proanthocyanidin in the presence of phloroglucinol and analysis of cleavage products

Proanthocyanidins were analysed and quantified after acid-catalysis in the presence of phloroglucinolysis as described in Jakobek et al. (2013), with slight modification. Briefly, a solution of 0.1 N HCl in methanol containing 50 g/L phloroglucinol and 10 g/L ascorbic acid was freshly prepared, and 6 mL of this solution was added to a 15 mL assay tube that contained 50 mg of lyophilised sample. The resultant reaction was conducted for 20 minutes at 50 °C. The reaction was stopped by diluting the reaction medium with 7.5 mL of 40 mmol/L sodium acetate solution. The solution was centrifuged for 10 minutes at 5311 g at room temperature and filtered on a 0.22 µm nylon filter. Cleavage products were analysed according to the flavan-3-ols method described previously, and quantities were estimated using their relative response factor (Koerner et al. 2009). To calculate the mean degree of polymerisation of proanthocyanidins, the sum of all subunits (flavan-3-ol monomer and phloroglucinol adduct, in moles) was divided by the sum of all flavan-3-ol monomers (in moles) corrected by subtracting the content of flavan-3-ols monomers (in moles) previously measured in the phenolic extract. Total proanthocyanidin content was calculated by conversion of subunit moles to proanthocyanidins weight using molar masses, excluding the phloroglucinol portion of the phloroglucinol adducts (Kennedy and Jones 2001).

3.4.7 Statistical analyses

Statistical analyses were performed using the R software, version 4.1.2 (R Development Core Team 2021). To avoid a pseudoreplication bias, the data were averaged by site for all analyses except the linear mixed models, for which it was possible to correct this bias by including a random site effect.

Potential differences in flavonoid profiles in *R. groenlandicum* between the three territories were investigated with a hierarchical bottom-up classification using Ward's criterion based on a Euclidean matrix of the similarities between sampling sites according to their flavonoid concentrations. The stability of the groups was tested by a bootstrap procedure with 10,000 replicates using the pvclust R package (Suzuki et al. 2019). The clustering was coupled with a principal component analysis (PCA) performed with the vegan R package (Oksanen et al. 2020) to visually examine the relationships between the concentrations of different flavonoids, disturbance types, and territories. The approximate forest cover percentage at each site was also added to the PCA to visually assess the effect of forest canopy density on flavonoid concentration. The forest cover percentage was extracted from the MFFP database, and sites under hydroelectric power lines were assigned a forest cover of 0%.

The effect of disturbance type, territory, and their interaction on flavonoid profile was assessed using a permutational analysis of variance (PERMANOVA) performed with the adonis function of the vegan R package. Differences in flavonoid concentration between all sites were quantified using Euclidean distance, then 9999 permutations were performed on the dataset to create a random distribution. This random distribution was used to determine the probability of obtaining the observed distribution by chance. A PERMANOVA was preferred to a MANOVA because some of the flavonoids analyzed violated the prerequisite of multivariate normality.

Correlations between the site-averaged concentrations of different flavonoids were then assessed to retain only flavonoids that were weakly correlated with others for the following analyses. We used Spearman correlation analysis with the Hmisc R package (Harrell Jr and Dupont 2021) to measure the correlation between the concentrations of different flavonoids. Flavonoids highly significantly correlated with one another were removed ($P \leq 0.001$). Spearman's method was preferred over Pearson's because some flavonoid concentrations had outliers.

Finally, to further examine the variation in flavonoid profiles of the samples as a function of disturbance and territory, a linear mixed-effect model was created for each retained flavonoid, using the following structure:

$$(1) \quad y_{ij} = \beta_0 + \beta_1 \text{Dist}_{ij} + \beta_2 \text{Terr}_{ij} + \beta_3 \text{Dist}_{ij} \text{Terr}_{ij} + u_i + \varepsilon_{ij}$$

where y_{ij} is the concentration of each flavonoid in sample j in site i , Dist_{ij} is disturbance type, Terr_{ij} is territory, $\text{Dist}_{ij} \text{Terr}_{ij}$ the interaction between disturbance type and territory, u_i is the random effect of site i on the intercept, and ε_{ij} is the residual error. Contrasts were adjusted so that disturbances were compared to controls (dummy coding), and territories were compared to the mean for all territories (deviation coding). These models were constructed with the lmer function of the lme4 R package (Bates et al. 2015).

3.5 Results

3.5.1 Flavonoid content

The majority of the flavonoid content in the samples is represented by catechin (mean of 13.67 mg/g), proanthocyanidins A1 (12.42 mg/g), and epicatechin (8.59 mg/g) (Figure 3.2; Table S3.4).

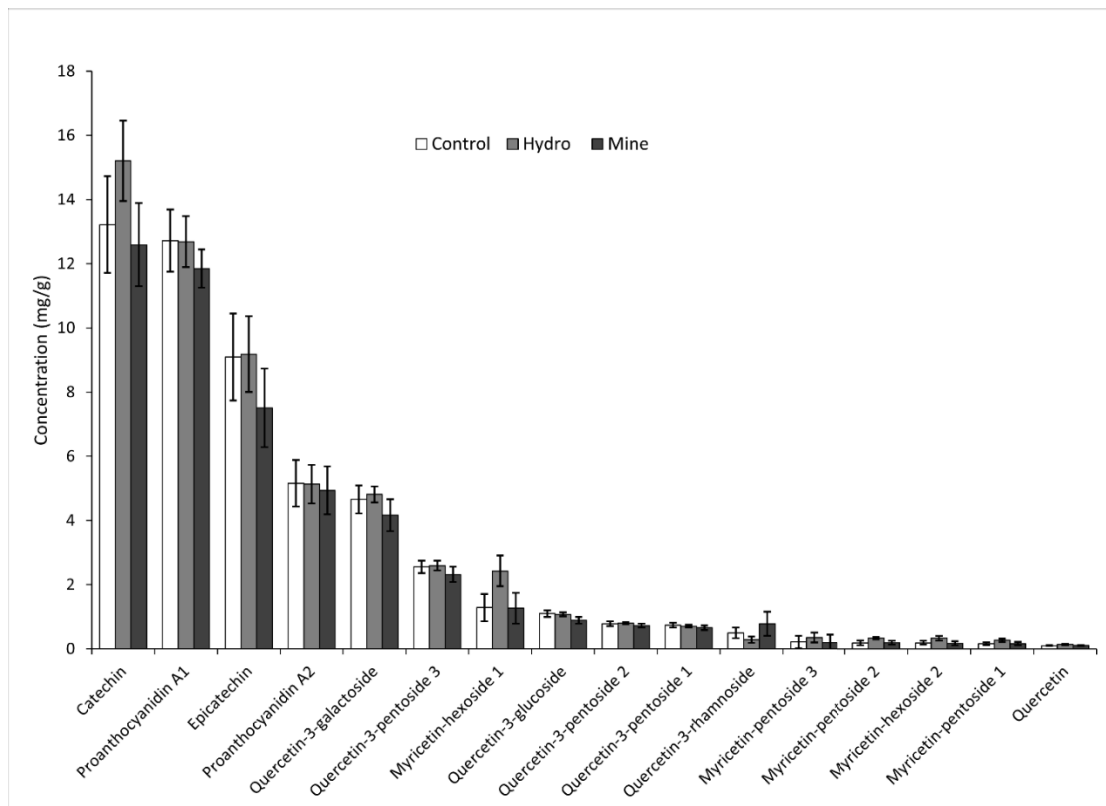


Figure 3.2 Average concentration of the different flavonoids measured in the samples in each disturbance type in milligrams per gram of dry matter with the associated standard deviation.

3.5.2 Variation of the flavonoid profile

The hierarchical classification highlighted two relatively stable main groups of sample sites (Figure 3.3). Sites under hydroelectric power lines from Mistissini and all sites from Nemaska are clustered together (83% probability), whereas all the other sites from Mistissini and all the sites from Abitibiwinni form another cluster (82% probability). In order to further explore this clustering, a PCA analysis was carried out (Figure 3.4). The first two principal components (PCs) accounted for 77.36% of the total variability observed in the concentration of flavonoids. Sites from Nemaska and hydro sites from

Mistissini were on the right of the PC1 axis, and most of the other sites were on the left of the same axis (Figure 3.4). The concentrations of most flavonoids were positively associated with PC1, which also corresponded to a gradient in forest canopy openness. The sites with the densest canopies were located on the left of the graph (most sites from Abitibiwinni and mine sites from Mistissini), and the sites with the most open canopies were on the right (sites from Nemaska and hydro sites from Mistissini). This observation is supported by significant Spearman correlations between the coordinates on the PC1 axis and the percentage of forest cover at the sites ($r = -0.52$, $P = 0.027$). In contrast to all other flavonoids, quercetin-3-rhamnoside was negatively associated with the PC1 axis, being more concentrated in closed environments, which seems to partly explain the clustering of sites from Abitibiwinni.

There was little variability along the PC2 axis. It was negatively associated with quercetin-3-glucoside, quercetin-3-galactoside, quercetin-3-pentosides, and to a lesser extent proanthocyanidin A1, and positively associated with all other flavonoids. While sites from the same territory were clustered together for Nemaska and Abitibiwinni, there was a high variability among sites from Mistissini (Figure 3.4), which seemed to reflect higher heterogeneity in concentrations of several flavonoids, notably quercetin-3-rhamnoside and flavan-3-ols.

A PERMANOVA indicated significant differences in flavonoid concentrations by territory and disturbance type (Table 3.1), with the effect of territory being much stronger than that of disturbance type.

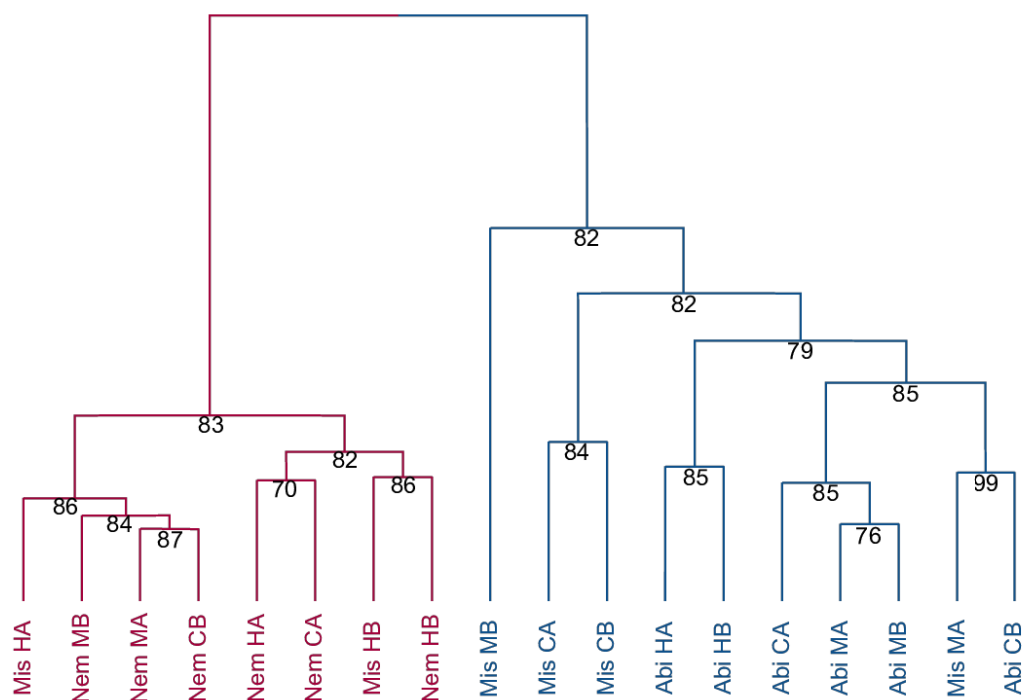


Figure 3.3 Hierarchical classification of the sampling sites based on the concentration in flavonoids. The first three letters of each sample code indicate the territory (Mis = Mistissini, Nem = Nemaska, Abi = Abitibiwinni). The fourth letter indicates disturbance type (M = mine, H = hydroelectric power line, C = control) and the last letter indicates replicate (A or B). The two main clusters are shown in different colors. Numbers indicate the stability (in %) of clusters over all bootstrap replicates calculated using the approximately unbiased probability method.

3.5.3 Variations in the concentrations of individual flavonoids

Before constructing linear mixed models to estimate the effects of territory, disturbance type, and their interaction on the concentrations of individual flavonoids, we used the Spearman correlation analysis to detect flavonoids with high correlations with other flavonoids, indicating redundancy in the dataset (Table 3.2). Hence, we did not construct models for proanthocyanidins and all the myricetin-glycosides because their

concentrations were highly correlated with that of epicatechin. Although quercetin-3-rhamnoside was also highly correlated with epicatechin, it was retained for analysis because it is the only flavonoid that correlated negatively with the others. Models were not constructed either for quercetin-3-galactoside and quercetin-3-pentoside 2 and 3 because their concentrations were strongly correlated with that of quercetin-3-glucoside. Thus, linear mixed models were constructed for six flavonoids: epicatechin, catechin, quercetin, quercetin-3-glucoside, quercetin-3-pentoside 1 and quercetin-3-rhamnoside. These flavonoids were not necessarily the most concentrated or biologically active in the samples, but they are the ones best representing the whole flavonoid profile.

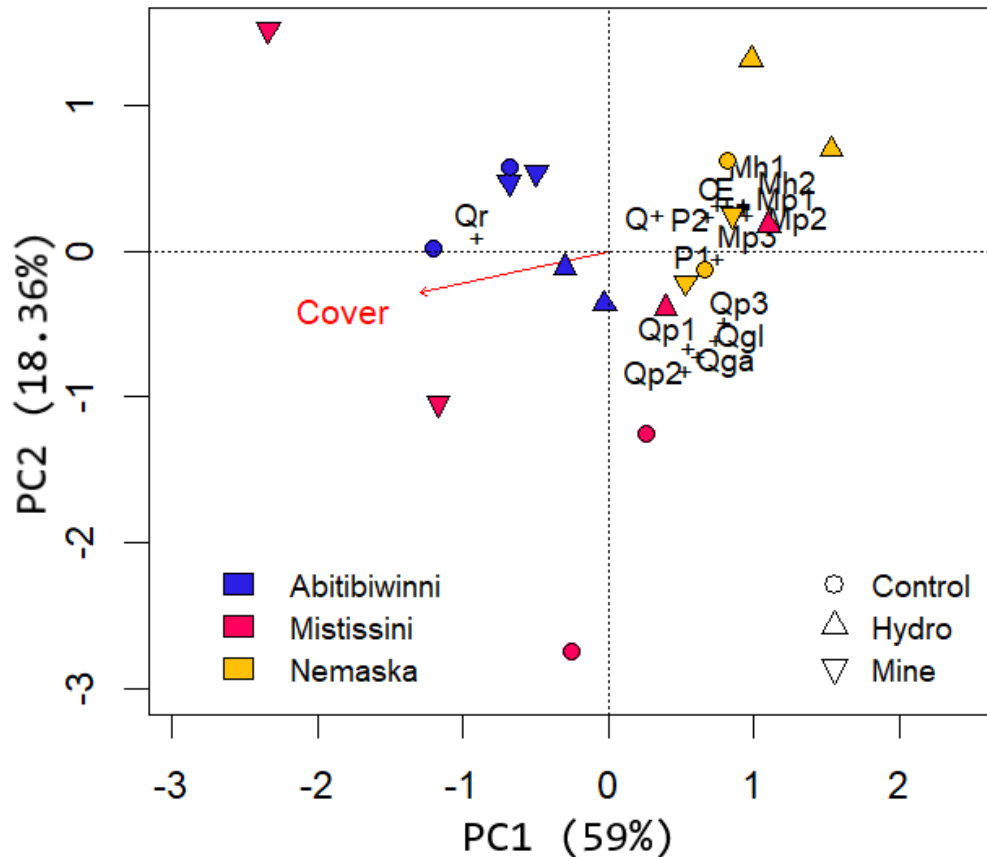


Figure 3.4 Principal component analysis (PCA) of the variation in the concentration of flavonoids in the samples (averaged by site) as a function of disturbance type and territory. The black crosses and letters indicate the different flavonoids. C, catechin; E, epicatechin; P1, proanthocyanidin A1; P2, proanthocyanidin A2; Q, quercetin; Qga, quercetin-3-galactoside; Qgl, quercetin-3-glucoside; Qp1, quercetin-3-pentoside 1; Qp2, quercetin-3-pentoside 2; Qp3, quercetin-3-pentoside 3; Qr, quercetin-3-rhamnoside; Mh1, myricetin-hexoside 1; Mh2, myricetin-hexoside 2; Mp1, myricetin-pentoside 1; Mp2, myricetin-pentoside 2; Mp3, myricetin-pentoside 3. The red arrow indicates the trend in the average % canopy cover for a given site in relation to the flavonoid pattern.

The linear mixed models constructed for each flavonoid showed that samples collected near mining sites were significantly less concentrated in quercetin-3-glucoside than control (-19%, $P = 0.0121$), marginally less concentrated in quercetin-3-pentoside 1

and epicatechin ($P < 0.10$), and marginally more concentrated in quercetin-3-rhamnoside (Table 3.3). Samples collected under hydroelectric power lines had a significantly higher concentration of quercetin than control (+15%; $P = 0.0193$) and a marginally higher concentration of catechin. The samples collected in Nemaska were significantly more concentrated than average in epicatechin (+23%, $P = 0.0317$) and significantly less concentrated in quercetin-3-rhamnoside (-68%, $P = 0.0039$). Samples collected in Mistissini were significantly more concentrated than average in quercetin-3-pentoside 1 (+17%, $P = 0.0117$) and marginally more concentrated in quercetin-3-glucoside. Samples collected in Abitibiwinni were significantly less concentrated than average in quercetin-3-glucoside (-17%, $P = 0.0183$) and quercetin-3-pentoside (-14%, $P = 0.0360$). The effect of mining showed a significant interaction with territory in Mistissini and Abitibiwinni for three of the flavonoids (quercetin-3-glucoside, quercetin-3-pentoside 1 and quercetin-3-rhamnoside). Samples from mining sites in Mistissini were less concentrated in quercetin-3-glucoside and quercetin-3-pentoside 1 than expected under the effect of mining alone, whereas samples from mining sites in Abitibiwinni were more concentrated in these flavonoids than expected under the effect of mining alone. The opposite pattern was observed for quercetin-3-rhamnoside, mining effect increasing concentrations more than expected in Mistissini, and decreasing concentrations more than expected in Abitibiwinni. The positive effect of hydroelectric power lines on quercetin concentration was amplified by a significant interaction with the territory in Abitibiwinni. The variance associated with grouping samples by site was less than or equal to the residual variance, indicating that grouping was appropriate.

Table 3.1 PERMANOVA of the variation in flavonoid concentration as a function of territory, disturbance, and their interaction.

	Df	Sums of Squares	Mean Squares	<i>F</i> Model	<i>R</i> ²	Pr(> <i>F</i>)
Territory	2	0.06	0.03	9.03	0.43	0.0005
Disturbance	2	0.02	0.01	3.89	0.18	0.0260
Territory:Disturbance	4	0.02	0.01	1.85	0.18	0.1444
Residuals	9	0.03	0.003		0.21	
Total	17	0.13			1	

Table 3.2 Spearman correlation between the concentrations of the different flavonoids studied. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. To improve readability, highly significant correlations are shown in bold, as are compounds retained for subsequent analyses

Flavonoids	Catechin	Epi-catechin	Proanthocyanidin A1	Proanthocyanidin A2	Quercetin
Epicatechin	0.66**	1			
Proanthocyanidin A1	0.46	0.71***	1		
Proanthocyanidin A2	0.62**	0.88***	0.57*	1	
Quercetin	0.60**	0.43	0.00	0.26	1
Quercetin-3-galactoside	0.20	0.13	0.40	0.02	0.14
Quercetin-3-glucoside	0.36	0.41	0.62**	0.21	0.16
Quercetin-3-pentoside 1	0.20	0.39	0.46	0.46	0.01
Quercetin-3-pentoside 2	0.13	0.07	0.38	0.02	0.08
Quercetin-3-pentoside 3	0.22	0.45	0.74***	0.36	-0.15
Quercetin-3-rhamnoside	-0.57*	-0.75***	-0.64**	-0.60**	-0.44
Myricetin-hexoside 1	0.69**	0.77***	0.61**	0.61**	0.50*
Myricetin-hexoside 2	0.70**	0.77***	0.62**	0.61**	0.51*

Table 3.2 (continued)

Flavonoids	Catechin	Epi-catechin	Proantho- cyanidin A1	Proantho- cyanidin A2	Quercetin
Myricetin-hexoside 1	0.69**	0.77***	0.61**	0.61**	0.50*
Myricetin-hexoside 2	0.70**	0.77***	0.62**	0.61**	0.51*
Myricetin-pentoside 1	0.70**	0.81***	0.64**	0.67**	0.49*
Myricetin-pentoside 2	0.70**	0.76***	0.62**	0.60**	0.49*
Myricetin-pentoside 3	0.70**	0.75***	0.68**	0.64**	0.45
Flavonoids	Quercetin-3- galactoside	Quercetin-3- glucoside	Quercetin-3-pentosi- de 1	Quercetin-3-pentosi- de 2	Quercetin-3-pentosi- de 3
Quercetin-3- glucoside	0.76***	1			
Quercetin-3- pentoside 1	0.38	0.58*	1		
Quercetin-3- pentoside 2	0.76***	0.74***	0.50*	1	
Quercetin-3- pentoside 3	0.69**	0.75***	0.47*	0.64**	1
Quercetin-3- rhamnoside	-0.33	-0.59*	-0.35	-0.22	-0.64**
Myricetin-hexoside 1	0.23	0.48*	0.23	0.20	0.59**
Myricetin-hexoside 2	0.26	0.51*	0.22	0.22	0.59**
Myricetin-pentoside 1	0.18	0.43	0.26	0.16	0.56**
Myricetin-pentoside 2	0.25	0.50*	0.23	0.21	0.60**
Myricetin-pentoside 3	0.32	0.50*	0.32	0.30	0.65**

Table 3.2 (continued)

Flavonoids	Quercetin-3-rhamnoside	Myricetin-hexoside 1	Myricetin-hexoside 2	Myricetin-pentoside 1	Myricetin-pentoside 2
Myricetin-hexoside 1	-0.93***	1			
Myricetin-hexoside 2	-0.93***	1.00***	1		
Myricetin-pentoside 1	-0.92***	0.99***	0.99***	1	
Myricetin-pentoside 2	-0.93***	1.00***	1.00***	0.99***	1
Myricetin-pentoside 3	-0.87***	0.97***	0.96***	0.97***	0.97***

Table 3.3 Linear mixed models estimating the effects of territory, disturbance type, and their interaction on the concentration of flavonoids. The effect of disturbance type is given relative to the control (no disturbance). The effect of territory is given relative to the average effect for all territories. To improve readability, significant effects are shown in bold.

Catechin			Epicatechin		
Random effects	Variance	Std. Dev.	Random effects	Variance	Std. Dev.
Site	1.63	1.28	Site	1.56	1.25
Residuals	5.48	2.34	Residuals	2.23	1.49
Fixed effects	Estimate	Pr(> t)	Fixed effects	Estimate	Pr(> t)
(Intercept)	13.22	1.08e-08	(Intercept)	9.09	7.45e-08
Mine	-0.63	0.5275	Mine	-1.59	0.0836
Hydro	1.99	0.0669	Hydro	0.08	0.921
Abitibiwinni	-0.63	0.5275	Abitibiwinni	-1.34	0.1347
Mistissini	-1.02	0.3141	Mistissini	-0.73	0.393
Nemaska	1.64	0.1189	Nemaska	2.08	0.0317
Mine:Abitibiwinni	0.48	0.7319	Mine:Abitibiwinni	1.50	0.2267
Hydro:Abitibiwinni	0.67	0.6295	Hydro:Abitibiwinni	-0.78	0.5150
Mine:Mistissini	-0.75	0.59	Mine:Mistissini	-1.58	0.2048
Hydro:Mistissini	0.22	0.8721	Hydro:Mistissini	0.01	0.9955
Mine:Nemaska	0.28	0.842	Mine:Nemaska	0.08	0.9463
Hydro:Nemaska	-0.90	0.52	Hydro:Nemaska	0.78	0.52
Quercetin			Quercetin-3-glucoside		
Random effects	Variance	Std. Dev.	Random effects	Variance	Std. Dev.
Site	4e-04	0.02	Site	0.01	0.10
Residuals	7e-04	0.03	Residuals	0.02	0.13
Fixed effects	Estimate	Pr(> t)	Fixed effects	Estimate	Pr(> t)
(Intercept)	0.10	1.36e-06	(Intercept)	1.10	2.08e-09
Mine	0.01	0.6881	Mine	-0.21	0.0121
Hydro	0.04	0.0193	Hydro	-0.02	0.7324
Abitibiwinni	-0.01	0.4181	Abitibiwinni	-0.19	0.0183
Mistissini	-0.01	0.3518	Mistissini	0.14	0.0693
Nemaska	0.02	0.1004	Nemaska	0.05	0.4365
Mine:Abitibiwinni	0.02	0.2465	Mine:Abitibiwinni	0.16	0.1167

Table 3.3 (continued)

Quercetin			Quercetin-3-glucoside		
Fixed effects	Estimate	Pr(> t)	Fixed effects	Estimate	Pr(> t)
Hydro: Abitibiwinni	0.05	0.0156	Hydro: Abitibiwinni	0.18	0.0838
Mine:Mistissini	-0.01	0.3444	Mine:Mistissini	-0.30	0.0097
Hydro:Mistissini	-0.03	0.1816	Hydro:Mistissini	-0.10	0.2930
Mine:Nemaska	-4.4e-3	0.8144	Mine:Nemaska	0.14	0.1590
Hydro:Nemaska	-0.03	0.1613	Hydro:Nemaska	-0.08	0.4296
Quercetin-3-pentoside 1			Quercetin-3-rhamnoside		
Random effects	Variance	Std. Dev.	Random effects	Variance	Std. Dev.
Site	-2.2e-3	0.05	Site	0.06	0.24
Residuals	0.01	0.11	Residuals	0.04	0.21
Fixed effects	Estimate	Pr(> t)	Fixed effects	Estimate	Pr(> t)
(Intercept)	0.74	7.35e-10	(Intercept)	0.49	0.0011
Mine	-0.09	0.0582	Mine	0.29	0.0854
Hydro	-0.04	0.3536	Hydro	-0.21	0.1863
Abitibiwinni	-0.10	0.0360	Abitibiwinni	0.26	0.1071
Mistissini	0.12	0.0117	Mistissini	0.07	0.6334
Nemaska	-0.03	0.5069	Nemaska	-0.34	0.0483
Mine:Abitibiwinni	0.15	0.0262	Mine:Abitibiwinni	-0.53	0.0332
Hydro:Abitibiwinni	0.09	0.1328	Hydro:Abitibiwinni	-0.04	0.8437
Mine:Mistissini	-0.23	0.0027	Mine:Mistissini	0.80	0.0039
Hydro:Mistissini	-0.12	0.0650	Hydro:Mistissini	-0.16	0.4690
Mine:Nemaska	0.08	0.1856	Mine:Nemaska	-0.28	0.2150
Hydro:Nemaska	0.03	0.6643	Hydro:Nemaska	0.20	0.3627

3.6 Discussion

3.6.1 Effect of mining on flavonoid concentration

While we hypothesized that heavy metal oxidative stress would activate flavonoid biosynthesis, *R. groenlandicum* individuals near mining sites actually had lower

concentrations of most flavonoids. Quercetin-3-rhamnoside, however, showed higher concentrations near mine sites than in control sites, but the reason for this peculiar response to heavy metal stress (compared with other flavonoids) is not clear, as no differences in functionality have been reported between quercetin-3-rhamnoside and other structurally related flavonoids (Jiang et al. 2021). In addition, quercetin-3-rhamnoside concentrations were not especially high near mine sites (0.78 mg/g) when compared with other studies in the same area of western Québec on the flavonoids of *R. groenlandicum* (between 0.38 and 1.41 mg/g) (Saleem et al. 2010; Rapinski et al. 2014). Interestingly, mine sites from different territories had different effects on some flavonoids. The interaction between mine and Abitibiwinni had a positive effect on quercetin-3-pentoside concentrations and a negative effect on quercetin-3-rhamnoside concentrations, while it was the opposite at Mistissini (Table 3.3). This may be due to the difference in the operating stage between the two mines, as it has been shown that the effect of mining on the environment can vary at different stages of the mine life cycle (Yao et al. 2021; Boisvert et al. 2021; Yin et al. 2022, 2023a). In addition, the two mines process different ores with different methods, leading to the production of different mining waste (Nakić et al. 2017), which could also have an effect as different heavy metals do not always affect plants in the same way (Asare et al. 2023; Jańczak-Pieniążek et al. 2023). For example, copper mines (Mistissini) typically produce copper and cadmium pollution (Chen et al. 2022b), whereas gold mines (Abitibiwinni) typically produce cadmium, mercury, and lead pollution (Gagnon et al. 2020; Chen et al. 2022a), although pollution may vary from mine to mine. However, while the effects of different heavy metals have been investigated on the metabolism of some plant species (Ibrahim et al. 2017; AbdElgawad et al. 2020; Asare et al. 2023; Jańczak-Pieniążek et al. 2023), there is a lack of such studies for ericaceous shrubs in general and *R. groenlandicum* specifically.

The overall negative effect of mining on the concentrations of most flavonoids was unexpected. One possible way to explain this result would be the depletion of

flavonoids due to their contribution to heavy metal chelation (Michalak 2006) and the reduction of lipid oxidation, as hypothesised in other studies with similar results on other species (Dutta and Maharia 2012; Sleptsov et al. 2021). In addition, heavy metals can inhibit enzymatic activity in plants (Nagajyoti et al. 2010), which could further reduce flavonoid concentrations by affecting their biosynthesis. However, since we do not have data on heavy metal concentrations near the mining sites, we cannot rule out that the observed effect of mines is due to disturbances other than heavy metal pollution.

In addition to the effect of mine sites on flavonoids, there could have been an effect of canopy closure, as some of the mine sites were surrounded by a dense forest cover, and samples from sites with dense forest cover were less concentrated in most flavonoids (Figure 3.4).

3.6.2 Effect of canopy openness on flavonoid concentration

As hypothesised, *R. groenlandicum* individuals growing in more open environments (i.e., under hydropower lines) had higher concentrations of most flavonoids, notably flavan-3-ols. This was the case of sites in Nemaska that were more open than those in the Mistissini and Abitibiwinni territories (Figure 3.5) because they were located in the transition zone between the closed and open boreal forest and experienced major wildfires over the last decades (Zelnicker 2001; Bonspiel 2006). The effect of canopy openness is likely due to sunlight exposure (Peng et al. 2017; Zhou et al. 2021), as shown by a previous study which found that the concentrations of phenolic compounds in *R. groenlandicum* were related to solar radiation and photoperiod (Rapinski et al. 2014). However, the positive effect of canopy openness may decrease in the context of climate change, as the additive effect of climate change and sunlight exposure in open environments may cause extreme local temperatures, which can decrease flavonoid concentrations in plants (Chung et al. 2006). Interestingly, flavan-3-ols concentrations

were quite high in our samples when compared to other studies on the flavonoids of *R. groenlandicum*. The concentration of our samples in catechin and epicatechin ranged from 10.82 to 15.95 mg/g and from 5.19 to 12.03 mg/g respectively, while previous studies reported concentrations between 2.16 and 12.01 mg/g for catechin and between 1.1 and 5 mg/g for epicatechin (Saleem et al. 2010; Rapinski et al. 2014; Eid et al. 2016). This difference may be due to the exceptionally late frost in the spring during our sampling year, which may have affected the flavonoid concentrations in our samples. The concentrations in flavonoids reported in this study are unlikely to cause any toxicity in humans, as there are no observed adverse effects of flavonoids in mammals under 500 mg per kilogram of body weight per day (Chan et al. 2010; Cladis et al. 2022). However, besides increasing flavonoid concentrations, openings in the forest canopy caused by disturbances can also have other undesirable effects that were not measured here. For example, hydroelectric power line maintenance includes the application of phytocides potentially toxic to humans, such as triclopyr and glyphosate (Gosselin et al. 2005; Kyong et al. 2010; Ojelade et al. 2022). In addition, disturbances may also increase other compounds in *R. groenlandicum*, which do have adverse effects on human health, such as ledol and grayanotoxins, which are toxic at high doses (Dampc and Luczkiewicz 2015).

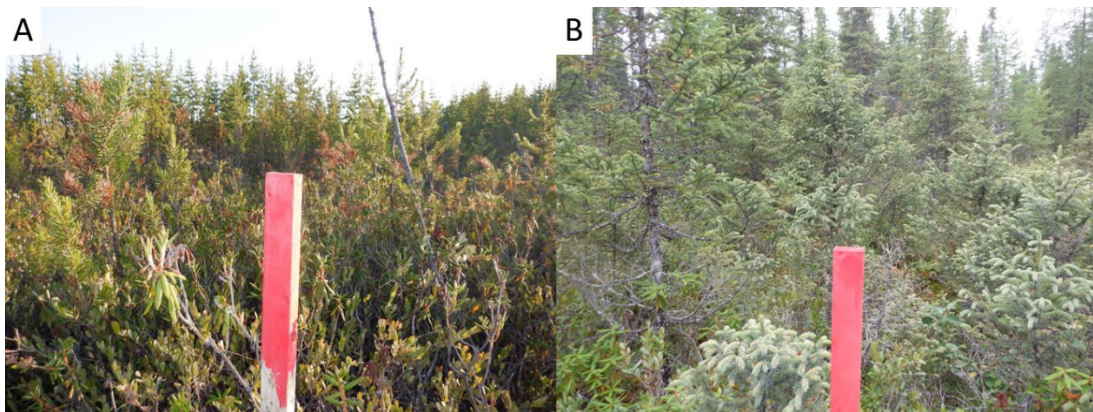


Figure 3.5 Comparison of control sites in Nemaska (A) and Mistissini (B) with regard to canopy openness. Photo credit: Maxime Thomas.

3.6.3 Differences in flavonoid concentrations between territories

The differences in flavonoid concentrations observed between territories could be the result of differences in local environmental conditions contributing to oxidative stress, such as in solar radiation intensity or temperature range (Choudhury et al. 2013; Hasanuzzaman et al. 2020) (Figure 3.4). Nemaska and Mistissini displayed marked differences in their flavonoid profiles: samples collected in Nemaska were more concentrated in flavan-3-ols, proanthocyanidins, and myricetin-glycosides, while samples from Mistissini were globally more concentrated in quercetin-3-glycosides (Figure 3.4). Sites from Mistissini showed a large variation compared to sites from the other two territories. This variation can partly be explained by canopy openness, as sites under hydroelectric lines in Mistissini are more similar to sites from Nemaska (Figure 3.4 and Table S3.1). However, we could not find a pattern in climatic data alone to explain the remaining variation (Table S3.3), which could be due to other factors we did not measure, such as soil composition or understory vegetation. Rapinski et al. (2014) also measured some marked differences in the phenolic profiles of *R. groenlandicum* from Nemaska, Mistissini, and other territories. According to our results, the difference in flavonoid profiles between these territories seems to mainly reflect a difference between sites with closed and open forest canopies.

The differences between territories and the effect of disturbances on *R. groenlandicum* could be further elucidated in future studies with untargeted metabolomics techniques allowing to measure simultaneously a large number of metabolites, including flavonoids (Patti et al. 2012). This approach would be able to determine the effects of disturbances on *R. groenlandicum*'s growth, development, and on other biologically active compounds that were not considered in the present study.

3.6.4 Conclusion

The Indigenous communities living in the boreal forest have a strong connection to their territories and depend on the forest for many traditional activities, which implies vulnerability to environmental changes of both natural and anthropogenic origins. This is why our objective was to assess the effects of anthropogenic disturbances on the flavonoid concentrations (linked to nutritive and medicinal properties) of *R. groenlandicum* on the territories of three Indigenous communities.

Anthropogenic disturbances have a complex effect on *R. groenlandicum*'s flavonoid concentrations. On the one hand, mining disturbances have a negative effect on the concentration of flavonoids of this species, which we did not expect. We suggest this might be due to flavonoid depletion as well as a decrease in their biosynthesis due to the accumulation of heavy metals in the plant tissue. On the other hand, the opening of the forest canopy due to some disturbances (e.g., hydropower lines) increases the concentration of flavonoids in *R. groenlandicum*. However, this does not mean that canopy opening by disturbances increases the health benefits associated with the consumption of *R. groenlandicum*. The increased concentrations of flavonoids could be outbalanced by the potential presence of harmful pollutants due to anthropogenic disturbances. Furthermore, increased flavonoid concentrations may be accompanied by higher concentrations of other compounds with adverse effects on human health, such as ledol and grayanotoxins. Therefore, further studies should complement our results before concluding on the total effects of anthropogenic disturbances on the medicinal properties of *R. groenlandicum*.

Rhododendron groenlandicum is known to respond positively to most disturbances through aggressive clonal propagation (Hébert and Thiffault 2011). Thus, while anthropogenic disturbances can be beneficial to *R. groenlandicum*, they could be detrimental to other culturally salient species. For example, in British Columbia, two

Indigenous communities expressed concerns regarding the adverse effect of industrial development on berry plants and other culturally salient species (Booth and Skelton 2011). Hence, it is important to measure the cumulative effects of disturbances (natural and anthropogenic) on several culturally salient species in order to better assess their effects on Indigenous values.

This study not only provides insight into the complex biochemical response of plants to disturbances in the boreal forest but also raises new questions regarding the mechanisms and factors affecting this response. Therefore, future research could test the following hypotheses:

- The effect of heavy metal pollution on plant phenolics depends on metal type, as different metals may affect plant metabolism in different ways.
- Soil properties, for example, microbiome composition and nutrients availability, interact with disturbances to determine plant biochemical response.
- The beneficial effects on human health of an increase in plant phenolics can be offset due to the accumulation of harmful pollutants in the plant.

3.7 Acknowledgements

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3.8 Community involvement statement

The Indigenous communities of Abitibiwinni, Mistissini and Nemaska were involved in project development. We discussed with members of the three communities in order for them to select the species of interest as well as the disturbances of concern on their territories. We also checked if the sampling locations were relevant by confirming they were used by the communities. We communicated some of our results in conferences destined to partners of the project, including the communities. We also plan to go back to the communities in 2023 to summarize our results.

CHAPITRE IV

DÉMÊLER L'INTERACTION ENTRE LE MICROBIOME DU SOL ET LE
CONTENU EN (POLY)PHÉNOLS DES BLEUETS EN RÉPONSE AUX
PERTURBATIONS

UNRAVELING THE INTERPLAY OF THE SOIL MICROBIOME AND
(POLY)PHENOL CONTENT IN BLUEBERRY IN RESPONSE TO
DISTURBANCES

Maxime Thomas¹, Mebarek Lamara¹, Yves Desjardins², Hugo Asselin³, Nicole J.
Fenton¹

¹Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

²Institut sur la Nutrition et les Aliments Fonctionnels, Université Laval, Québec,
Québec, Canada

³École d'études autochtones, Université du Québec en Abitibi-Témiscamingue,
Rouyn-Noranda, Québec, Canada.

Corresponding author: Maxime Thomas (maxime.thomas@uqat.ca)

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4.1 Résumé

Objectifs Les perturbations anthropiques exercent des effets directs et indirects sur les plantes en modifiant les propriétés et la composition en microorganismes du sol. Cela peut induire un stress, entraînant des modifications du profil phytochimique des plantes. Cela peut à son tour affecter la possibilité pour les populations indigènes de pratiquer des activités culturelles qui dépendent des plantes sauvages utilisées comme nourriture ou comme médecine. Dans le cadre d'une étude de cas, nous avons évalué l'effet des perturbations dues aux activités minières et hydroélectriques sur les propriétés du sol, le microbiome du sol, et les (poly)phénols des fruits de *Vaccinium angustifolium*.

Méthodes Nous avons collecté des échantillons de fruits et de sol sur les territoires de trois communautés autochtones de l'est du Canada. Les fruits ont été analysés pour leurs concentrations en anthocyanines, proanthocyanidines et autres (poly)phénols. L'ADN microbien du sol a été extrait pour reconstituer les communautés bactériennes et fongiques. Un sous-ensemble secondaire d'échantillons de sol a été utilisé pour mesurer les propriétés du sol. Les relations entre le sol, les perturbations et les (poly)phénols ont été étudiées à l'aide d'analyses multivariées.

Résultats Les perturbations affectaient les propriétés du sol et le microbiome, mais pas la teneur en (poly)phénols des fruits. Deux classes de bactéries du sol non affectées par les perturbations, Bacilli et Desulfitobacteriia, étaient positivement corrélées avec les niveaux de proanthocyanidines et de delphinidine-, cyanidine-, et pétunidine-3-glucoside dans les fruits.

Conclusion Les perturbations n'affectent pas la teneur en (poly)phénols des fruits de *V. angustifolium*. Certaines classes de bactéries du sol semblent améliorer le contenu (poly)phénolique des fruits de *V. angustifolium*, ce qui suggère qu'une stratégie pourrait

être développée pour améliorer les propriétés nutritionnelles et médicinales de cette espèce culturellement importante.

Mots-clés : Bleuet, communautés autochtones, microbiome du sol, (poly)phénols, mines, lignes de transport hydroélectrique.

4.2 Abstract

Aims Anthropogenic disturbances exert direct and indirect effects on plants through alterations of soil properties and microbiota composition. This can induce stress, resulting in modifications of plants' phytochemical profile. This in turn can affect the possibility for Indigenous people to engage in cultural activities depending on wild plants used as food or medicine. As a case study, we evaluated the effect of disturbances from mining and hydroelectric activities on soil properties, soil microbiome, and the (poly)phenols in *Vaccinium angustifolium* fruits.

Methods We collected fruit and soil samples in the territories of three Indigenous communities in eastern Canada. Fruits were analyzed for their concentrations in anthocyanins, proanthocyanidins and other (poly)phenols. Soil microbial DNA was extracted to reconstruct bacterial and fungal communities. A secondary subset of soil samples was used to measure soil properties. Relationships between soil, disturbances and (poly)phenols were investigated using multivariate analyses.

Results Disturbances affected soil properties and microbiome, but not fruit (poly)phenol content. Two soil bacterial classes unaffected by disturbances, Bacilli and Desulfitobacteriia, were positively correlated with levels of proanthocyanidines and delphinidin-, cyanidin-, and petunidin-3-glucoside in fruits.

Conclusion Disturbances did not affect (poly)phenol content in *V. angustifolium* fruits. Some soil bacterial classes seem to enhance the (poly)phenolic content of *V. angustifolium* fruits, suggesting that a strategy could be developed for enhancing the nutritional and medicinal properties of this culturally salient species.

Keywords: Blueberry, Indigenous communities, soil microbiome, (poly)phenols, mines, hydroelectric power lines.

4.3 Introduction

Mining and hydroelectric development are two of the main industrial activities taking place in the Canadian boreal forest (Venier et al. 2014; Gauthier et al. 2015; Bélisle and Asselin 2021). These activities result in disturbances that affect the boreal landscape, including animal and plant species. The establishment of a mining site or a hydroelectric power line entails the clearance of forests and the destruction of wildlife habitats to make room for infrastructure construction (Sonter et al. 2018; Haddaway et al. 2019; Li and Lin 2019).

Mining also generates heavy metal pollution that can contaminate the soil, water, and plants surrounding a mining site (Yin et al. 2023a,b; Yu and Zahidi 2023). Exposure to heavy metal pollution poses significant risks to plants, as heavy metals can disrupt metabolic processes, germination rates, and reproductive capabilities (Adeel et al. 2019; Yin et al. 2021). The installation of hydroelectric power lines can also induce stress in plants. Indeed, the removal of trees for the creation of a power transmission line increases the exposure of understory plants to light, including ultraviolet (UV) radiation. Elevated exposure to UV radiation can impair plant metabolic functions and lead to tissue damage (Bergamini et al. 2004).

Plants acclimate to disturbances, notably by synthesizing secondary metabolites, such as (poly)phenols (Sytar et al. 2013; Kumar and Pandey 2013; Thakur et al. 2019). Secondary metabolites in plants play a crucial role in mitigating the detrimental effects of stresses, including exposure to heavy metals and increased levels of UV radiation (Agati and Tattini 2010; Naing and Kim 2021).

Disturbances can also affect plants indirectly by modifying soil properties and microbiome composition. For instance, mining activities have been shown to lower soil pH (Dudka and Adriano 1997; Johnson and Hallberg 2005), a change to which the soil

microbiome is highly sensitive (Fierer and Jackson 2006; Ali et al. 2017). Disturbances can also indirectly influence plant health and development through their effects on the soil microbiome, which interacts with plant roots (Ali et al. 2017; Trivedi et al. 2020). The influence of the soil microbiome extends beyond the roots to affect aerial plant parts as well (Salla et al. 2014; Rahman et al. 2018). For instance, the majority of plants engage in symbiotic relationships with mycorrhizal fungi to enhance nutrient uptake from the soil, illustrating a critical interaction that benefits plant growth and health (Jeffries et al. 2003; Brundrett 2009). Bacteria too can have beneficial effects on plants, notably by improving nutrition and response to stresses (Franche et al. 2009; Ali et al. 2017; Rahman et al. 2018). The soil microbiome also harbors bacterial and fungal pathogens capable of reducing plant growth (Štraus et al. 2023). By altering soil characteristics, environmental disturbances can provoke shifts in the composition of the soil microbiome (Seitz et al. 2021). This, in turn, can influence a range of plant processes including growth, nutrition, and the production of secondary metabolites (Treutter 2006; Kumar and Pandey 2013; Trivedi et al. 2020; Thomas et al. 2023).

Disturbances can also affect plant nutritional and medicinal properties, since these attributes are closely linked to the presence and concentration of secondary metabolites (Del Rio et al. 2013; Durazzo et al. 2019). For example, anthocyanins, a group of secondary metabolites, provide numerous health benefits to humans; notably helping in the prevention of cardiovascular disease, cancer, and diabetes (de Pascual-Teresa and Sanchez-Ballesta 2008). Proanthocyanidins are another example of compounds conferring health benefits, such as anti-inflammatory effects and kidney protection (Ivey et al. 2013; Yokota et al. 2016; Dasiman et al. 2022).

Modifications in plant properties can affect the livelihood and culture of different populations, notably Indigenous peoples. Indeed, certain plant species are central to cultural activities, such as food or medicine, underscoring the profound connection between Indigenous cultures and specific flora (Garibaldi and Turner 2004; Parlee et

al. 2005; Ladle et al. 2019; Boulanger-Lapointe et al. 2019). Investigating how such culturally salient species respond to disturbances is thus key to the preservation of Indigenous ways of life.

The early lowbush blueberry (*Vaccinium angustifolium* (Aiton)) is a culturally salient species for several Indigenous peoples in eastern Canada. This species is culturally salient because of its importance as a key food item (Arnason et al. 1981; Batal et al. 2021). *V. angustifolium* contributes to reinforcing the connection of Indigenous peoples with their territories and traditions, through blueberry picking outings and the preparation of traditional food such as blueberry paste (Boulanger-Lapointe et al. 2019; Basile et al. 2022; Pelletier 2022). Blueberries are also rich in phenolic acids, anthocyanins and proanthocyanidins, among other secondary metabolites, which possess antioxidant and antidiabetic properties (Uprety et al. 2012; Norberto et al. 2013; Grace et al. 2019; Weber 2022).

Disturbances affect soil properties, soil microbiome composition, and plant secondary metabolism, which are intricately linked. Although each of these elements have been the subject of individual studies (Lahdesmaki 1990; Tahkokorpi et al. 2010; Francioli et al. 2021; Zaborowska et al. 2021), their interrelations are seldom examined collectively, highlighting a gap in comprehensive understanding of their synergistic effects on ecosystem and plant health. Thus, the objective of this study was to assess the effect of two disturbances (mining and hydroelectric power lines) on the complex interplay between (poly)phenols in the fruits of *V. angustifolium*, soil properties and the soil microbiome in the eastern Canadian boreal forest. More specifically, we asked the questions: i) Do disturbances directly affect fruit (poly)phenol content, and if so, how? ii) Which soil microbial taxa, if any, affect fruit (poly)phenol content and how? iii) Do disturbances indirectly affect plant (poly)phenol content through their effect on soil properties and bacterial and fungal communities?

4.4 Material and Methods

4.4.1 Study area

This study took place in western Quebec (Canada) on the traditional territories of the Abitibiwinni (Anishnaabe), Mistissini (Cree), and Nemaska (Cree) Indigenous communities (Figure 4.1). The Abitibiwinni First Nation's territory is located near the Ontario border, mainly in the black spruce – feather moss bioclimatic domain, except for its southern part located in the balsam fir – paper birch bioclimatic domain (Bélisle and Asselin 2021). The Mistissini Cree Nation's territory is located further north and is very large, with its southern part in the black spruce – feather moss bioclimatic domain and its northern part in the spruce – lichen woodland bioclimatic domain. The territory of the Nemaska Cree Nation is located at the northern boundary of the black spruce – feather moss bioclimatic domain. This territory has experienced frequent fires in the past decades, which led to younger and more open stands (Eeyou Planning Commission 2017).

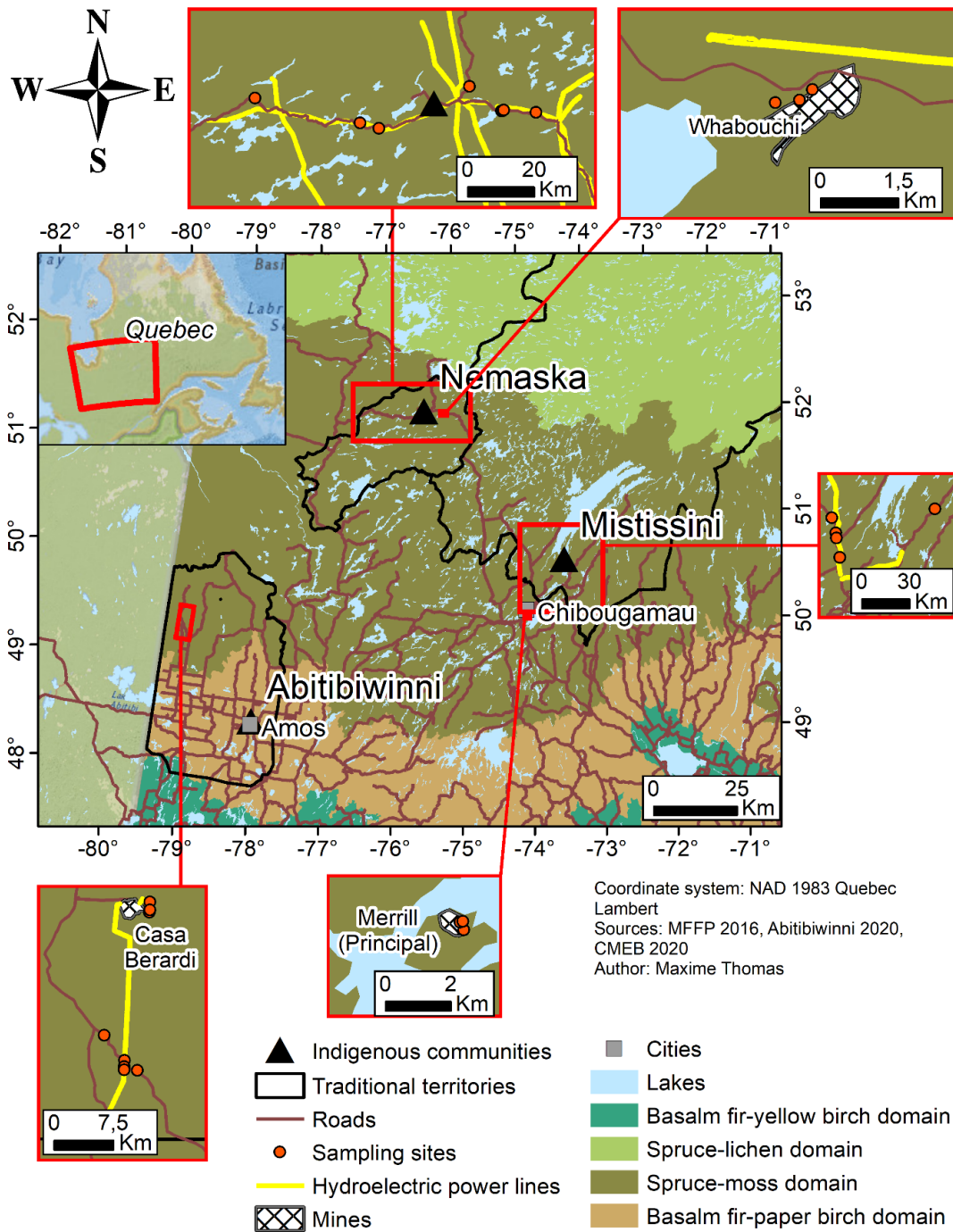


Figure 4.1 Location of the study area in Quebec, eastern Canada. The red inserts around the main map indicate the locations of sampling sites in relation to hydroelectric power lines, mines, and roads.

4.5 Fruit and soil sampling

Samples were collected on the territories of the Abitibiwinni, Mistissini and Nemaska communities on August 2nd, 16-17th, and 20th 2022, respectively. The difference in timing between territories was planned to collect fruits at the same phenological stage, accounting for latitude differences. All samples were collected in the black spruce – feather moss bioclimatic domain (Figure 4.1), more specifically in black spruce stands, to limit the influence of potential confounding environmental variables. A total of 24 sites were sampled, that is 8 in each territory: 3 under hydroelectric power lines, 3 near a mine (200 m or less), and 2 control sites at least 1 km away from these disturbances. The selection of the distance around mining sites for analysis was informed by findings from prior studies, which determined that the effect of mining activities on vegetation extended to an average distance of 200 m (Boisvert et al. 2021; Yin et al. 2023a). All sites were located at least 100 m from roads to limit edge effects, trampling, and disturbances due to traffic.

At each site, 4 fruit samples were collected from different plant individuals for analysis of (poly)phenol compounds. Three organic soil samples were also collected with an auger in a triangular fashion around the fruit sampling locations, for analysis of soil microbiome and soil properties. The three soil samples were combined into a composite sample representative of the soil around the sampled plants. All samples (fruit and soil) were preserved in a cooler immediately after collection, then transferred to a -80 °C freezer after each sampling day until extraction.

4.5.1 Extraction and analysis of (poly)phenol compounds

Fruit samples were sent to INAF's chemical analysis laboratory (Institute of Nutrition and Functional Foods, Laval University, Quebec City, Canada) where they were extracted for analysis of flavonoids and total (poly)phenol compounds.

4.5.1.1 Flavonoids

The proanthocyanidins (PACs) content of the samples was measured by phloroglucinolysis followed by a UPLC-UV-MS/MS analysis. Phloroglucinolysis is a process in which PACs are cleaved into their base units, flavan-3-ols, using phloroglucinol (Kennedy and Jones 2001). This allows to quantify PACs and to determine their polymerization degree. A catechin standard was used to quantify PACs by UPLC-UV. The identification of detected compounds was then confirmed by triple quadrupole mass spectrometry.

The flavonol content of the samples was measured using the same procedure as for PACs, albeit with the omission of phloroglucinolysis and the use of a quercetin-3-glucoside standard for the purpose of quantification.

4.5.1.2 Total (poly)phenols

Total (poly)phenolic content was determined according to the Folin-Ciocalteu method as described in Dudonné et al. (2015) using gallic acid as a standard. Extract solutions (20 mL in 20 % methanol 0.1 % TFA) were mixed with 100 mL of 10-fold diluted Folin-Ciocalteu reagent and 80 mL of sodium carbonate solution (75 g/L). After 1 h of

incubation at room temperature, the absorbance was measured at 765 nm using a BMG Labtech Fluostar Omega microplate reader (Offenburg, Germany).

4.5.2 Physicochemical analyses

Before proceeding to physicochemical analyses, soil samples were oven-dried at 35 °C for 3 days, then passed through a 5.6 mm sieve to remove large debris, and stored in a -80 °C freezer until analysis. Soil samples were analyzed for mineral contents (calcium, aluminum, potassium, phosphorus, magnesium, boron, copper, iron, manganese, zinc, sodium), pH, cation exchange capacity (CEC), organic matter content, as well as nitrogen and carbon content. Minerals were extracted with a Mehlich III solution and quantified by ICP-Optical Emission Spectrometry with the appropriate standard for each mineral (Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec 2014). Soil pH was determined in water with a pH-meter (Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs 2023). The organic matter percentage in the soil was calculated by loss on ignition (Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec 2017).

4.5.3 Microbiome analysis

4.5.3.1 DNA extraction

The DNA of the soil samples was extracted from 250 mg of sampled soil using the Qiagen DNeasy Powersoil Pro kit (QIAGEN 2022) following the manufacturer's protocol. Two negative extraction controls with no soil were also processed following

the same protocol. The extracted DNA was stored immediately in a -80 °C freezer until further processing. DNA samples were then sent to Genome Quebec Innovation Center (Montreal, Canada) for amplification and sequencing.

4.5.3.2 Amplification and sequencing

The metabarcoding method was used to detect and quantify bacteria and fungi in the organic soil. For bacteria, the extracted DNA samples were amplified using the primers 515b-FwR1 forward (GTGYCAGCMGCCGCGGTAA) and 926-RvR2 reverse (CCGYCAATTYMTTTRAGTTT) (Parada et al. 2016). For fungi, the primers used were ITS-9F forward (GAACGCAGCRAAIIGYGA) and ITS4R reverse (TCCTCCGCTTATTGATATGC) (White et al. 1990; Ihrmark et al. 2012). PCR amplifications were performed with 5 minutes of initial denaturation at 95 °C, 34 cycles (bacteria) or 40 cycles (fungi) of 30 seconds at 94 °C, 30 seconds at 50 °C, and 1 minute at 72 °C, then a final elongation step of 10 minutes at 72 °C. Prior to amplification and sequencing, DNA quality was checked using 1 % agarose gel electrophoresis.

Amplicons were sequenced on the Illumina MiSeq platform for paired-end reads. A negative control was included in the sequencing for both bacteria and fungi, to ensure that the extraction step did not result in contamination of the samples.

4.5.4 Bioinformatic workflow

The DADA2 R-package was used to build amplicon sequence variants (ASVs) from the raw sequences (Callahan et al. 2016). For bacteria, sequence primers were removed by trimming the first 19 nucleotides of forward reads and first 20 nucleotides of reverse

reads in DADA2. After checking reads quality, 16S reads were also truncated at position 260 for forward reads and 190 for reverse reads, as there was a drop in read quality after these points. For fungi, ITS sequences primers were removed with cutadapt (Martin 2011) prior to assembly with DADA2. As the ITS sequence length is variable, ITS reads of lesser quality were not truncated to ensure that forward and reverse read could merge, but ITS read quality was decent overall. For 16S and ITS analyses, reads were pseudo-pooled during the ASVs assembly step in order to allow for the detection of rare ASVs. External contaminants were then removed using the decontam R-package using the prevalence method (Davis et al. 2018). Taxonomy was assigned using the Silva v138.1 database formatted for DADA2 for the bacterial sequences (McLaren and Callahan 2021) and the UNITE v.9.0 database for the fungal sequences (Abarenkov et al. 2022).

Once ASVs were built, data were transferred into a phyloseq object with the phyloseq R-package for handling (McMurdie and Holmes 2013). Quality control led to removing ASVs that were found in only one sample, and those that were found less than 10 times across all samples. A phylogenetic heat tree of the taxa found in the samples was built using the metacoder R-package for visualization of taxonomic diversity across all samples (Figure S4.1 and Figure S4.2) (Foster et al. 2017). Before downstream analyses, the library of each sample was repeatedly rarefied to the library size of the smallest sample by drawing random ASVs without replacement with 1000 repetitions with the mirlyn R-package (Figure S4.3 and Figure S4.4) (Cameron et al. 2021), to control for biases in richness induced by differences in library sizes between samples. As the analyses available in the mirlyn package are limited, the multiple libraries created by the repeated rarefaction were then condensed into a single phyloseq object for compatibility with further packages. To do so, a table of ASV abundance was constructed by rounding the mean abundance of each ASV after 1000 rarefactions for each sample.

4.5.5 Statistical analyses

All analyses were performed using the R software version 4.3.1 (R Core Team 2023). Bacteria and fungi were treated separately for all analyses.

4.5.5.1 Effect of disturbances and territory on (poly)phenol concentrations

The effect of disturbance type, territory, and their interaction on (poly)phenol concentrations was evaluated with a PERMANOVA using the *adonis2* function of the vegan R-package (Oksanen et al. 2022). The random effect of the sampling sites was accounted for by constraining permutations: sampling sites could be permuted, but not samples between sites. A total of 9999 permutations were performed using Euclidean distances.

4.5.5.2 Effect of disturbances and territory on soil properties and microbime

The effect of disturbance type, territory, and their interaction on soil properties was also analyzed with a PERMANOVA using the *adonis2* function from the vegan R-package (Oksanen et al. 2022). Variables were normalized by scaling prior to the PERMANOVA, and 9999 permutations were performed using Euclidean distances. To further study the response of soil properties to disturbances, an ANOVA followed by a Tukey test was performed for each soil property.

Differences in alpha diversity between disturbance types and territories were plotted using the *plot_richness* function of the phyloseq R-package. Non-metric multidimensional scaling (NMDS) ordination plots were also produced, using the

vegan package (Oksanen et al. 2022) on Hellinger transformed data to visualize the relation between phylum abundance, soil properties and sampling sites. Finally, a linear discriminant analysis effect size analysis (LEfSe) was performed to detect taxa that were differentially abundant between disturbance types (Segata et al. 2011). Since this analysis has a high false discovery rate (Nearing et al. 2022), the LDA threshold was conservatively set to 3.5. The LEfSe was computed in R using the microbiomeMarker package (Cao et al. 2022).

4.5.5.3 Effect of soil properties on microbiome

The effect of soil properties on soil microbiome composition was evaluated using a distance-based redundancy analysis (db-RDA) using the vegan R-package (Oksanen et al. 2022). The explanatory variables used in the model were the following: pH, contents of nitrogen, carbon, phosphorus, magnesium, potassium, iron, copper, manganese, zinc, aluminum, calcium, and sodium, and CEC. Explanatory variables were scaled prior to analysis, and the dissimilarity matrix of microbiome abundance was calculated using the Hellinger distance. Significance of the db-RDA model, axis, and terms was then evaluated by permutation, using the *anova* function of the vegan R-package with 9999 permutations (Borcard et al. 2018). *P*-values were adjusted with the Benjamini-Hochberg correction (Benjamini and Hochberg 1995).

4.5.5.4 Effect of microbiome on (poly)phenol concentrations

(Poly)phenol concentrations were not scaled prior to analyses, as concentration was the best available proxy for (poly)phenol bioavailability.

The effect of soil bacterial abundance on (poly)phenol concentrations was evaluated. For each site, the average concentration of each (poly)phenol compound was calculated. The rarefied ASV abundances were summed to the phylum level, and phyla with less than 500 observations across all samples were removed from the analysis, as they were unlikely to meaningfully affect plant (poly)phenols. Then, a redundancy analysis (RDA) was used to investigate the effect of the abundance of each phylum on (poly)phenol concentrations using the *vegan* R-package. Significance of the model, axis and explanatory variables was then evaluated by permutation, with the *anova* function of the *vegan* R-package using 9999 permutations (Borcard et al. 2018). *P*-values were adjusted with the Benjamini-Hochberg correction (Benjamini and Hochberg 1995). If a significant effect was found at the phylum level, another RDA was conducted with the abundance of the classes of this phylum, and so on with inferior taxonomic levels. In addition, the Proteobacteria and Firmicutes phyla were further explored as they contain plant growth promoting bacteria (Bulgarelli et al. 2013; Youseif 2018; Getahun et al. 2020). The same procedure was followed to evaluate the effect of fungi abundance on (poly)phenols, except with a threshold of 300 observations across all samples, as fungi were less abundant in general. In addition, the Ascomycota and Basidiomycota phyla were also explored as they contain ericoid mycorrhiza (Dong et al. 2022). FUNGuild v1.1 (accessed on August 3rd 2023) was used to get fungi putative functional assignments in order to help discuss the results (Nguyen et al. 2015).

When an RDA highlighted a taxon as having a significant effect on the (poly)phenol profile, the effect of this taxon on individual (poly)phenol was further evaluated by constructing linear models. It was then possible to quantify the effect of this taxon on each individual (poly)phenol content.

4.6 Results

4.6.1 (Poly)phenol content

The majority of the (poly)phenols quantified in the samples consisted of PACs, and to a lesser degree, anthocyanins featuring a 3-glucoside moiety, including delphinidin, malvidin, and cyanidin-3-glucoside (Figure 4.2). No differences were observed in the concentrations of (poly)phenols among the various environmental disturbances examined. Interestingly, concentrations had a lower standard deviation for control sites than for disturbances, especially for PACs and anthocyanin with a 3-glucoside moiety, which may indicate a higher variability of environmental conditions near disturbed sites.

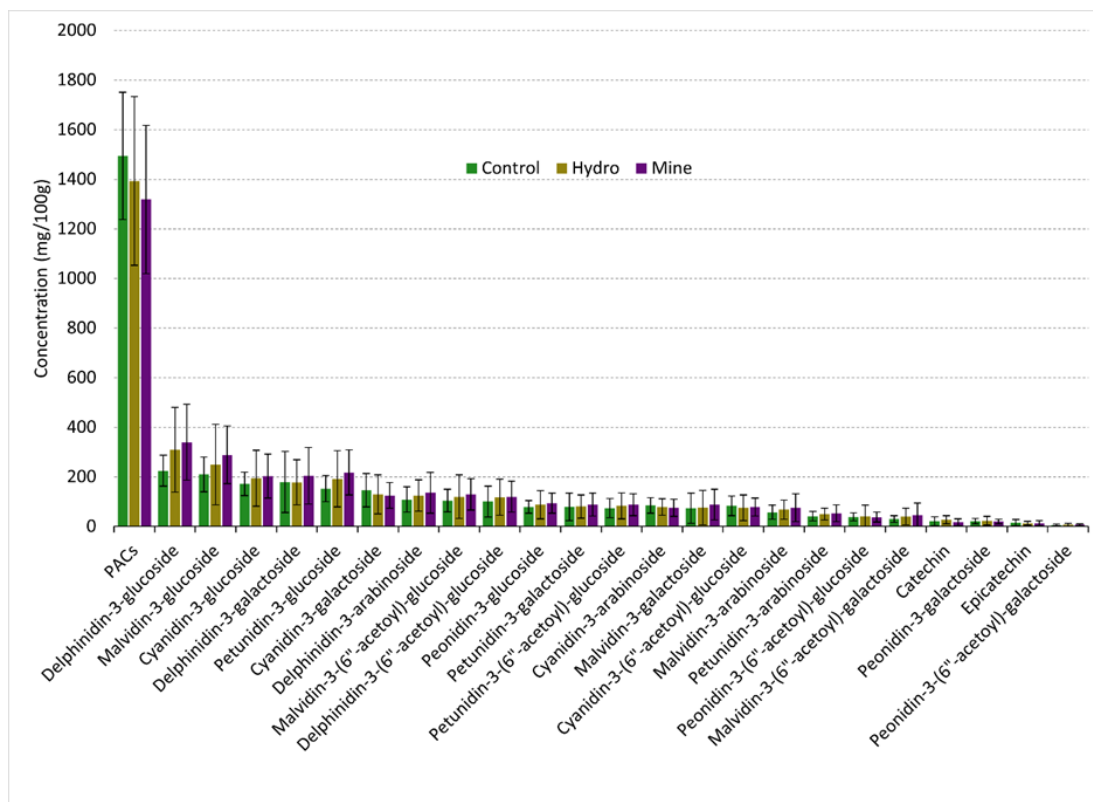


Figure 4.2 Average concentration of the different (poly)phenols measured in the samples for each disturbance type in milligram per 100 grams of dry matter with the associated standard deviation. PACs: proanthocyanidins.

4.6.2 Effect of disturbances

4.6.2.1 Effect of disturbances on (poly)phenol content

The content of (poly)phenols was not significantly influenced by disturbance type, territory, or the interaction between these two factors, although the effect of territory was marginally notable ($P=0.0573$; Table S4.1).

4.6.2.2 Effect of disturbances on soil properties

Disturbance type and territory had a significant effect on soil properties, while the effect of their interaction was not significant (Table 4.1).

Table 4.1 PERMANOVA of the variation in soil properties as a function of disturbance type, territory, and their interaction.

	Df	Sum of Squares	R ²	F	Pr(>F)
Disturbance	2	71.38	0.19	3.12	0.0004
Territory	2	64.8	0.18	2.83	0.0009
Disturbance:Territory	4	60.1	0.16	1.31	0.1403
Residual	15	171.71	0.47		
Total	23	368	1		

Samples collected from mining sites exhibited significantly higher levels of copper (8.4 ppm) and iron (354 ppm) compared to other locations (0.7 ppm and 162 ppm for control, 0.8 ppm and 179 ppm for hydro), and also contained significantly more carbon (284 g/kg), nitrogen (6.8 g/kg), and organic matter (49%) than sites associated with hydroelectric power lines (133 g/kg, 3.3 g/kg and 22% respectively). They also had a higher pH than control sites (4 vs 3.6). Regarding differences between territories, samples from Nemaska were more concentrated in aluminum and sodium than those from Mistissini (1014 ppm vs 492 ppm and 33.8 ppm vs 19.1 ppm respectively), and less concentrated in magnesium and zinc than those from Abitibiwinni (104 ppm vs 269 ppm and 3.8 ppm vs 7.5 ppm respectively). Samples from Mistissini contained more copper than those from other territories (9.2 ppm vs 0.9 ppm for Abitibiwinni and Nemaska).

4.6.2.3 Effect of disturbances on soil bacteria

Control site samples tended to have a lower bacterial abundance in general, and a lower abundance of bacteria from the *Xanthobacteraceae* family in particular (Figure 4.3).

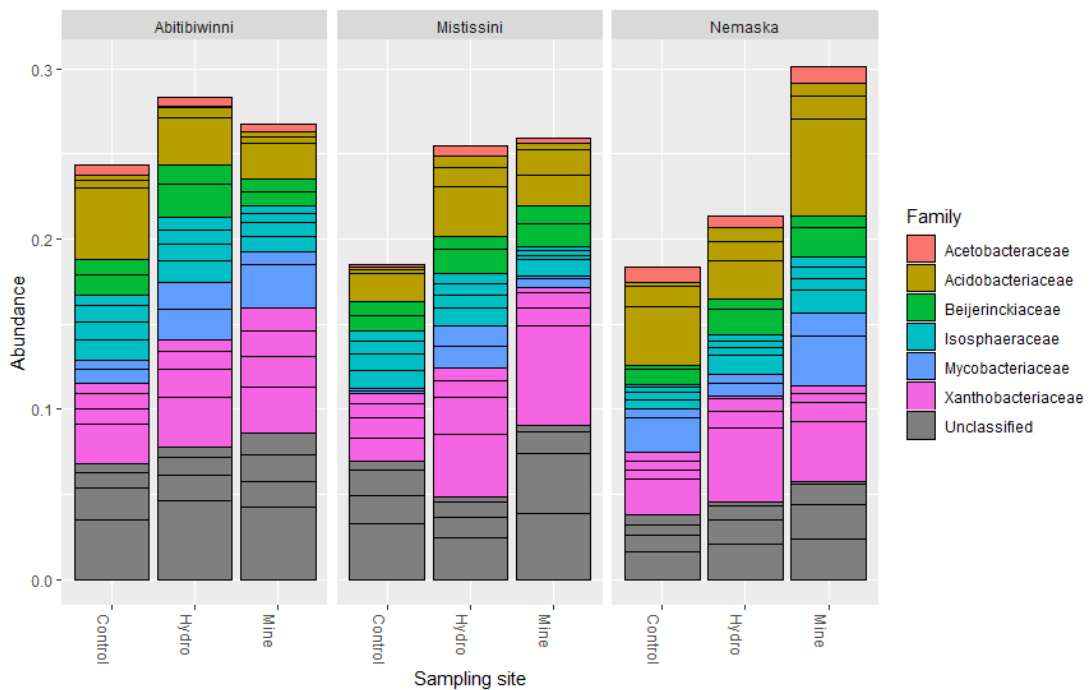


Figure 4.3 Mean relative abundance of the 20 most abundant bacteria taxa (stacked boxes) classified by family (colors) in samples subjected to different disturbances and from different territories.

Samples from mine sites were associated with bacteria from the Fibrobacterota, Desulfobacterota and Spirochaetota phyla (Figure 4.4). Trends regarding bacterial phyla were less obvious for hydro sites, as they were mainly clustered closer to the center of the ordination graph. Samples from control sites tended to have a lower abundance of all bacterial phyla, as suggested by the lower abundance in all bacteria families seen in Figure 4.3.

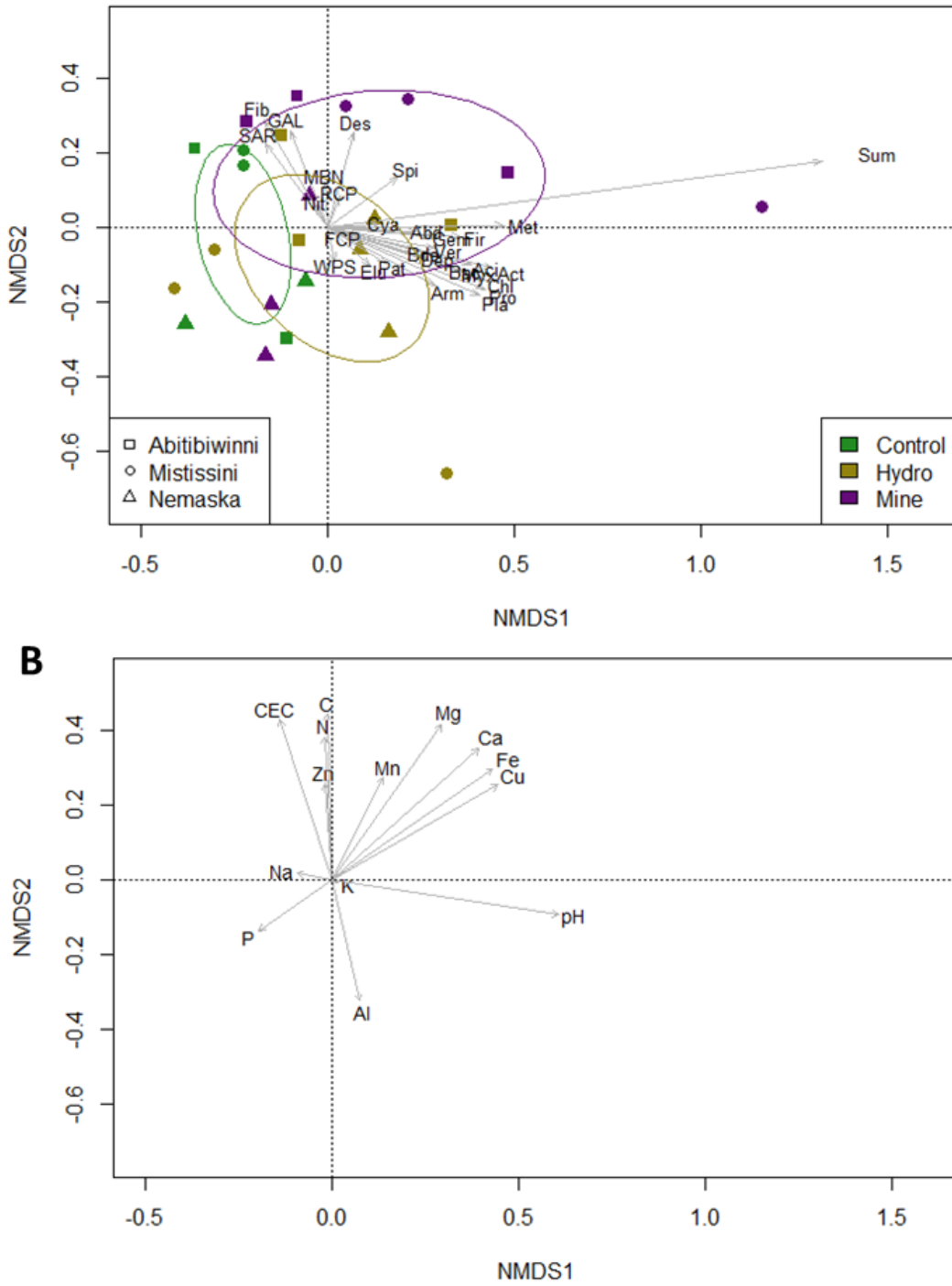


Figure 4.4 Non-metric multidimensional scaling of the abundance of bacterial phyla. Stress = 0.16. A) Points represent the sampling sites. Ellipses represent the standard

deviation around each disturbance type. Abd: Abditibacteriota, Aci: Acidobacteriota, Act: Actinobacteriota, Arm: Armatimonadota, Bac: Bacteroidota, Bde: Bdellovibrionota, Chl: Chloroflexi, Cya: Cyanobacteria, Dep: Dependientiae, Des: Desulfobacterota, Elu: Elusimicrobiota, FCP: FCP426, Fib: Fibrobacterota, Fir: Firmicutes, GAL: GAL15, Gem: Gemmatimonadota, MBN: MBNT15, Met: Methylophilota, Myx: Myxococcota, Nit: Nitrospirota, Pat: Patescibacteria, Pla: Planctomycetota, Pro: Proteobacteria, RCP: RCP2-54, SAR: SAR324 clade(Marine group B), Spi: Spirochaetota, Sum: Sumerlaeota, Ver: Verrucomicrobiota, WPS: WPS-2. B) Soil properties and composition in metals and oligo-elements. Cu: copper, Fe: iron, C: carbon, N: nitrogen, Mg: magnesium, Ca: calcium, CEC: Cation Exchange Capacity, Mn: manganese, K: potassium, Zn: zinc, P: phosphorus, Al: aluminum.

Only hydro sites had significant differentially abundant bacterial taxa (Figure 4.5). Soil from these sites contained significantly more bacteria from the Verrucomicrobiae class, especially of the Chthoniobacterales order, and more bacteria from the Ktedonobacteria class, especially of the Ktedonobacterales order and *Ktedonobacteriaceae* family.

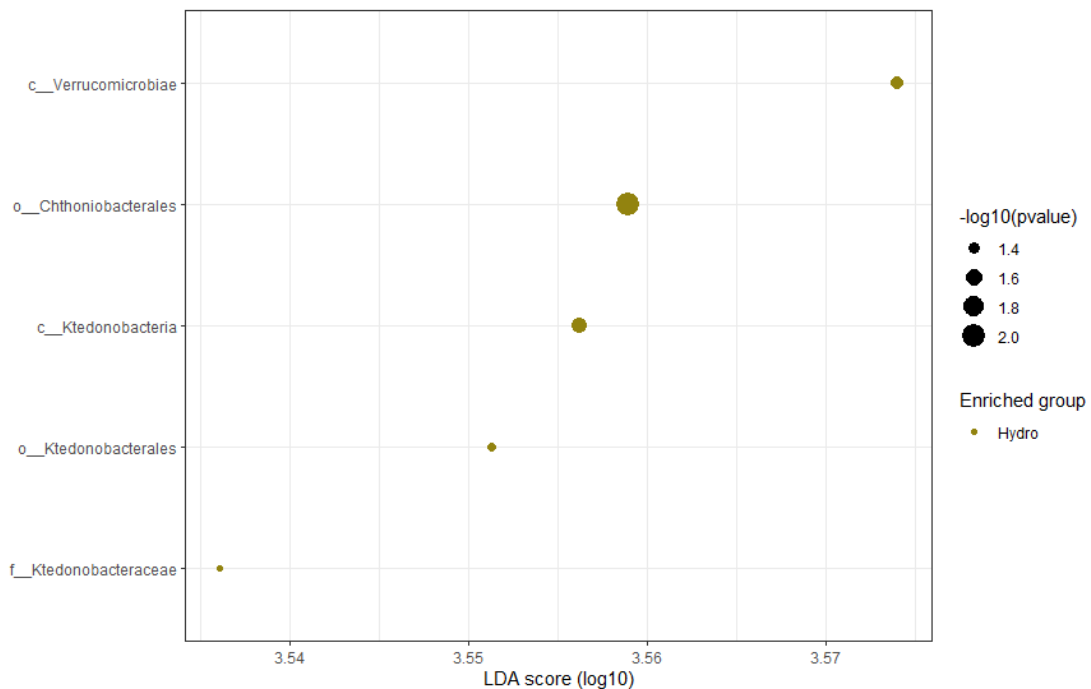


Figure 4.5 Bacterial taxa differentially abundant for different disturbance types. Only hydro is represented as other disturbances did not have differentially abundant taxa.

The letter before the name of the taxa indicates the taxonomic level: o: order, c: class, f: family.

4.6.2.4 Effect of disturbances on soil fungi

Samples near a mining site tended to contain more *Myxotrichaceae* (Figure 4.6). The fungal composition of mining sites within the Abitibiwinni territory differed from the other mining sites, which could be due to differences in mine operation stage or processed ores between the mines. Interestingly, samples from control sites in Mistissini contained a large proportion of *Pilodermataceae*.

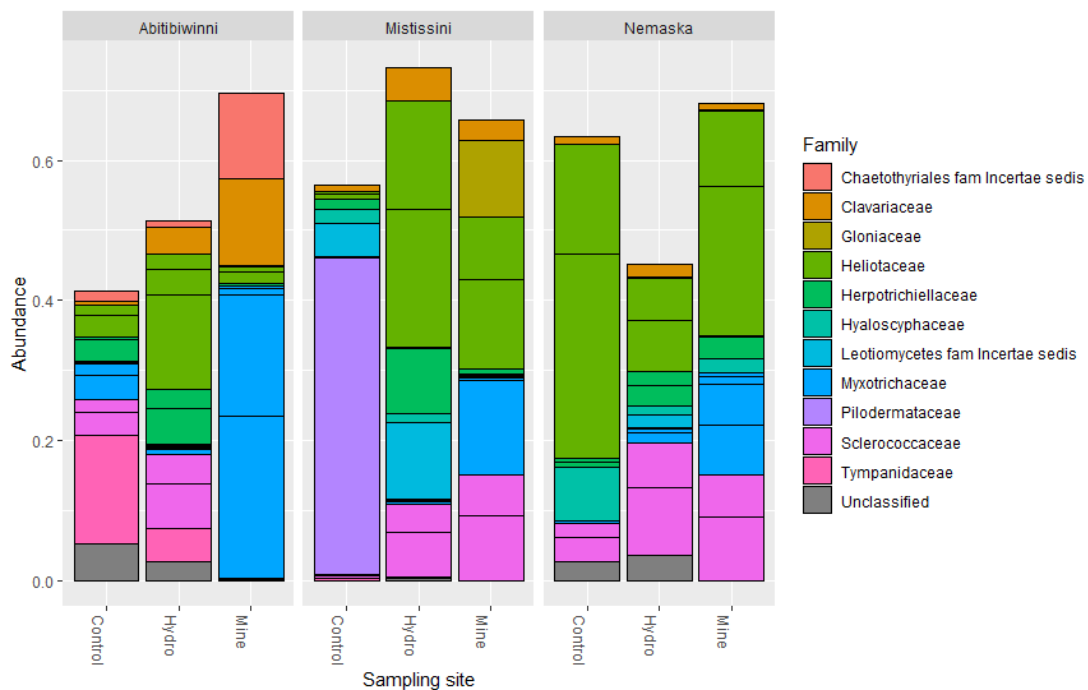


Figure 4.6 Mean relative abundance of the 20 most abundant fungi taxa (stacked boxes) classified by family (colors) in samples subjected to different disturbances and from different territories.

The majority of ASVs belonged to the Ascomycota phylum. Abundances of Ascomycota, Basidiomycota, Mortierellomycota, and Mucoromycota were correlated (Figure 4.7). These phyla tended to be more abundant in sites near mines and sites from Abitibiwinni.

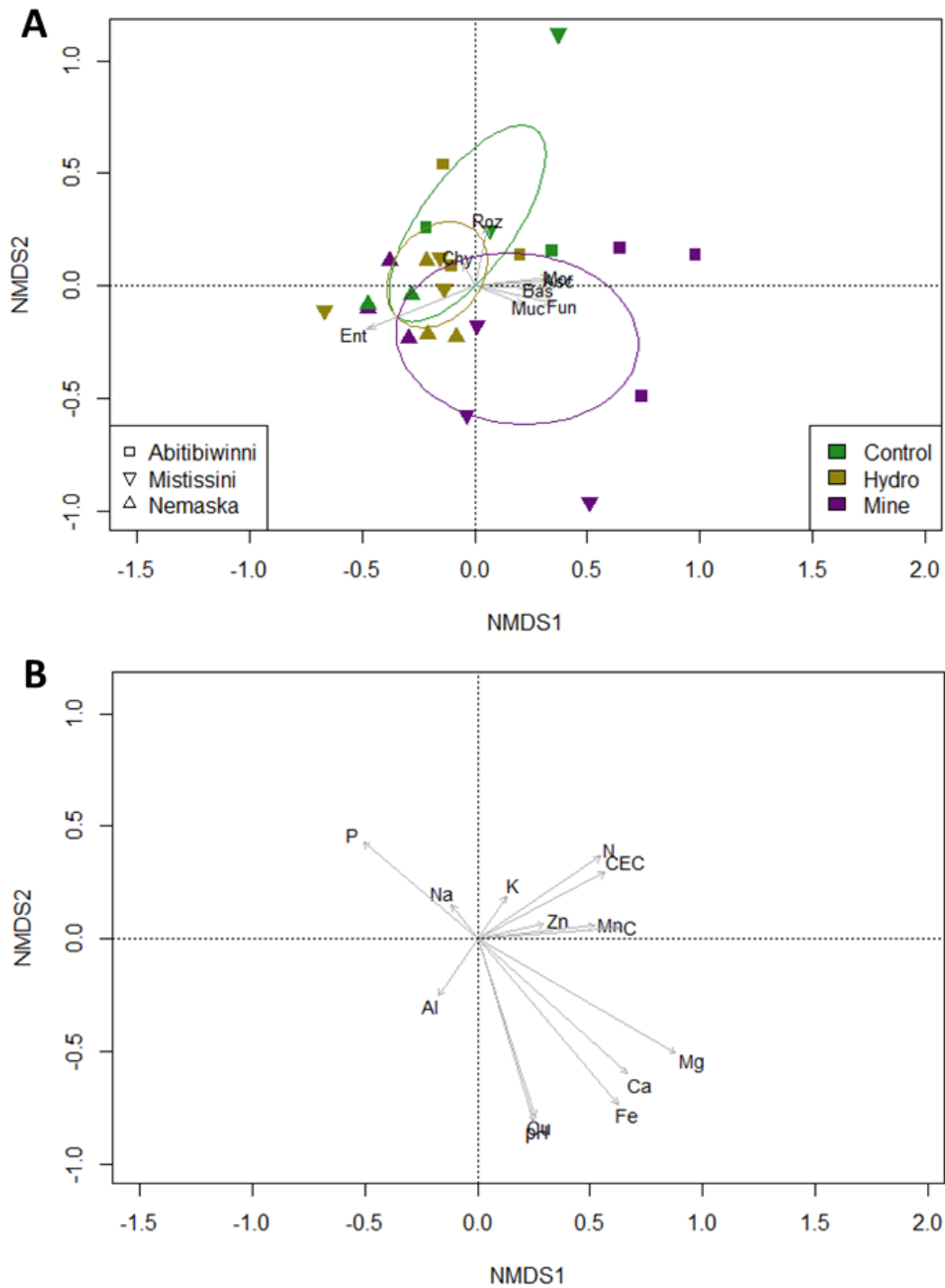


Figure 4.7 Non-metric multidimensional scaling of the abundance of fungal phyla. Stress = 0.17. A) Points represent the sampling sites. Ellipses represent the standard

deviation around each disturbance type. Asc: Ascomycota, Bas: Basidiomycota, Chy: Chytridiomycota, Ent: Entorrhizomycota, Fun: Fungi Phylum Incertae sedis, Mor: Mortierellomycota, Muc: Mucoromycota, Roz: Rozellomycota. B) Soil properties and composition in metals and oligo-elements. Cu: copper, Fe: iron, C: carbon, N: nitrogen, Mg: magnesium, Ca: calcium, CEC: Cation Exchange Capacity, Mn: manganese, K: potassium, Zn: zinc, P: phosphorus, Al: aluminum.

Most of the differentially abundant taxa were found in sites under hydroelectric power lines (Figure 4.8). Fungi from the Geoglossomycetes class, especially from Geoglossales order, the *Geoglossaceae* family, and the *Sarcoleotia* genus were more abundant in hydro sites. They also contained more fungi from several taxa of the Helotiales order, specifically from the *Dermateaceae* family, and from the *Humicolopsis* genus in the Sordariomycetes class. Fungi from the *Myxotrichaceae* family, especially from the *Oidiodendron* genus, which also belong to the Heliotiales order were more abundant in mine sites. One specific species, *Brahmaculus moonlighticus* was more abundant in control sites.

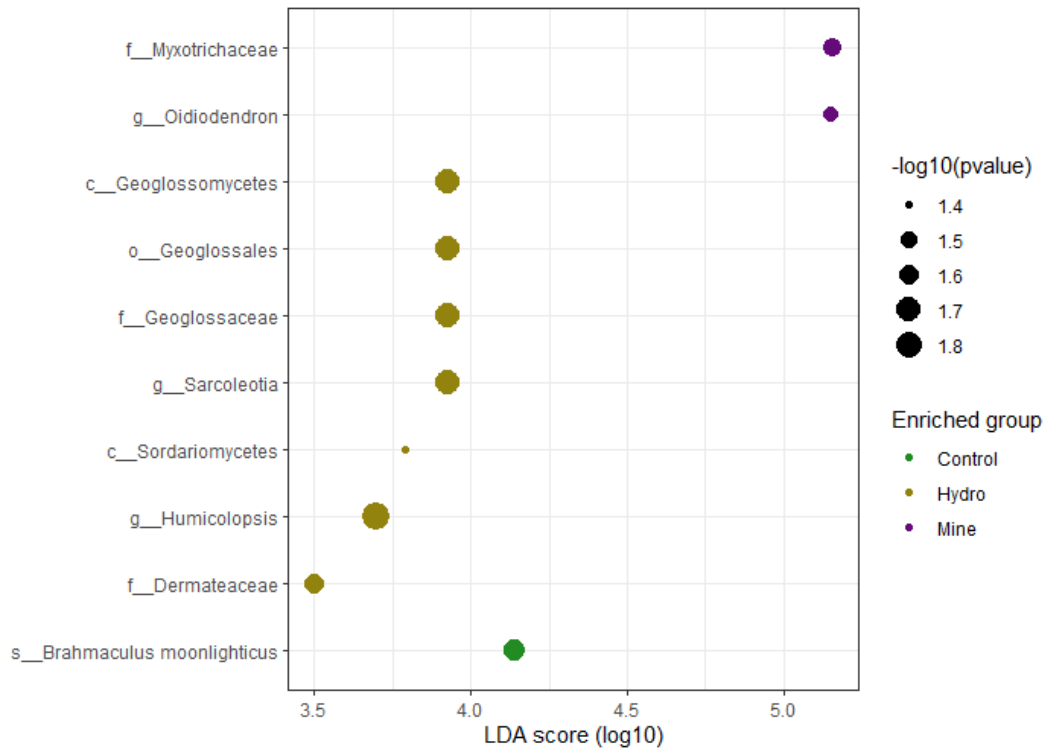


Figure 4.8 Fungal taxa differentially abundant for different disturbance types. Different colors indicate different disturbance types. The letter before the name of the taxa indicates the taxonomic level: o: order, c: class, f: family, g: genus, s: species.

4.6.3 Effect of soil properties on the soil microbiome

4.6.3.1 Effect of soil properties on bacteria

Soil pH emerged as the sole soil property exerting a significant influence on the composition of soil bacteria ($P=0.0014$, Table 4.2). An increase in soil pH was associated with a rise in the abundance of bacteria belonging to the WD260 order and several species within the *Bradyrhizobium* genus. Conversely, higher pH levels led to a decrease in the abundance of bacteria from the Acidobacteriales order and various genera within the *Acidobacteriaceae* family (Figure 4.9).

Table 4.2 Distance-based redundancy analysis (RDA) of the effect of soil properties on soil bacterial community. Bacteria dissimilarity matrix was calculated using the Hellinger distance. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values, and significant (< 0.05) adjusted *P*-values are shown in bold. Model adjusted $R^2 = 0.15$. For the sake of brevity, only the first 4 of the 15 axes are presented.

		Df	Sum of squares	F	Pr(>F)
Global	Model	14	7.2889	1.2987	0.0018
	Residual	9	3.6079		
Axes	dbRDA1	1	1.3336	3.3267	0.0098
	dbRDA2	1	1.09	2.719	0.5474
	dbRDA3	1	0.7978	1.9902	1
	dbRDA4	1	0.6264	1.5625	1
Terms	pH	1	1.219	3.0409	0.0014
	Nitrogen	1	0.6562	1.6369	0.1794
	Carbon	1	0.5865	1.463	0.385
	Phosphorus	1	0.3412	0.8511	1
	Magnesium	1	0.6340	1.5816	0.2196
	Potassium	1	0.386	0.963	1
	Iron	1	0.5552	1.385	0.552
	Copper	1	0.4962	1.2377	1
	Manganese	1	0.3873	0.9662	1
	Zinc	1	0.3799	0.9477	1
	Aluminum	1	0.431	1.0751	1
	Calcium	1	0.4493	1.1207	1
	Sodium	1	0.3266	0.8148	1
CEC	1	0.4405	1.0989	1	

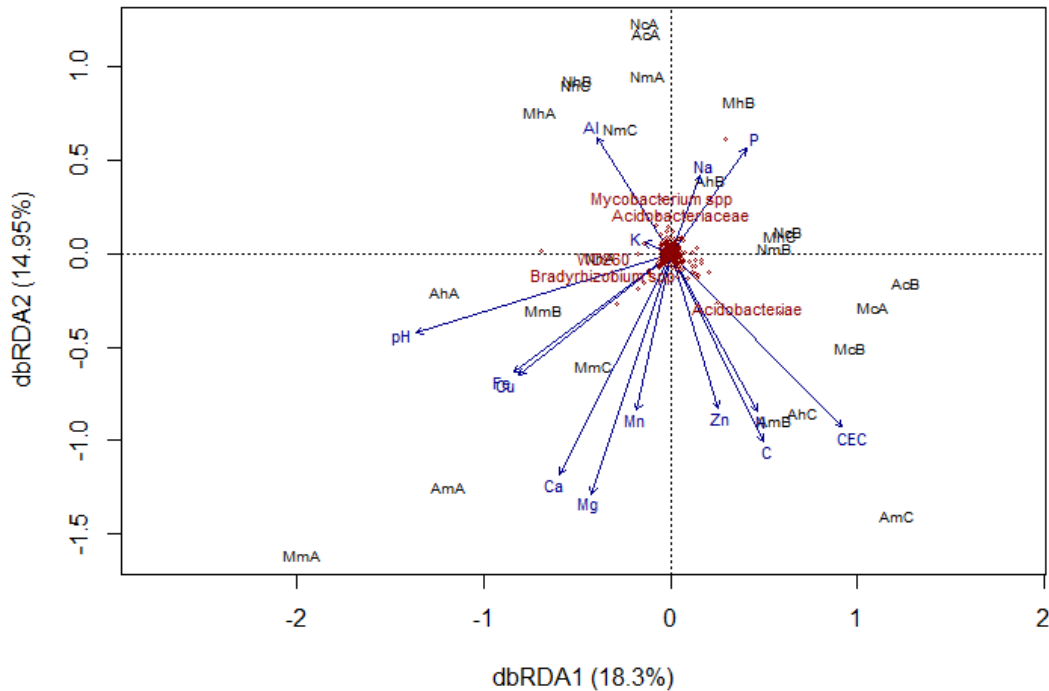


Figure 4.9 Distance-based redundancy analysis (RDA) of the effect of soil properties (blue arrows) on soil bacterial community (red). Cu: copper, Fe: iron, C: carbon, N: nitrogen, Mg: magnesium, Ca: calcium, CEC: Cation Exchange Capacity, Mn: manganese, K: potassium, Zn: zinc, P: phosphorus, Al: aluminum. Bacteria dissimilarity matrix was calculated using the Hellinger distance. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to p -values. Only the first axis and the pH variable are significant. Model adjusted $R^2 = 0.15$. To improve readability, bacterial taxa further from the center of the ordination are represented by red text, while the remaining taxa are represented by red points. When a labeled taxa is found in more than one ASV, the label is placed at their centroid. Sampling sites are in black; the first letter indicates the territory (A: Abitibiwinni, M: Mistissini, N: Nemaska), the second letter indicates the disturbance (c: control, h: hydroelectric line, m: mine), while the last letter indicates the replicate.

4.6.3.2 Effect of soil properties on fungi

Soil fungal composition was affected significantly by pH ($P=0.0195$), but also by nitrogen content ($P=0.0028$) (Table 4.3). Nitrogen content was correlated with carbon, magnesium, and calcium content, and mainly associated with increased abundances of fungi from the *Piloderma* genus, and from the *Oidiodendron pilicola* species, and with decreased abundances of fungi from the *Scytalidium vaccinii* species (Figure 4.10). The pH was correlated with copper content and was associated with increased abundances of fungi from the *Piloderma* and *Oidiodendron* genera, and with decreased abundances of fungi from the *Mycosymbioco*s genus (Figure 4.10).

Table 4.3 Distance-based redundancy analysis (RDA) of the effect of soil properties on soil fungal community. Bacteria dissimilarity matrix was calculated using the Hellinger distance. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to P -values, and significant (< 0.05) adjusted P -values are shown in bold. Model adjusted $R^2 = 0.18$. For the sake of brevity, only the first 4 of the 15 axes are presented in the table.

		Df	Sum of squares	F	Pr(>F)
Global	Model	14	11.2182	1.364	0.0001
	Residual	9	5.2873		
Axes	dbRDA1	1	1.7237	2.9341	0.0266
	dbRDA2	1	1.2332	2.0991	0.0469
	dbRDA3	1	1.0541	1.7942	0.9492
	dbRDA4	1	1.0443	1.7777	0.9996
Terms	pH	1	1.0493	1.7861	0.0195
	Nitrogen	1	1.2123	2.0635	0.0028
	Carbon	1	0.8902	1.5153	0.0890
	Phosphorus	1	0.5908	1.0057	1
	Magnesium	1	0.9514	1.6195	0.0768
	Potassium	1	0.6803	1.1580	0.9840
	Iron	1	0.6436	1.0955	1
	Copper	1	0.8704	1.4815	0.0890
	Manganese	1	0.8087	1.3766	0.2597

Table 4.3 (continued)

Terms	Df	Sum of squares	F	Pr(>F)
Zinc	1	0.5897	1.0038	1
Aluminum	1	0.9173	1.5614	0.0768
Calcium	1	0.8322	1.4166	0.1880
Sodium	1	0.6696	1.1399	1
CEC	1	0.5123	0.7253	1

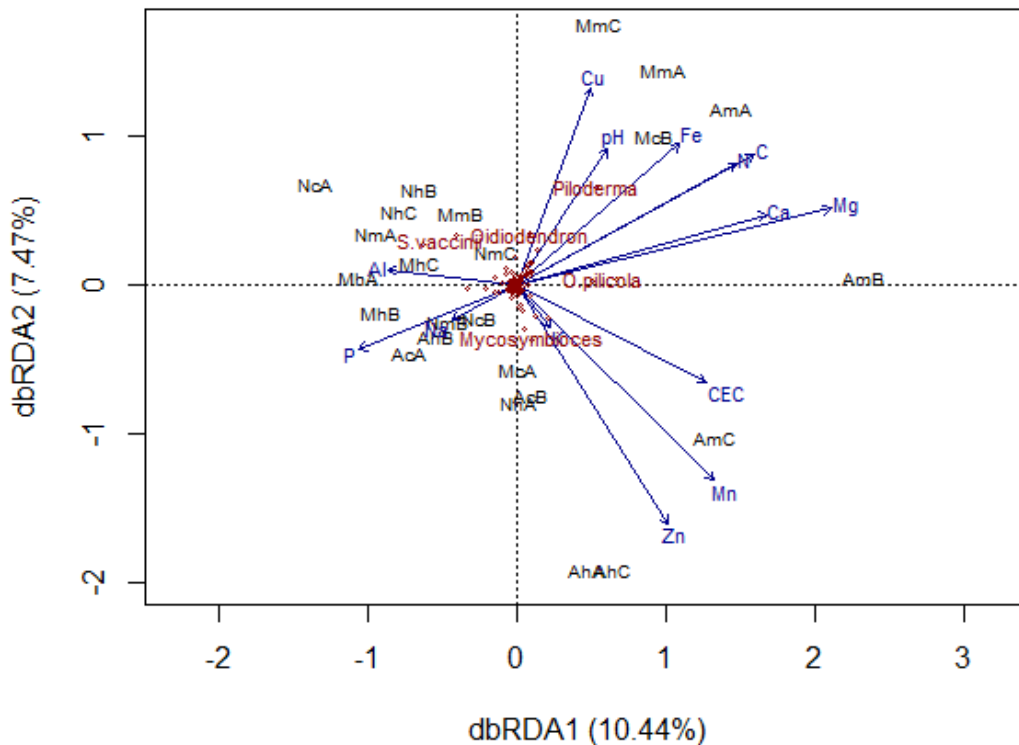


Figure 4.10 Distance-based redundancy analysis (RDA) of the effect of soil properties (blue arrows) on soil fungal community (red). Cu: copper, Fe: iron, C: carbon, N: nitrogen, Mg: magnesium, Ca: calcium, CEC: Cation Exchange Capacity, Mn: manganese, K: potassium, Zn: zinc, P: phosphorus, Al: aluminum. Fungi dissimilarity matrix was calculated using the Hellinger distance. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg

correction was applied to *p*-values. The two axes and the pH and nitrogen variables are significant. Model adjusted $R^2 = 0.18$. To improve readability, fungal taxa further from the center of the ordination are represented by red text, while the remaining taxa are represented by red points. When a labeled taxa is found in more than one ASV, the label is placed at their centroid. Sampling sites are in black; the first letter indicates the territory (A: Abitibiwinni, M: Mistissini, N: Nemaska), the second letter indicates the disturbance (c: control, h: hydroelectric line, m: mine) while the last letter indicates the replicate.

4.6.4 Effect of microbiome on (poly)phenol concentrations

The abundance of bacteria phyla in the soil did not have a significant effect on (poly)phenol concentrations (Table S4.2). However, when breaking down the Firmicutes phylum into its classes, we found a significant effect of the abundance of Bacilli ($P=0.0356$) and Desulfitobacteriia ($P=0.0056$) on (poly)phenol concentrations (Table 4.4 and Figure 4.11). Increased abundances of the Bacilli and Desulfitobacteriia were associated to higher concentrations of PACs (Figure 4.11). Increased abundances of Desulfitobacteriia were also associated with higher concentrations of delphinidin-3-glucoside, cyanidin-3-glucoside, and petunidin-3-glucoside (Figure 4.11). We did not find a significant effect of classes of Proteobacteria on (poly)phenol concentrations (Table S4.3). We also explored the Acidobacteriota, RCP2-54, WPS-2, Bacteroidota, Chloroflexi and Myxococcota phyla as they were near significant (Table S4.2), but it was inconclusive.

Table 4.4 Redundancy analysis (RDA) of the effect of Firmicutes Classes abundance on the concentration in (poly)phenolics of *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values, and significant (< 0.05) adjusted *P*-values are shown in bold. Model adjusted $R^2 = 0.25$.

		Df	Variance	F	Pr(>F)
Global	Model	4	46486	2.8798	0.0028
	Residual	19	76676		
Axes	RDA1	1	31213	7.7346	0.0300
	RDA2	1	11954	2.9622	0.4092
	RDA3	1	2035	0.5044	0.9523
	RDA4	1	1284	0.3181	0.9523
Terms	Bacilli	1	14987	3.7138	0.0356
	Negativicutes	1	8951	2.2179	0.1732
	Desulfitobacteriia	1	19654	4.8702	0.0056
	Clostridia	1	2895	0.7174	0.5566

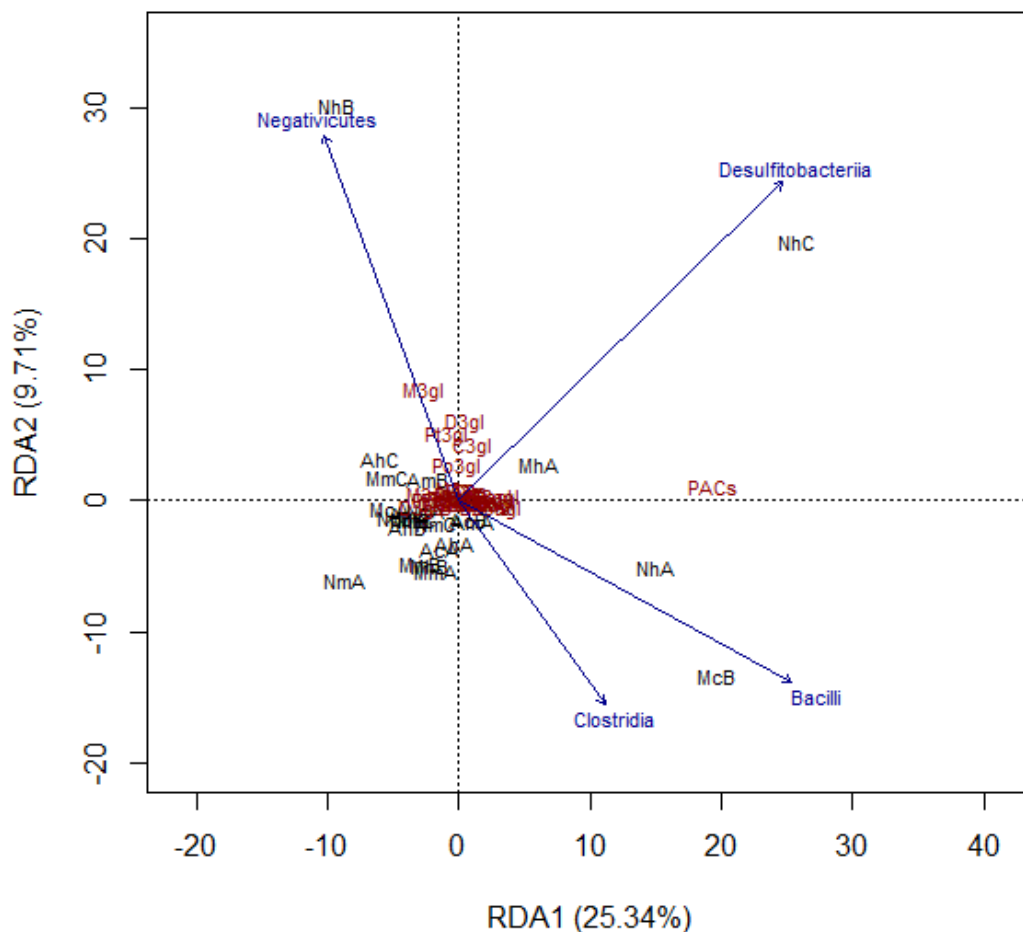


Figure 4.11 Redundancy analysis (RDA) ordination representing the effect of the abundance of classes from the Firmicutes phylum (blue arrows) on the phenolic profile of samples (red). Only the first axis was statistically significant ($P=0.0300$). The abundance of Bacilli and Desulfotobacteriia had a significant effect on the phenolic profile ($P=0.0356$ and $P=0.0056$ respectively). (Poly)phenolic compounds are displayed in red; Dga: delphinidin-3-galactoside, Dgl: delphinidin-3-glucoside, Cga: cyanidin-3-galactoside, Dar: delphinidin-3-arabinoside, Cgl: cyanidin-3-glucoside, Ptga: petunidin-3-galactoside, Car: cyanidin-3-arabinoside, Ptgl: petunidin-3-glucoside, Pnga: peonidin-3-galactoside, Ptar: petunidin-3-arabinoside, Pngl: peonidin-3-glucoside, Mga: malvidin-3-galactoside, Mgl: malvidin-3-glucoside, Mar: malvidin-3-arabinoside, D36agl: delphinidin-3-(6''-acetylglucoside), Pn36aga: peonidin-3-(6''-

acetylglactoside), C36agl: cyanidin-3-(6''-acetylglucoside), M36aga: malvidin-3-(6''-acetylglactoside), Pt36agl: petunidin-3-(6''-acetylglucoside), Pn36agl: peonidin-3-(6''-acetylglucoside), M36agl: malvidin-3-(6''-acetylglucoside), Cat: catechin, Epicat: epicatechin, PACs: proanthocyanidins. Sampling sites are in black; the first letter indicates the territory (A: Abitibiwinni, M: Mistissini, N: Nemaska), the second letter indicates the disturbance (c: control, h: hydroelectric line, m: mine) while the last letter indicates the replicate.

The abundance of fungi phyla did not have a significant effect on (poly)phenol concentrations (Table S4.4). Abundances of classes from the Ascomycota and Basidiomycota phyla did not have a significant effect on (poly)phenol concentrations either (Table S4.55 and Table S4.66). We further investigated classes from the Chytridiomycota phylum, as they approached significance (Table S4.4), but the findings remained inconclusive.

4.7 Discussion

Disturbances affected the composition of soil microorganisms, primarily due to alterations in soil characteristics. However, these changes did not influence plant (poly)phenol content. Indeed, the microbiome taxa responding to disturbances were not the same as the taxa that affected plant (poly)phenols.

4.7.1 Effect of disturbances on (poly)phenol content

Disturbances had no significant effect on the (poly)phenol content of *V. angustifolium*. This outcome is unexpected given that plants commonly react to stressors, including heavy metal contamination or ultraviolet (UV) radiation, by increasing the synthesis of (poly)phenols (Šamec et al. 2021; Jańczak-Pieniżek et al. 2023). This observation

could be attributed to the specific organ examined in the current study (fruits), as the response of plant secondary metabolism to stress factors can vary depending on the organ (Schreiner et al. 2009; Larbat et al. 2012; de Miguel et al. 2016; Smirnov et al. 2021). Indeed, various plant organs may not experience stressors to the same degree and may produce different compounds to counteract stress (Larbat et al. 2012; Simek et al. 2016). For instance, tomato plants (*Solanum lycopersicum* L.) infected by *Alternaria solani*, a pathogenic fungus, exhibit reduced flavonoid levels in the leaves, whereas the concentrations in the fruits remain unaffected (Quiterio-Gutiérrez et al. 2019). Similarly, in the olive tree (*Olea europaea* L.), water stress leads to diverse and occasionally contradictory changes in the concentrations of (poly)phenols across different organs, such as leaves and fruits (Jiménez-Herrera et al. 2019). Therefore, it is conceivable that the studied disturbances affected other parts of *V. angustifolium* but did not affect its fruits.

4.7.2 Effect of disturbances on soil microbiome

The construction of hydroelectric lines and the subsequent vegetation management under the lines creates distinctive soil conditions, particularly as wood from trimmed or felled trees is frequently left on site to decompose naturally (Hydro-Québec 2023c). According to our analyses, soil from sites under hydroelectric lines was relatively poor in carbon and nitrogen. It is thus possible that woody debris were the main carbon source at these sites. This may explain the higher abundance of saprotroph taxa or taxa able to degrade cellulose and lignin. Bacterial taxa such as Verrucomicrobiae and Ktedonobacteria at the class level, Chthoniobacterales and Ktedonobacterales at the order level, and *Ktedonobacteriaceae* at the family level, possess the capability to degrade lignin, cellulose, and other complex forms of carbon (Köberl et al. 2020; Zhao et al. 2020; Li et al. 2021; Zheng et al. 2021; Rachmania et al. 2022).

The abundance of the Ktedonobacteria class and its descendant taxa is higher under elevated levels of UV radiation (Maccario et al. 2019; Bañeras et al. 2022). This phenomenon could account for their higher abundance in sites under hydroelectric lines, where the absence of tree cover results in greater exposure to UV radiation.

Regarding fungi, members of the Sordariomycetes class, *Dermateaceae* family, and *Humicolopsis* genus are known for their ability to break down complex carbon structures (Osono and Hirose 2009; Eliades et al. 2015; Zhou et al. 2016; Li et al. 2020; Miao et al. 2022; Xing et al. 2022; Rao et al. 2023). Fungi from the Geoglossomycetes class and their children taxa have also been described as saprotrophic (Tedersoo et al. 2014). However, more recent studies found that they are rather mutualistic and able to form ericoid mycorrhizae (Baba et al. 2021; Melie et al. 2023). During our field observations, we noted that areas beneath hydroelectric lines exhibited a high abundance of ericaceous shrubs. This environmental characteristic may account for the observed increase in the abundance of ericoid mycorrhizal fungi, which are known to form symbiotic associations with the roots of ericaceous plants. Therefore, marker taxa found under hydroelectric lines could be the result of particular carbon conditions and of the high abundance of ericaceous shrubs.

Mining also affects soil conditions, notably by increasing metal concentrations. According to our analyses, soil from mining sites contained higher copper and iron concentrations. This may explain the higher abundance of fungi from the *Oidiodendron* genus, which are metal-tolerant (Vallino et al. 2009; Chiapello et al. 2015). However, these sites also had high abundance of fungi from the *Myxotrichaceae* family, which includes species forming mycorrhizal relationships (Kernaghan and Patriquin 2011) as well as functioning as saprotrophs (Dalpé 1989; Sigler et al. 2000; Rice et al. 2006). Yet, it is noteworthy that these fungi are not documented as being tolerant to metals.

Regarding bacteria, Sumerlaeota tended to be more abundant near mining sites, although this was not significant. This phylum is relatively unexplored, but is known

to be extremophile, thus probably adapted to the particular soil conditions of mining sites (Fang et al. 2021). Taxa associated with mining sites are thus partly explained by the specific edaphic conditions generated by mining activity.

Finally, the only taxon with higher abundance in control sites, the fungi *Brahmaculus moonlighticus*, has unfortunately not been studied with regards to its functions or habitat requirements. Interestingly, control sites also had less bacteria from the *Xanthobacteraceae* family than mining and hydroelectric sites. This is consistent with the characteristics of *Xanthobacteraceae*, as they are tolerant to polluted soil, and are able to degrade various pollutants including metals (Petrus et al. 2015; Martínez et al. 2022; Li et al. 2023), which could explain their lower abundance in undisturbed sites.

4.7.3 Effect of soil properties on the microbiome

Some microbial taxa were not associated with a particular disturbance type but responded to variations in soil properties. Concerning soil properties, only pH was found to significantly affect the abundance of bacterial taxa. Acidobacteriae at the class level and *Acidobacteriaceae* at the family level decreased in abundance with increasing pH, reflecting their acidophilic nature (Campbell 2014; Bartram et al. 2014; De Jonge et al. 2021). The genus *Bradyrhizobium* increased in abundance with rising pH levels. *Bradyrhizobium* species can tolerate a broad spectrum of pH conditions (Meghvansi et al. 2005) but their optimal pH for growth varies depending on species and strain (Graham et al. 1994; Indrasumunar et al. 2012). Given that the pH of the study sites was relatively acidic, ranging from 3.4 to 4.7, it is plausible that the *Bradyrhizobium* strains encountered in this study possess an optimal growth pH closer to neutral conditions. This adaptation could explain their increased abundance in conjunction with rising pH levels within the observed range.

The abundance of fungal taxa was influenced not only by soil pH, but also by nitrogen, and marginally by carbon, magnesium, aluminum, and copper content. Unfortunately, the current body of research concerning the optimal edaphic conditions and recognized functions of the majority of the studied taxa has only provided sufficient information to elucidate the response of a single taxon to soil properties. The *Piloderma* genus increased in abundance with magnesium and other metal concentrations in the soil. This particular genus is documented to thrive in soils with a high magnesium content (Glowa et al. 2003).

4.7.4 Effect of microbiome on plant (poly)phenols

(Poly)phenols in *V. angustifolium* fruits were not affected by any of the microbial taxa shown to vary with disturbances or soil properties, but were nevertheless affected by other taxa. (Poly)phenols were significantly affected by the abundance of two classes from the Firmicutes bacterial phylum: Bacilli and Desulfotobacteriia. Both these bacterial classes contain plant growth-promoting rhizobacteria (PGPR). Bacilli within the soil, particularly the *Bacillus* genus, are recognized for their diverse range of functions that are vital to plants (Hrynkiewicz et al. 2010; Saxena et al. 2020). Among others, they promote plant nutrition through nitrogen fixation, phosphorus and potassium solubilization (Sharma et al. 2013; Verma et al. 2015; Asari et al. 2017; Yousuf et al. 2017), and they help plants combat pathogens and mitigate the effects of metal pollution (Ramadoss et al. 2013; Goswami et al. 2014, 2016; Borriss et al. 2019). Desulfotobacteriia, specifically of the genus *Desulfotobacterium* increase in abundance following NH_4^+ addition, thus could have a role in nitrogen cycling (Xiao et al. 2023), and can also detoxify mycotoxins (He et al. 2020). In addition, PGPR can enhance plant (poly)phenol production under various stresses, notably by activating the phenylpropanoid pathway (Ait Barka et al. 2006; Zhang et al. 2023). Therefore, it is

likely that these two classes of bacteria, Bacilli and Actinobacteria, influenced the (poly)phenolic content of *V. angustifolium* fruits through their multifaceted effects on plant metabolism and their role in pathogen control.

4.7.5 Conclusion

Disturbances influence soil properties and the composition of the soil microbiome. However, intriguingly, these changes did not result in discernible differences in the (poly)phenolic compounds found in the fruits of *V. angustifolium*. Thus, disturbances due to mining and hydroelectric lines do not appear to affect the nutritional and medicinal properties of blueberries associated with (poly)phenols. However, this does not imply that disturbances have no effect on the overall nutritional and medicinal properties of the fruits. For example, presence of heavy metals in the fruits (due to mining activities) could lead to deleterious consequences for those who consume them (Okerefor et al. 2020; Yin et al. 2021). Hence, it is imperative to conduct assessments for the presence of pollutants in *V. angustifolium* fruits before making definitive conclusions regarding the effect of disturbances on the innocuity of these fruits and their nutritional and medicinal properties.

Aside from the effects of disturbances and soil properties, two bacterial classes, Bacilli and Desulfotobacteriia, were associated with increased abundance of fruit (poly)phenols. Identifying the environmental conditions that are conducive to the growth of Bacilli and Desulfotobacteriia and actively promoting these conditions could represent a potential strategy for enhancing the nutritional and medicinal properties of *V. angustifolium*.

CHAPITRE V

CONCLUSION GÉNÉRALE

L'objectif général de cette thèse était de comprendre l'effet des perturbations anthropiques sur deux espèces végétales d'importance culturelle, *Rhododendron groenlandicum* et *Vaccinium angustifolium*. Ces deux espèces ont été choisies par des communautés autochtones collaborant aux études de cette thèse, et servent de cas d'étude pour mieux comprendre l'effet des perturbations anthropiques sur les espèces culturelles clés et la végétation de sous-bois en général. Afin d'étudier l'effet des perturbations de la façon la plus exhaustive possible, différentes perturbations à différentes échelles (changements climatiques, coupes forestières, mines et lignes hydroélectriques) ont été considérées, ainsi que leurs effets sur différents éléments des plantes ou interagissant avec les plantes (présence des plantes, profil phénolique, microbiome et propriétés du sol).

5.1 Résumé des résultats des trois chapitres

L'effet des changements climatiques et des coupes forestières sur la présence de *R. groenlandicum* et *V. angustifolium* a pu être mieux compris en modélisant l'évolution de leur habitat (Chapitre II). L'exercice de modélisation a montré que les changements climatiques et les coupes contribueront à la diminution des peuplements de conifères en faveur de peuplements décidus et de zones non forestières. En effet, dans l'ouest du Québec, les changements climatiques, surtout s'ils sont importants (RCP 8.5),

conduiront à une augmentation de la sévérité et la fréquence des feux (Boulangier et al. 2017b, 2022; Augustin et al. 2022), ce qui, à l'échelle du paysage, mènerait les peuplements vers des stades de succession plus précoces, typiquement décidus (Bergeron 2000; Shenoy et al. 2011; Paudel et al. 2015). Cela diminuerait la présence de *R. groenlandicum* et *V. angustifolium* dans le paysage, car ces espèces ne sont pas associées avec les peuplements décidus (Humbert et al. 2007; Hébert and Thiffault 2011; Thiffault et al. 2015). La coupe exacerberait l'effet des changements climatiques, en contribuant également à augmenter la proportion de peuplements décidus dans le paysage, tels que les peupliers qui peuvent se reproduire par marcottage après une coupe (Laquerre et al. 2011; Marchais et al. 2022). Un levier d'action pour préserver la présence de *R. groenlandicum* et *V. angustifolium* dans le paysage serait de limiter l'augmentation des peuplements décidus, par exemple en prenant en compte les peuplements qui pourraient brûler lors de la planification des coupes pour éviter les échecs de régénération (Acuna et al. 2010; Daniel et al. 2017) , ou en plantant des conifères plus adaptés à des feux fréquents tels que le pin gris (*Pinus banksiana* Lambert) (Cyr et al. 2022).

Dans les chapitres III et IV, l'effet des mines et des lignes hydroélectriques sur le profil phénolique de *R. groenlandicum* et *V. angustifolium* a été examiné. Pour *R. groenlandicum*, l'activité minière diminue la concentration en différents phénols, tandis que la présence d'une ligne hydroélectrique l'augmente. La diminution de concentration associée aux mines peut être expliquée par l'épuisement des phénols pour chélater les métaux lourds (Michalak 2006; Sleptsov et al. 2021), ainsi que par l'inhibition de la biosynthèse des phénols par les métaux lourds (Nagajyoti et al. 2010). L'augmentation des concentrations associée avec les lignes hydroélectriques peut être expliquée par l'exposition accrue au soleil, et donc aux rayons UV, qui provoque la biosynthèse des composés phénoliques dans la plante pour s'adapter à ces conditions d'ensoleillement accru (Rapinski et al. 2014; Peng et al. 2017; Zhou et al. 2021). Concernant *V. angustifolium*, ni les mines, ni les lignes hydroélectriques n'influencent

de façon significative la teneur en composés phénoliques de ses fruits. Cette absence d'effet comparativement à *R. groenlandicum* peut s'expliquer à la fois par la différence d'espèce et la différence d'organe considéré. En effet, différentes espèces, même proches, n'utilisent pas forcément les mêmes composés pour répondre aux stress environnementaux (Riihinen et al. 2008), et les différents organes des plantes ne répondent pas toujours de la même manière aux stress environnementaux (Larbat et al. 2012; de Miguel et al. 2016; Smirnov et al. 2021). Il se peut donc que les fruits de *V. angustifolium* répondent aux perturbations étudiées via d'autres composés que les composés phénoliques (Larbat et al. 2012; Simek et al. 2016).

Enfin, avec le chapitre IV, nous avons montré que les mines et les lignes hydroélectriques influençaient les propriétés du sol et le microbiome du sol. Le sol sous les lignes hydroélectriques était relativement pauvre en carbone, mais riche en débris ligneux générés par les coupes d'entretien sous les lignes (Hydro-Québec 2023c). Ces débris ligneux représentaient donc possiblement la principale source de carbone du sol, ce qui explique la plus forte présence de microorganismes capables de dégrader la cellulose sous les lignes hydroélectriques, tels que les Ktedonobacteria ou les Sordariomycetes (Zheng et al. 2021; Miao et al. 2022; Rachmania et al. 2022; Rao et al. 2023). Le sol des mines était plus concentré en cuivre et en fer, résultant en une abondance plus élevée de microorganismes tolérants aux métaux ou extrémophiles, tels que les champignons du genre *Oidiodendron* et les bactéries du Phylum Sumerlaota (Vallino et al. 2009; Chiapello et al. 2015; Fang et al. 2021).

Nous avons également montré que deux classes de bactéries qui ne répondaient pas aux perturbations, Bacilli et Desulfotobacteriia, étaient liées à des concentrations plus élevées de phénols dans les fruits de *V. angustifolium*. Ces classes bactériennes contiennent des rhizobactéries promotrices de la croissance des plantes (PGPR) qui favorisent la nutrition des plantes, détoxifient les métaux, et aident à combattre les pathogènes (Yousuf et al. 2017; Borriss et al. 2019; He et al. 2020; Saxena et al. 2020;

Xiao et al. 2023). De plus, les PGPR sont connues pour augmenter la production de phénols dans les plantes lorsque celles-ci sont exposées à différents stress (Ait Barka et al. 2006; Zhang et al. 2023). Ces deux classes de bactéries ont donc le potentiel d'augmenter les concentrations en phénols des fruits de *V.angustifolium*, ce qui pourrait être intéressant d'un point de vue nutritionnel.

5.2 Synthèse et implications

Avec les résultats de cette thèse, nous avons montré que les perturbations anthropiques peuvent affecter les deux espèces étudiées à large échelle comme à fine échelle, avec des conséquences environnementales et culturelles.

La diminution de la présence *R. groenlandicum* et *V. angustifolium* en réponse à des changements climatiques élevés et aux coupes forestières pourrait entraîner à son tour des changements dans le paysage. En effet, ces deux espèces limitent la colonisation et la croissance des arbres, ce qui crée des zones moins denses en arbres dans le paysage (Mallik 2003; Hébert and Thiffault 2011). Il est donc possible qu'une diminution de la présence de ces deux espèces entraîne une diminution de certains habitats dans le paysage forestier. Une diminution de la présence de *R. groenlandicum* et *V. angustifolium* aurait également des conséquences sur les pratiques culturelles associées avec ces deux espèces. En effet, *R. groenlandicum* est utilisée en médecine traditionnelle par les communautés autochtones du Canada, notamment pour préparer des infusions médicinales (Uprety et al. 2012). Les fruits de *V. angustifolium* font partie intégrante de la diète autochtone, et sont également consommés par des espèces chassées telles que l'ours noir (Boulanger-Lapointe et al. 2019; Basile et al. 2022; Pelletier 2022). Une diminution de la présence de *R. groenlandicum* et *V. angustifolium* pourrait donc non seulement entraîner des changements dans l'écosystème, mais également menacer différentes pratiques traditionnelles.

L'effet des mines et des lignes hydroélectriques sur les phénols de *R. groenlandicum* montre qu'une plante en apparence non stressée peut être soumise à des pressions liées aux perturbations. L'analyse des phénols, et du métabolisme secondaire de façon générale, pourrait donc être une piste prometteuse pour évaluer de façon plus précise, et plus précoce, l'effet des perturbations sur l'environnement.

La plus faible concentration en phénols des feuilles de *R. groenlandicum* à proximité des mines pourrait avoir des répercussions pour les communautés autochtones. En effet, les propriétés médicinales associées avec cette plante dépendent en grande partie des phénols contenus dans ses feuilles (Saleem et al. 2010; Eid et al. 2016; Dasiman et al. 2022). La proximité d'une mine pourrait donc diminuer le potentiel médicinal de cette plante. À l'inverse, la présence d'une ligne hydroélectrique, et l'exposition accrue au soleil qui en résulte, pourrait améliorer le potentiel médicinal de *R. groenlandicum*. Il est cependant important de considérer que les phénols ne représentent qu'un aspect du potentiel médicinal de la plante. D'autres composés, bénéfiques comme néfastes, de même que l'effet d'une potentielle contamination liée aux perturbations (p. ex. herbicides sous les lignes hydroélectriques), sont à considérer avant de conclure sur l'effet des perturbations sur les propriétés médicinales de l'espèce (Kyong et al. 2010; Dampc and Luczkiewicz 2015; Ojelade et al. 2022).

L'effet variable des mines et des lignes hydroélectriques sur les phénols de *R. groenlandicum* et *V. angustifolium* met également en lumière la complexité de la réponse des plantes aux perturbations. En effet, les mêmes perturbations n'entraînent pas les mêmes réponses chez ces deux espèces végétales proches. L'absence d'effet des perturbations sur les phénols de *V. angustifolium* pourrait être due à une réponse aux stress associés avec ces perturbations via d'autres métabolites secondaires non étudiés ici. En effet, bien que les composés analysés dans notre étude (phénols) soient importants chez *V. angustifolium* (Norberto et al. 2013; Grace et al. 2019), les plantes disposent d'autres mécanismes pour s'adapter à leur environnement qui n'ont pas été

analysés, comme des enzymes antioxydantes (Syta et al. 2013; Qamer et al. 2021). Une autre explication serait une différence de réponse liée à l'organe considéré, c'est-à-dire les fruits plutôt que les feuilles. Les différents organes d'une plante ne subissent pas toujours les stress de la même manière, et peuvent donc utiliser des composés différents pour répondre aux stress (Larbat et al. 2012; Simek et al. 2016).

L'effet du microbiome du sol sur les phénols des fruits de *V. angustifolium* offre une avenue prometteuse pour améliorer ses propriétés nutritionnelles. Les Bacilli et les Desulfotobacteriia, les deux classes de bactéries augmentant les concentrations en phénols des fruits, ne réagissent pas aux perturbations. Cependant, il serait possible de trouver et favoriser les conditions environnementales qui leur sont favorables afin d'améliorer les propriétés nutritionnelles de *V. angustifolium*.

Les perturbations étudiées n'avaient pas d'effet sur *V. angustifolium* via le microbiome du sol, mais cela ne veut pas dire que cet effet indirect des perturbations n'existe pas dans d'autres circonstances. Étant donné la complexité du processus d'assemblage des communautés microbiennes du sol, l'effet des perturbations sur la composition microbienne pourrait différer en fonction de différentes variables environnementales, telles que les propriétés du sol pré-perturbation (Kaminsky et al. 2021; Philippot et al. 2023). L'espèce végétale considérée peut également avoir une influence, car différentes espèces végétales n'interagissent pas forcément avec les mêmes microorganismes (Sánchez-Cañizares et al. 2017; DiLegge et al. 2022). Ainsi, dans d'autres conditions, il est possible que l'effet des perturbations sur le microbiome du sol engendre des changements dans les plantes (Seitz et al. 2021).

Les effets des différentes perturbations étudiées pourraient également se cumuler. Par exemple, les changements climatiques et la coupe forestière risquent de diminuer la présence de *R. groenlandicum* dans les territoires étudiés, mais en plus une partie des individus restants se retrouverait soumise à des perturbations locales, et donc verrait ses propriétés altérées. De la même manière, il est possible que les coupes et les

changements climatiques n'entraînent pas seulement des changements dans la présence des espèces, mais aussi dans les propriétés des individus toujours présents. En effet, les coupes et les feux dégagent le paysage, générant de façon transitoire de nouvelles conditions d'ensoleillement, avec des conséquences qui pourraient donc s'apparenter à celles générées par la présence d'une ligne hydroélectrique. De plus, les phénols sont également impliqués dans la réponse des plantes aux stress thermiques et hydriques (Sharma et al. 2019; Šamec et al. 2021), leurs concentrations pourraient donc changer en réponse aux changements climatiques. Les conséquences seraient alors doubles pour les communautés autochtones : une espèce d'importance culturelle deviendrait moins disponible sur leur territoire, et une partie des individus restants auraient des propriétés altérées, les rendant potentiellement moins aptes à soutenir les activités traditionnelles liées à cette espèce.

5.3 Limites

Pour le chapitre II, nous avons pu modéliser la présence des deux espèces végétales, mais pas la fructification de *V. angustifolium*. Étant donné que la valeur culturelle de *V. angustifolium* repose principalement sur ses fruits (Boulanger-Lapointe et al. 2019; Basile et al. 2022), il serait nécessaire de modéliser la présence de fruits afin d'avoir une meilleure compréhension des conséquences des perturbations.

La complexité du processus de simulation nous a également forcé à simplifier les perturbations modélisées. Nous avons considéré toutes les coupes comme des coupes totales, la principale méthode utilisée dans l'aire d'étude. Cependant, d'autres pratiques, comme les coupes partielles et la préparation de site, pourraient avoir une influence plus négative sur les deux espèces étudiées, en limitant l'ouverture de la canopée et la colonisation post-coupe (Lorente et al. 2012; Bose et al. 2014; Thiffault and Hébert

2017). Il serait donc intéressant d'évaluer l'effet de ces pratiques dans un contexte où elles commencent à être utilisées plus fréquemment à l'échelle du paysage.

L'effet des feux a également été simplifié. Les régimes de feux répondaient à l'âge des peuplements, mais pas à leur composition. Comme les peuplements décidus brûlent moins bien que les peuplements de conifères (Krawchuk et al. 2006; Boulanger et al. 2018a; Marchal et al. 2020), il est possible que l'augmentation des décidus liée aux feux projetée par nos modèles soit en réalité en partie limitée par une boucle de rétroaction négative, ce qui résulterait en un meilleur maintien des conifères.

Pour les chapitres III et IV, les échantillonnages se déroulaient dans des milieux éloignés, et échantillons prélevés avaient besoin d'être préservés rapidement, ce qui a restreint le nombre de mesures que nous avons pu prendre sur le terrain. Par exemple, nous n'avons pas pu mesurer directement les modifications de l'environnement associées avec les perturbations étudiées. Il aurait été intéressant de mesurer la concentration en métaux lourds dans les plantes, la température ou l'ensoleillement du sous-bois afin d'obtenir un portrait plus précis du mode d'action des perturbations sur les plantes de sous-bois.

L'éloignement des sites d'échantillonnage a également rendu impossible l'étude de l'ARN, qui aurait pu s'avérer un outil utile pour étudier la réponse des plantes et du microbiome du sol aux perturbations. Analyser l'ARN des plantes aurait permis de mieux comprendre l'effet des perturbations sur les plantes, en mettant en lumière les gènes impliqués dans la variation des phénols. L'analyse de l'ARN aurait également pu être appliquée au microbiome, ce qui aurait permis de détecter uniquement les microorganismes vivants, et donc actifs, dans le sol, et d'avoir une meilleure idée de leur fonction.

5.4 Perspectives

R. groenlandicum et *V. angustifolium* sont deux espèces capables de bénéficier des perturbations grâce à leur capacité de reproduction végétative qui leur permet de recoloniser rapidement le milieu (Laberge Pelletier 2007; Hébert and Thiffault 2011; Marozau and Gordej 2019). D'autres espèces d'importance culturelle pourraient donc répondre plus négativement aux perturbations. En répliquant cette étude avec d'autres espèces avec des traits différents (incapables de reproduction végétative par exemple), il serait possible d'avoir une meilleure image de l'effet des perturbations sur les espèces d'importance culturelle.

L'étude de l'effet des perturbations sur les phénols pourrait être complétée en étudiant le métabolisme au complet grâce à la métabolomique non ciblée. Cette technique permet d'analyser un grand nombre de métabolites simultanément (Patti et al. 2012), ce qui permettrait une analyse différentielle de l'effet des perturbations sur le métabolisme des plantes. Il serait ainsi possible de déterminer l'effet des perturbations non seulement sur les phénols d'une plante, mais aussi sur d'autres métabolites secondaires, sur sa croissance, ou sur son développement.

Il serait également intéressant d'évaluer plus directement l'effet des perturbations sur les propriétés médicinales et nutritionnelles des espèces étudiées. La mesure des concentrations en phénols des parties consommées pourrait être couplée avec une évaluation de leur pouvoir antioxydant, par exemple avec une extraction au méthanol suivie d'un dosage au 2,2-diphényl 1-picrylhydrazyle (DPPH) (Xiao et al. 2020; Nawaz et al. 2022). Pour avoir un portrait plus complet des propriétés médicinales et nutritionnelles, il serait également nécessaire de mesurer les concentrations en polluants potentiels, par exemple différents métaux lourds ou herbicides, dans les parties consommées de la plante afin d'estimer leurs effets nocifs sur la santé.

Pour conclure, cette thèse a mis en lumière que les effets des perturbations sur les espèces végétales sont multiples, et que différentes approches doivent être utilisées de façon complémentaire pour étudier ces effets. Il est important de ne pas s'arrêter à l'effet des perturbations sur la présence des espèces, mais de considérer également leurs effets sur les propriétés des espèces, par exemple leur métabolisme secondaire. En effet, une modification dans le métabolisme secondaire d'une plante peut indiquer qu'elle répond à un stress environnemental, y compris dans des milieux qui semblent peu ou pas perturbés au premier abord. Dans ce cadre, étudier le métabolisme des plantes peut être un indicateur précoce et plus sensible des perturbations environnementales, ce qui permettrait aux décideurs d'agir plus efficacement pour préserver l'environnement. De plus, dans le cas de plantes consommées (p. ex. espèces d'importance culturelle), l'étude du métabolisme a également un intérêt culturel. En effet, les usagers du territoire, notamment les autochtones, consomment les plantes sauvages et en dépendent pour diverses activités traditionnelles. Étant donné les implications qu'ont les phénols pour la santé humaine, une variation dans leur concentration pourrait entraîner des conséquences chez ceux qui consomment ou utilisent ces plantes sauvages. De plus, les plantes sauvages sont également consommées par des espèces animales d'intérêt, comme des espèces chassées. Cela signifie qu'en plus de l'intérêt environnemental à étudier les phénols, il y a également un intérêt socio-culturel, avec la préservation des activités autochtones (p. ex. cueillette, chasse et médecine). Ainsi, il est important d'évaluer l'effet des perturbations sur les espèces végétales de façon complète afin de mieux comprendre les conséquences qui en découlent, et de prendre les décisions adaptées pour limiter ces conséquences.

APPENDICE A

MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE II

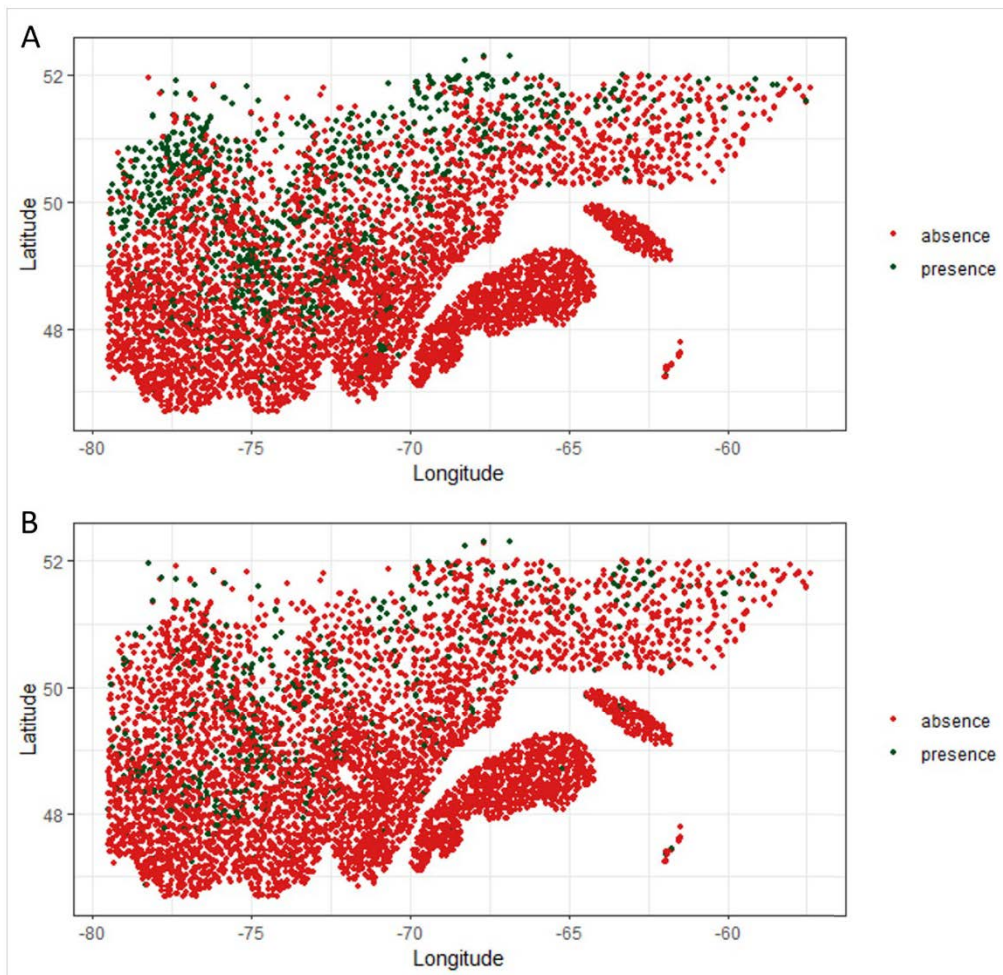


Figure S2.1 Presence/absence map of the data used to build the SDMs. A) *Rhododendron groenlandicum*. B) *Vaccinium angustifolium*.

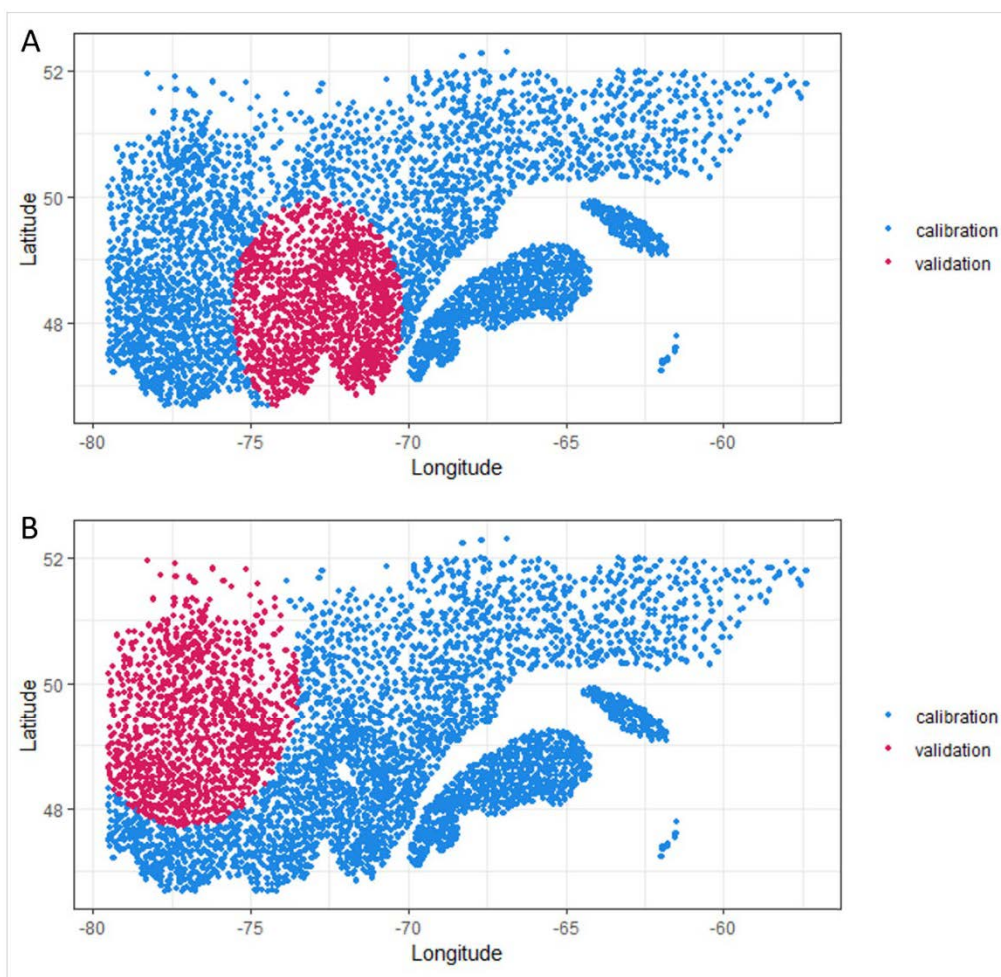


Figure S2.2 Calibration and validation blocks used in the SDMs. SDMs were calibrated with 75% of the data and validated on the remaining 25%. A) *Rhododendron groenlandicum*. B) *Vaccinium angustifolium*.

Table S2.1 Species distribution model scores for *R. groenlandicum*. The scores are the averages over all 3 replicates for each model type according to the True Skill Statistics metric. MAXENT: Maximum Entropy, GLM: Generalized Linear Model, GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

		Calibration	Validation	Evaluation	Cutoff	Sensitivity	Specificity
TSS	MAXENT	0.612	0.612	0.627	0.339	85.13	76.12
	GLM	0.614	0.617	0.619	0.534	82.90	78.48
	GAM	0.613	0.608	0.614	0.357	85.13	76.17
	RF	0.852	0.630	0.561	0.303	96.56	88.57
	GBM	0.695	0.638	0.597	0.492	88.85	80.61
AUC	MAXENT	0.884	0.883	0.885	0.337	85.31	76.00
	GLM	0.882	0.882	0.885	0.527	83.27	78.17
	GAM	0.881	0.879	0.878	0.358	85.07	76.23
	RF	0.977	0.888	0.852	0.303	96.52	88.65
	GBM	0.918	0.894	0.875	0.486	89.16	80.35

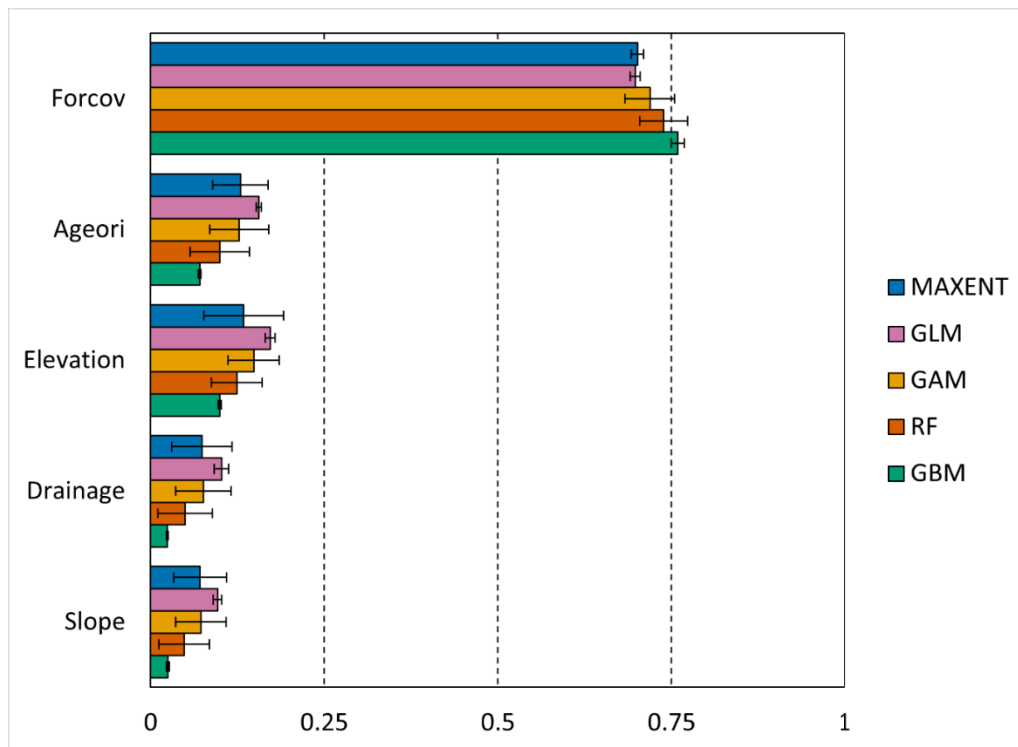


Figure S2.3 Average relative importance of explanatory variables for each type of model used in building the ensemble model for *R. groenlandicum*. Error bars represent the minimum and maximum values obtained in the replicates. MAXENT: Maximum Entropy, GLM: Generalized Linear Model; GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

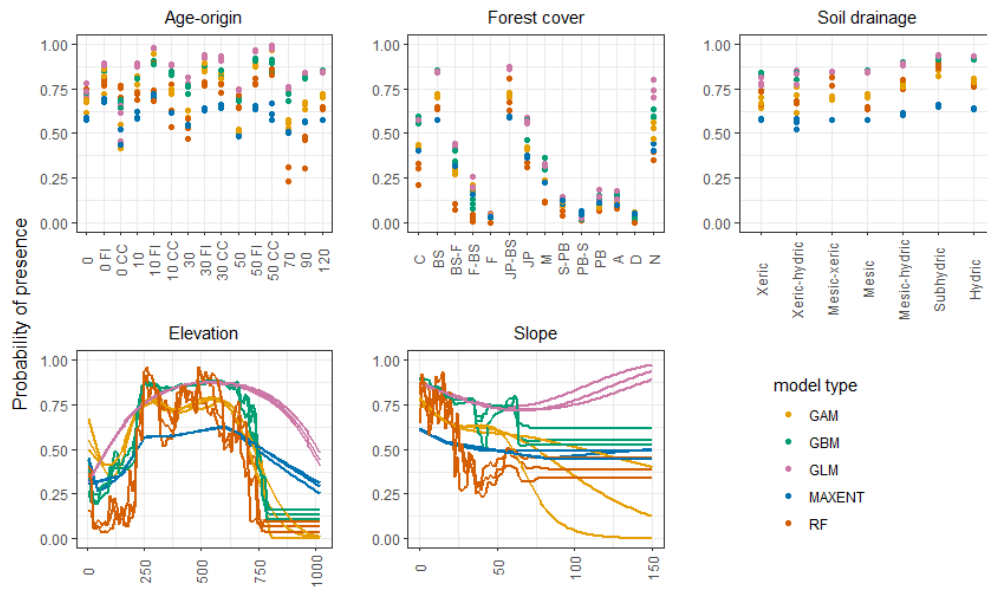


Figure S2.4 Predicted probability of presence of *R. groenlandicum* according to the different models used for each value of the explanatory variables. Elevation is expressed in meters. See Table 2.2 for the meaning of the codes for the variables age-origin and forest cover. MAXENT: Maximum Entropy, GLM: Generalized Linear Model, GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

Table S2.2 Species distribution model scores for *V. angustifolium*. The scores are the averages over all 3 replicates for each model type according to the True Skill Statistics metric. MAXENT: Maximum Entropy, GLM: Generalized Linear Model, GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

		Calibration	Validation	Evaluation	Cutoff	Sensitivity	Specificity
TSS	MAXENT	0.519	0.519	0.383	0.400	75.17	76.69
	GLM	0.526	0.53	0.376	0.483	80.62	71.89
	GAM	0.511	0.502	0.345	0.125	79.62	71.43
	RF	0.927	0.494	0.302	0.168	97.53	95.09
	GBM	0.611	0.538	0.371	0.479	85.22	75.95
AUC	MAXENT	0.853	0.831	0.745	0.416	73.39	78.57
	GLM	0.832	0.829	0.743	0.484	80.62	72.03
	GAM	0.826	0.820	0.723	0.124	80.25	71.22
	RF	0.992	0.822	0.703	0.161	96.30	94.76
	GBM	0.885	0.854	0.741	0.496	83.84	77.42

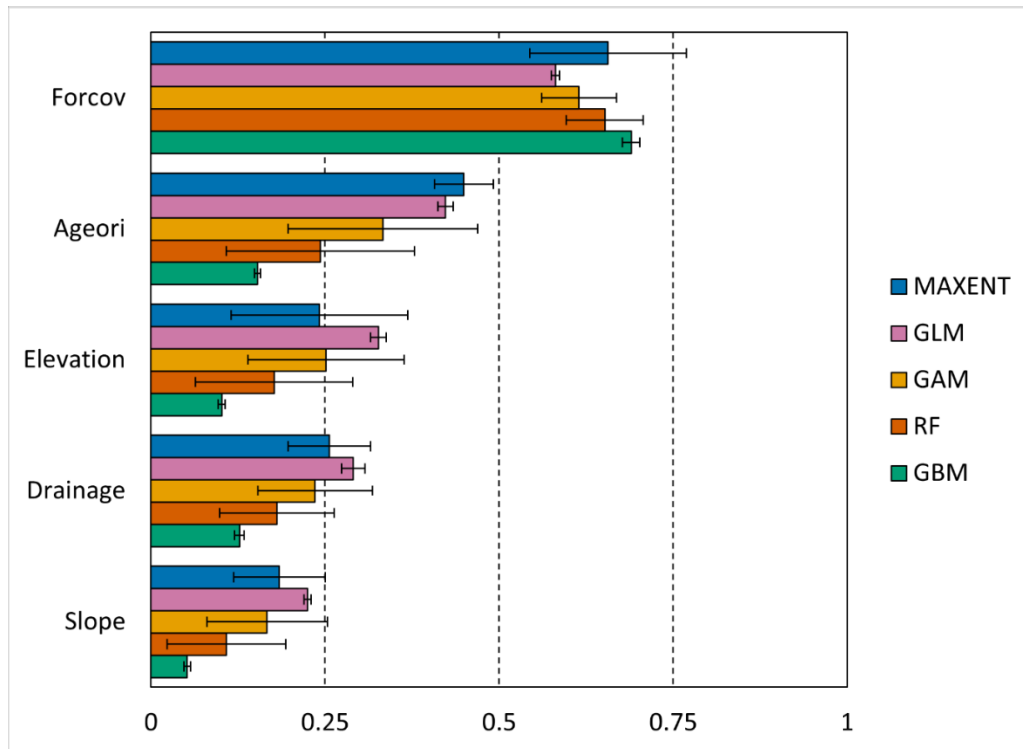


Figure S2.5 Average relative importance of explanatory variables for each type of model used in building the ensemble model for *V. angustifolium*. Error bars represent the minimum and maximum values obtained in the replicates. MAXENT: Maximum Entropy, GLM: Generalized Linear Model; GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

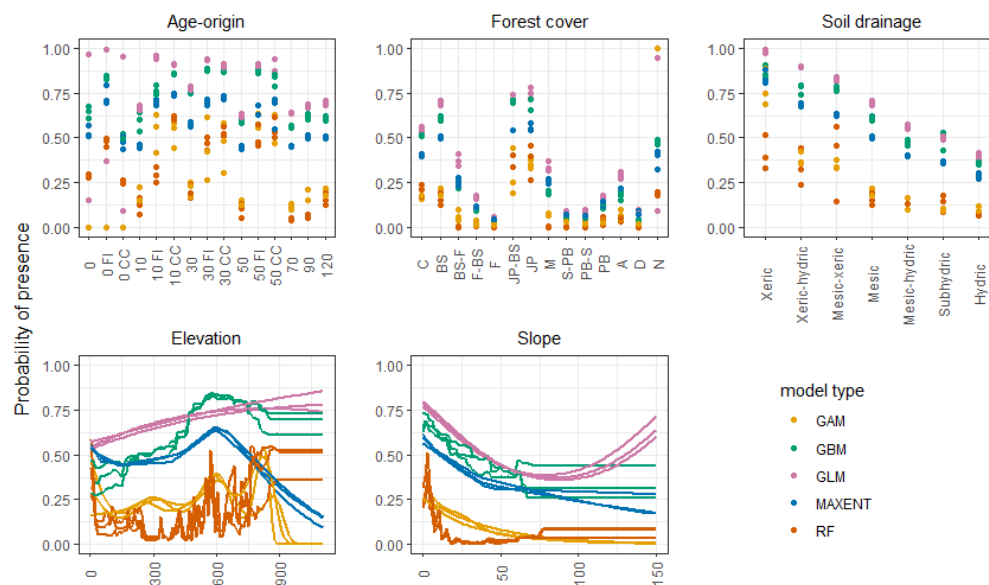


Figure S2.6 Predicted probability of presence of *V. angustifolium* according to the different models used for each value of the explanatory variables. Elevation is expressed in meters. See Table 2.2 for the meaning of the codes for the variables age-origin and forest cover. MAXENT: Maximum Entropy, GLM: Generalized Linear Model, GAM: Generalized Additive Model, RF: Random Forest, GBM: Generalized Boosted Model.

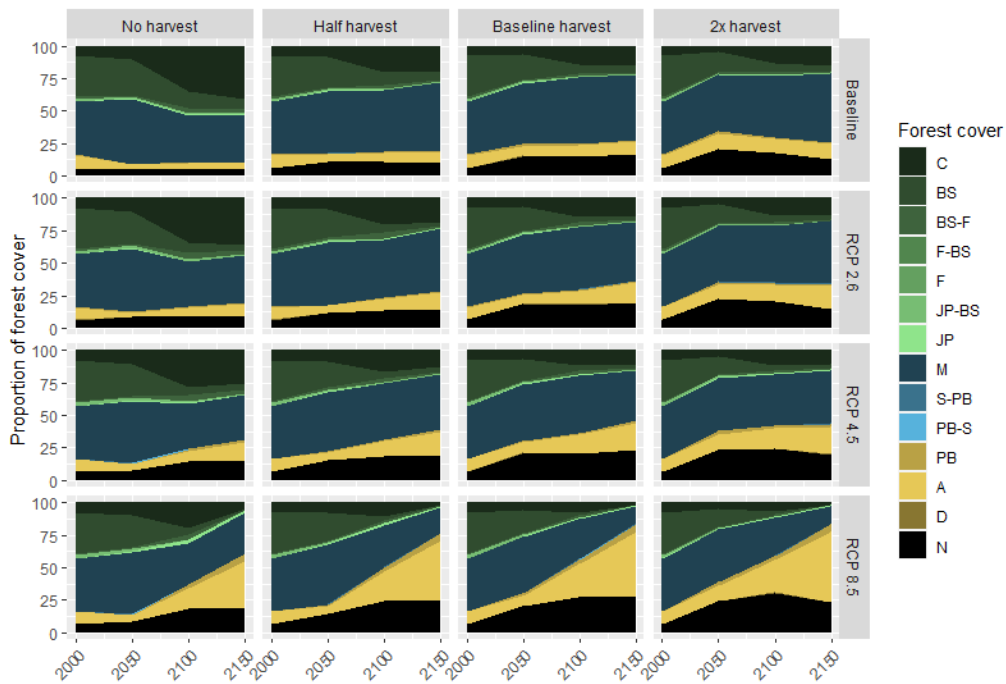


Figure S2.7 Changes in the proportion of forest cover on the Abitibiwiinni territory under different climate and forest harvesting scenarios. C: Coniferous species, BS: Black spruce, BS-F: Black spruce with fir or black spruce with white spruce, F-B: Fir-black spruce, F: Fir, JP-B: Jack pine with spruce, JP: Jack pine, M: Mixed forests, i.e. both deciduous and coniferous, S-P: Paper birch with fir or white spruce (coniferous dominance), P-B: Paper birch with fir or white spruce (deciduous dominance), P: Paper birch, A: Aspen, D: Deciduous species, N: Non-forested (no trees or trees too young/sparse).

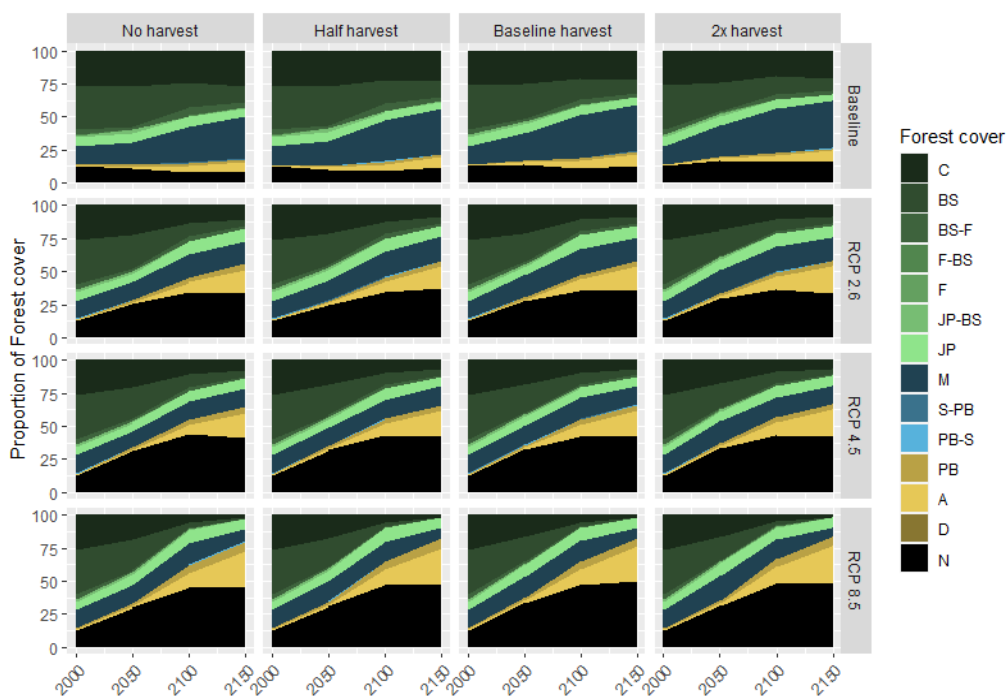


Figure S2.8 Changes in the proportion of forest cover on the Mistissini territory under different climate and forest harvesting scenarios. C: Coniferous species, BS: Black spruce, BS-F: Black spruce with fir or black spruce with white spruce, F-B: Fir-black spruce, F: Fir, JP-B: Jack pine with spruce, JP: Jack pine, M: Mixed forests, i.e. both deciduous and coniferous, S-PB: Paper birch with fir or white spruce (coniferous dominance), PB-S: Paper birch with fir or white spruce (deciduous dominance), PB: Paper birch, A: Aspen, D: Deciduous species, N: Non-forested (no trees or trees too young/sparse).

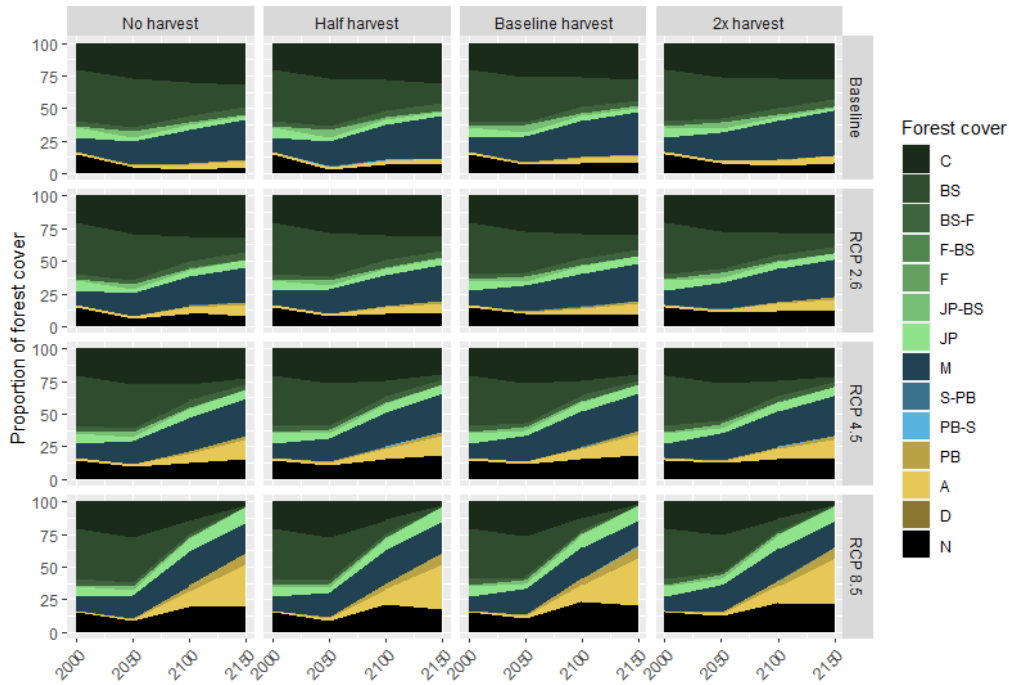


Figure S2.9 Changes in the proportion of forest cover on the Nemaska territory under different climate and forest harvesting scenarios. C: Coniferous species, BS: Black spruce, BS-F: Black spruce with fir or black spruce with white spruce, F-B: Fir-black spruce, F: Fir, JP-B: Jack pine with spruce, JP: Jack pine, M: Mixed forests, i.e. both deciduous and coniferous, S-PB: Paper birch with fir or white spruce (coniferous dominance), PB-S: Paper birch with fir or white spruce (deciduous dominance), PB: Paper birch, A: Aspen, D: Deciduous species, N: Non-forested (no trees or trees too young/sparse).

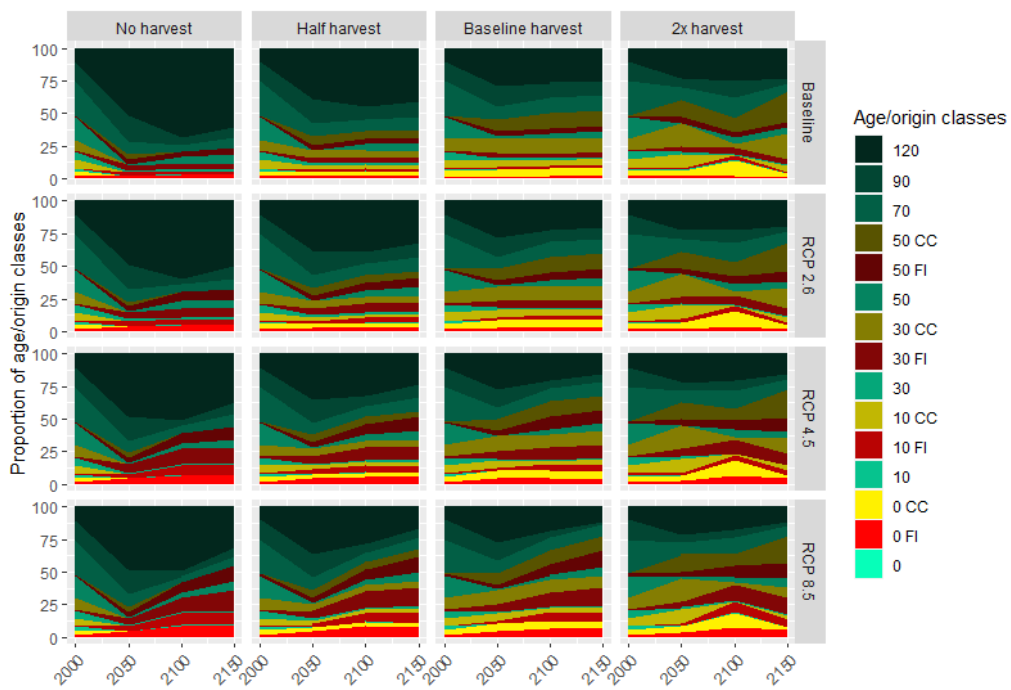


Figure S2.10 Evolution of the proportion of the different age-origin classes on the Abitibiwinni territory according to the different climate and forest harvesting scenarios. FI: Fire origin, CC: Clearcut origin.

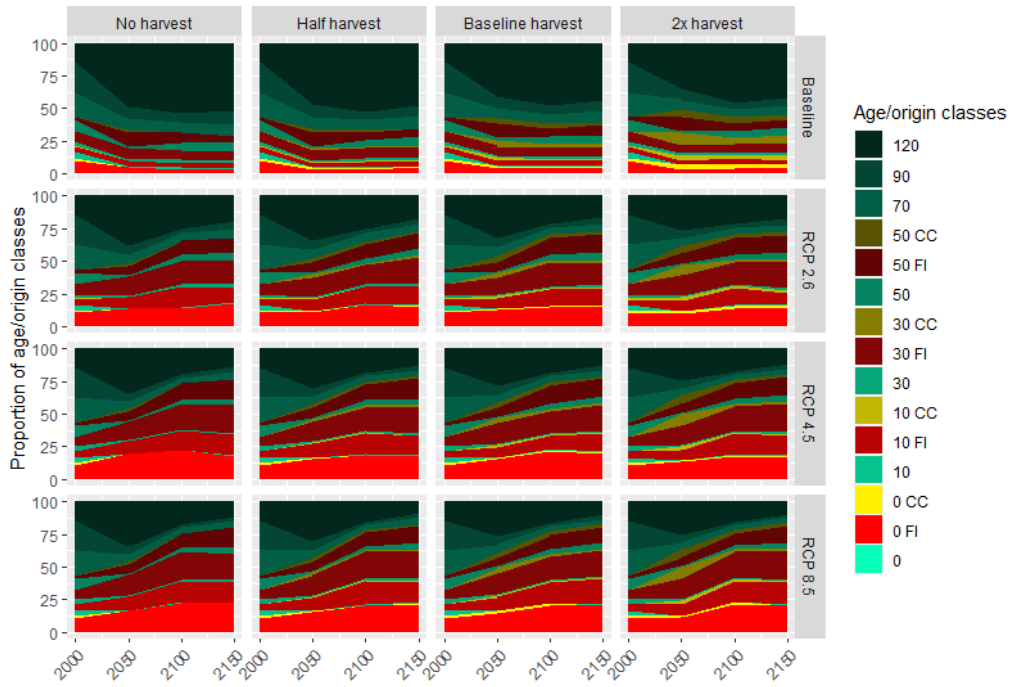


Figure S2.11 Evolution of the proportion of the different age-origin classes on the Mistissini territory according to the different climate and forest harvesting scenarios. FI: Fire origin, CC: Clearcut origin.

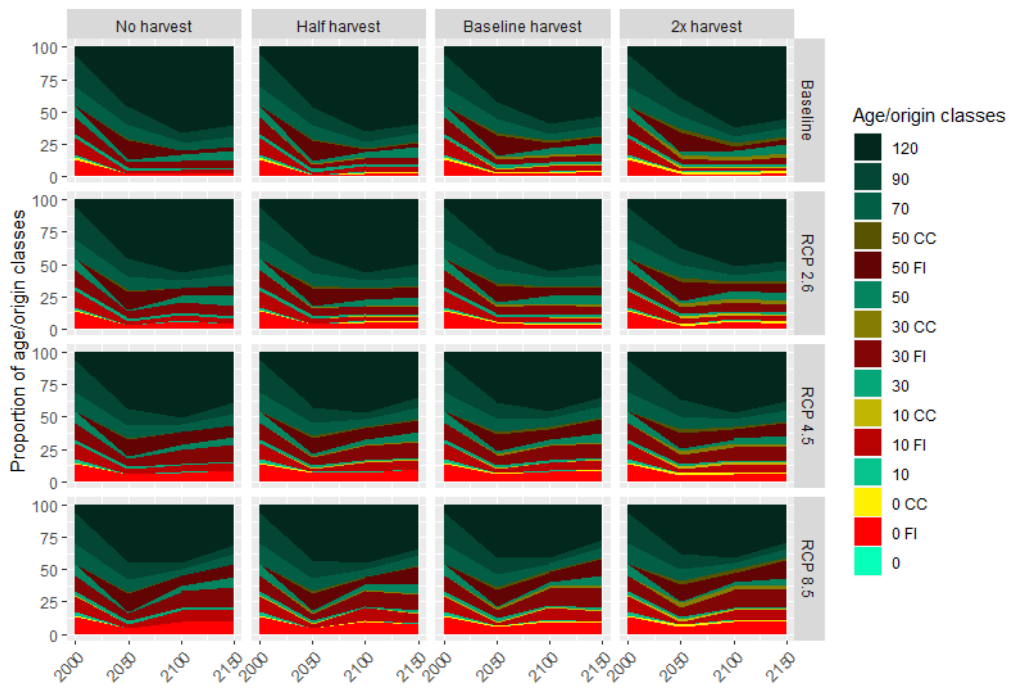


Figure S2.12 Evolution of the proportion of the different age-origin classes on the Nemaska territory according to the different climate and forest harvesting scenarios. FI: Fire origin, CC: Clearcut origin.

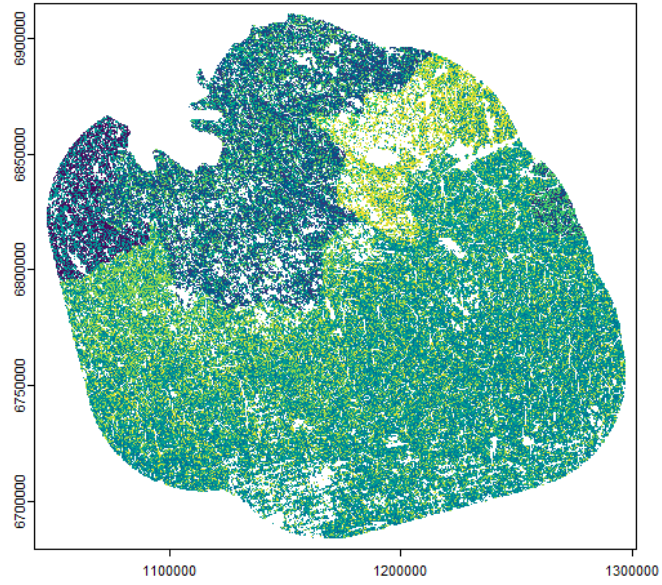


Figure S2.13 Map of ecoregions in the Abitibiwinni territory. Different colors represent different ecoregions.

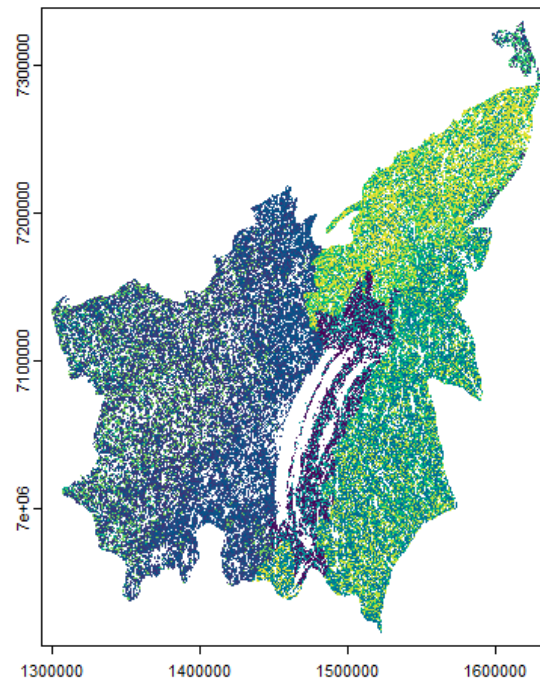


Figure S2.14 Map of ecoregions in the Mistissini territory. Different colors represent different ecoregions.

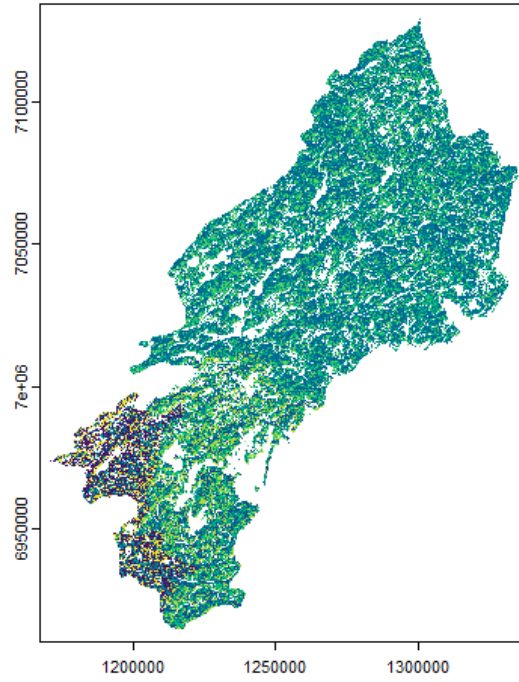


Figure S2.15 Map of ecoregions in the Nemaska territory. Different colors represent different ecoregions.

Table S2.3 LANDIS-II parameters for tree species simulated within the study area.

Species	Longevity	Age at maturity	Shade tolerance†	Effective seed dispersal (m)‡	Maximum seed dispersal (m)	Vegetative regeneration	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter	Thermal preference*	Successional stage**
<i>Abies balsamea</i>	150	30	5	250	250	No	Seeding	0	25	boreal	M/L- succ.
<i>Acer rubrum</i>	150	10	3	250	250	Yes	Resprout	0	25	Therm.	Pioneer
<i>Acer saccharum</i>	300	40	5	250	250	Yes	Resprout	1	15	Therm.	M/L- succ.
<i>Betula alleghaniensis</i>	300	40	3	250	400	Yes	Resprout	1	15	Therm.	M/L- succ.
<i>Betula papyrifera</i>	150	20	2	250	5000	Yes	Resprout	0	25	boreal	Pioneer
<i>Fagus grandifolia</i>	250	40	5	250	3000	Yes	Seeding	1	15	Therm.	M/L- succ.
<i>Larix laricina</i>	150	40	1	250	250	No	Seeding	0	25	boreal	Pioneer
<i>Picea glauca</i>	200	30	3	250	303	No	Seeding	1	15	boreal	M/L- succ.
<i>Picea mariana</i>	200	30	4	250	250	No	Serotiny	1	15	boreal	M/L- succ.
<i>Picea rubens</i>	300	30	4	250	303	No	Seeding	1	15	boreal	M/L- succ.

Table S2.3 (continued)

Species	Longevity	Age at maturity	Shade tolerance†	Effective seed dispersal (m)‡	Maximum seed dispersal (m)	Vegetative regeneration	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter	Thermal preference*	Successional stage**
<i>Pinus banksiana</i>	150	20	1	250	250	No	Serotiny	0	25	boreal	Pioneer
<i>Pinus resinosa</i>	200	40	2	250	275	No	Seeding	1	15	boreal	Pioneer
<i>Pinus strobus</i>	300	20	3	250	250	No	Seeding	1	15	Therm.	M/L- succ.
<i>Populus tremuloides</i>	150	20	1	1000	5000	Yes	Resprout	0	25	boreal	Pioneer
<i>Quercus rubra</i>	250	30	3	250	3000	Yes	Resprout	1	15	Therm.	M/L- succ.
<i>Thuja occidentalis</i>	300	30	5	250	250	No	Seeding	1	15	boreal	M/L- succ.
<i>Tsuga canadensis</i>	300	60	5	250	250	No	Seeding	1	15	Therm.	M/L- succ.

* Thermophilous (Therm.): $\text{minGDD} \geq 500$ AND $\text{maxGDD} \geq 4000$ (see table S2.4). All other species were considered boreal

** Pioneer: $\text{Shade tolerance} \leq 2$ and $\text{Longevity} \leq 200$ years. All other species were considered mid- to late-successional(M/L – succ.)

† Index of the ability of species to establish under varying light levels where 1 is the least shade tolerant and 5 is the most shade tolerant.

‡ Distance within which 95 % of seeds disperse. If reported seed dispersal distance in the literature was shorter than pixel resolution (250m), we nevertheless allow this species to seed to the adjacent pixel. As a consequence, minimum seed distance is set to 250m for all species.

Table S2.4 Species input parameters in PICUS.

Species	Soil nitrogen*	Minimum soil pH†	Maximum soil pH†	Minimum GDD (Base temp 5°C) ‡	Maximum GDD (Base temp 5°C) ‡	Maximum SMI§	Optimum SMI§
<i>Abies balsamea</i>	2	2	9	150	2723	0.3	0
<i>Acer rubrum</i>	2	2	9.5	500	6608	0.5	0.05
<i>Acer saccharum</i>	2	1.7	9.9	450	5093	0.3	0
<i>Betula alleghaniensis</i>	2	2	10	500	4517	0.5	0.05
<i>Betula papyrifera</i>	2	2.2	9.4	150	3081	0.5	0.05
<i>Fagus grandifolia</i>	2	2.1	9	500	5602	0.7	0.1
<i>Larix laricina</i>	1	3	9.6	150	2548	0.3	0
<i>Picea glauca</i>	3	2	10.2	150	2495	0.5	0.05
<i>Picea mariana</i>	2	2	8.5	150	2495	0.3	0
<i>Picea rubens</i>	2	2	7.8	450	3239	0.3	0
<i>Pinus banksiana</i>	1	2.5	10.2	300	3188	0.7	0.1
<i>Pinus resinosa</i>	1	2.5	8	500	3300	0.7	0.1

Table S2.4 (continued)

Species	Soil nitrogen*	Minimum soil pH†	Maximum soil pH†	Minimum GDD (Base temp 5°C) ‡	Maximum GDD (Base temp 5°C) ‡	Maximum SMI§	Optimum SMI§
<i>Pinus strobus</i>	2	2	9.3	500	4261	0.7	0.1
<i>Populus tremuloides</i>	1	2.3	9.3	500	5171	0.3	0
<i>Quercus rubra</i>	2	2.3	11	150	3024	0.5	0.05
<i>Thuja occidentalis</i>	2	3	10	500	3383	0.7	0.1
<i>Tsuga canadensis</i>	2	2.2	9	500	4660	0.5	0.05

* Nitrogen response curves: Three classes (1-3) with 1 being very tolerant

† USDA plant fact sheets (USDA 2016) and the Ontario Silvics Manual (Ontario Ministry of Natural Resources 2000) were used to derive the widest optimum pH range possible.

‡ Growing Degree Days (GDD). We used McKenney et al. (2011) growing season model, specifically the minimum GDD for the 0°C and growing season window with degree days over 5°C. For the maximum GDD, we used GDD Maximum from McKenney's previous growing season model (McKenney et al. 2007).

§ Soil Moisture Index (SMI). Determines each species tolerance to drought (Lexer and Hönninger 2001). HighTolerance (0.1 to 0.7), MedTolerance (0.05 to 0.5), LowTolerance (0 to 0.3).

APPENDICE B

MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE III

Table S3.1 Characteristics of the sampling sites. Stand age, dominant species and stand density are not given for Nemaska as this information was not available in northern inventories. When a characteristic was not available for a site, the value of adjacent forest units is given in italics instead. See Table S3.2 for signification of the abbreviations.

Site	Ecological type	Surficial deposit type	Surface drainage	Stand age (years)	Dominant species	Stand density
AbiCA	RE39	7E	Hydric	<i>120</i>	<i>ENEN</i>	<i>C</i>
AbiCB	RE39	7E	Hydric	<i>120</i>	<i>ENEN</i>	<i>C</i>
AbiHA	RE26	4GA	Mesic-Hydric	<i>30</i>	<i>ENSB</i>	<i>B</i>
AbiHB	RE21	2BE	Mesic	<i>30</i>	<i>PGPGPT</i>	<i>B</i>
AbiMA	RE39	7E	Hydric	<i>30</i>	<i>ENEN</i>	<i>C</i>
AbiMB	RE39	7T	Sub-hydric	90	ENEN	B
MisCA	RE37	2BE	Sub-hydric	<i>120</i>	<i>ENEN</i>	<i>D</i>
MisCB	RE39	7E	Hydric	120	ENEN	D
MisHA	RE39	7E	Hydric	<i>VIR</i>	<i>ENML</i>	<i>B</i>
MisHB	RE21	2BE	Mesic	<i>120</i>	<i>ENEN</i>	<i>C</i>
MisMA	RE39	7T	Sub-hydric	120	ENEN	C
MisMB	RS22	1A	Mesic	30	ENENPT	C
NemCA	RE39	7	Hydric			
NemCB	RE39	7	Hydric			
NemHA	RE22	1A	Mesic			
NemHB	RE22	1A	Mesic			
NemMA	RE22	1A	Mesic			
NemMB	RE22	1A	Mesic			

Table S3.2 Definition of the codes used in Table S3.1.

Ecological type	RE21: Black spruce-moss or black spruce-ericaceous stand on thin to thick mineral deposits, coarse texture, xeric or mesic drainage
	RE22: Black spruce-moss or black spruce-ericaceous stand on thin to thick mineral deposits, medium texture, mesic drainage
	RE26: Black spruce-moss or black spruce-ericaceous stand on thin to thick mineral deposits, fine texture, sub-hydric drainage
	RE37: Black spruce stand with sphagnum moss on thin to thick mineral deposits, hydric drainage, ombrotrophic
	RE39: Black spruce stand with sphagnum mosses on thin to thick organic deposits, hydric drainage, ombrotrophic
	RS22: Black spruce – fir stand on thin to thick mineral deposits, medium texture, mesic drainage
Surface deposit	1A: Glacial, no particular morphology, undifferentiated till
	2BE: Fluvio-glacial, pro-glacial, outwash
	4GA: Lacustrine, glacio-lacustrine
	7: Organic
	7E: Thick organic
Dominant species	7T: Thin organic
	ENEN: Black spruce
	ENENPT: Black spruce with trembling aspen
	ENML: Black spruce with tamarack
	ENSB: Black spruce with balsam fir
Stand density	PGPGPT: Jack pine with trembling aspen
	B: Between 60% and 80%
	C: Between 40% and 60%
	D: Between 25% and 40%

Table S3.3 Climate normals for each sampling site, extracted from BioSIM 11. MeanTmin: Annual mean of daily minimum temperature (°C); MeanTair: Annual mean of daily mean temperature (°C); MeanTmax: Annual mean of daily maximum temperature (°C); TotalPrp: Annual total precipitation (mm); TotalRadiation: Annual total radiation in MJ/m², computed by MTCLIM (estimation based on diurnal temperature range, latitude, elevation, slope, and aspect of the site).

Site	Latitude	Longitude	Elevation	Mean Tmin	Mean Tair	Mean Tmax	Total Prcp	Total Radiation
AbiHA	49.415	-79.241	304	-5	1	7	888.6	4611.6
AbiHB	49.389	-79.242	315	-5	1	7	884.9	4605.1
AbiMA	49.56	-79.277	284	-5.2	0.8	6.8	891.3	4610
AbiMB	49.558	-79.292	278	-5.2	0.8	6.8	892	4610.2
AbiTA	49.539	-79.32	272	-5.2	0.8	6.8	892.8	4610.7
AbiTB	49.428	-79.277	298	-5.1	0.9	6.9	888.9	4611.3
MisHA	50.34	-74.354	415	-5.1	0.4	5.9	967.2	4613.2
MisHB	50.23	-74.324	387	-4.8	0.6	6	971.6	4600.7
MisMA	50.24	-73.808	379	-4.8	0.6	6.1	967.4	4585.8
MisMB	50.241	-73.81	380	-4.9	0.6	6.1	967.4	4586.6
MisTA	50.247	-74.327	407	-5	0.5	6	969.1	4606.5
MisTB	50.257	-73.771	400	-5	0.5	6	963.7	4595.1
NemHA	51.69	-75.718	289	-5.5	-0.2	5.2	878.6	4470.4
NemHB	51.612	-76.526	243	-5.8	-0.3	5.2	856.5	4471
NemMA	51.685	-75.859	292	-5.6	-0.3	5	872.5	4481.6
NemMB	51.687	-75.848	294	-5.7	-0.3	5	872	4481.4
NemTA	51.592	-76.62	266	-5.9	-0.3	5.2	851.4	4490.8
NemTB	51.798	-76.01	279	-5.5	-0.2	5	837.4	4428.8

Table S3.4 Flavonoids identified in the sample of each combination of territory/disturbance type. Concentrations are means (\pm standard deviation).

		Concentrations		
		Abitibiwinni	Mistissini	Nemaska
Catechin	Control	12.59 (3.01)	12.20 (3.17)	14.86 (2.37)
	Hydro	15.25 (2.58)	14.41 (3.06)	15.95 (1.66)
	Mine	12.44 (1.72)	10.82 (2.47)	14.51 (2.23)
Proanthocyanidin A1	Control	10.87 (1.65)	13.13 (1.35)	14.16 (1.14)
	Hydro	11.02 (0.53)	13.87 (1.26)	13.17 (1.16)
	Mine	11.21 (1.24)	11.57 (0.87)	12.76 (0.86)
Epicatechin	Control	7.75 (2.12)	8.36 (2.56)	11.17 (2.31)
	Hydro	7.05 (1.00)	8.45 (1.08)	12.03 (1.03)
	Mine	7.66 (1.63)	5.19 (1.51)	9.66 (1.83)
Proanthocyanidin A2	Control	4.95 (1.88)	5.05 (1.44)	5.47 (0.99)
	Hydro	4.25 (0.89)	4.76 (0.65)	6.38 (0.80)
	Mine	5.12 (1.28)	3.74 (0.99)	5.95 (1.33)
Quercetin-3-galactoside	Control	3.85 (0.41)	5.38 (0.74)	4.75 (0.65)
	Hydro	4.97 (0.68)	4.90 (0.27)	4.56 (0.35)
	Mine	3.77 (0.58)	3.67 (1.19)	5.04 (0.34)
Quercetin-3-pentoside (3)	Control	2.22(0.21)	2.81 (0.36)	2.62 (0.32)
	Hydro	2.24 (0.17)	2.82 (0.20)	2.72 (0.14)
	Mine	2.12 (0.34)	2.09 (0.55)	2.74 (0.12)
Myricetin-hexoside (1)	Control	0.68 (0.23)	0.84 (0.50)	2.33 (0.42)
	Hydro	1.45 (0.34)	2.64 (0.78)	3.19 (0.65)
	Mine	1.18 (0.40)	0.23 (0.27)	2.37 (0.47)
Quercetin-3-glucoside	Control	0.91 (0.08)	1.23 (0.19)	1.15 (0.22)
	Hydro	1.06 (0.13)	1.10 (0.12)	1.05 (0.13)
	Mine	0.86 (0.12)	0.72 (0.19)	1.09 (0.12)
Quercetin-3-pentoside (2)	Control	0.66 (0.08)	0.93 (0.14)	0.75 (0.09)
	Hydro	0.83 (0.09)	0.81 (0.04)	0.78 (0.07)
	Mine	0.69 (0.09)	0.68 (0.17)	0.80 (0.04)
Quercetin-3-pentoside (1)	Control	0.64 (0.12)	0.86 (0.15)	0.71 (0.12)
	Hydro	0.70 (0.06)	0.71 (0.08)	0.70 (0.11)
	Mine	0.71 (0.11)	0.55 (0.13)	0.71 (0.13)
Quercetin-3-rhamnoside	Control	0.76 (0.32)	0.57 (0.20)	0.16 (0.06)
	Hydro	0.51 (0.20)	0.20 (0.04)	0.15 (0.05)
	Mine	0.52 (0.25)	1.66 (0.65)	0.16 (0.05)
Myricetin-pentoside (3)	Control	0.14 (0.21)	0.17 (0.36)	0.34 (0.32)
	Hydro	0.20 (0.17)	0.40 (0.20)	0.46 (0.14)
	Mine	0.19 (0.34)	0.06 (0.55)	0.34 (0.12)
Myricetin-pentoside (2)	Control	0.12 (0.08)	0.14 (0.14)	0.30 (0.09)
	Hydro	0.21 (0.09)	0.36 (0.04)	0.43 (0.07)
	Mine	0.20 (0.09)	0.06 (0.17)	0.32 (0.04)

Table S3.4 (continued)

		Concentrations		
		Abitibiwinni	Abitibiwinni	Abitibiwinni
Myricetin-hexoside (2)	Control	0.11 (0.04)	0.13 (0.07)	0.34 (0.06)
	Hydro	0.20 (0.05)	0.36 (0.14)	0.45 (0.10)
	Mine	0.18 (0.06)	0.04 (0.04)	0.31 (0.09)
Myricetin-pentoside (1)	Control	0.11 (0.04)	0.13 (0.07)	0.26 (0.05)
	Hydro	0.17 (0.04)	0.28 (0.07)	0.36 (0.07)
	Mine	0.18 (0.06)	0.05 (0.03)	0.26 (0.08)
Quercetin	Control	0.09 (0.03)	0.09 (0.02)	0.13 (0.02)
	Hydro	0.18 (0.05)	0.10 (0.03)	0.14 (0.03)
	Mine	0.12 (0.04)	0.08 (0.02)	0.13 (0.03)

APPENDICE C

MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE IV

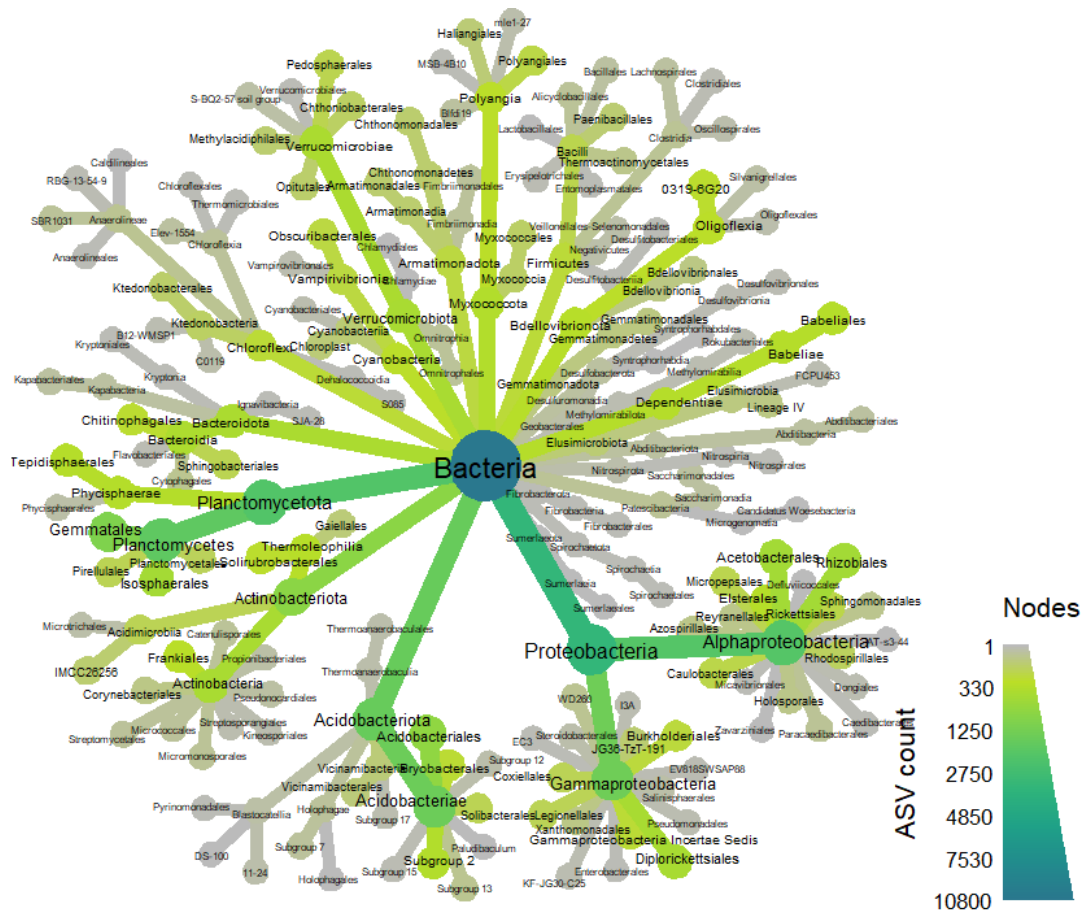


Figure S4.1 Phylogenetic heat tree of the bacterial diversity and abundance across all soil samples. ASVs below the order are not shown to declutter the figure. Point size and color represent the relative abundance of each taxon.

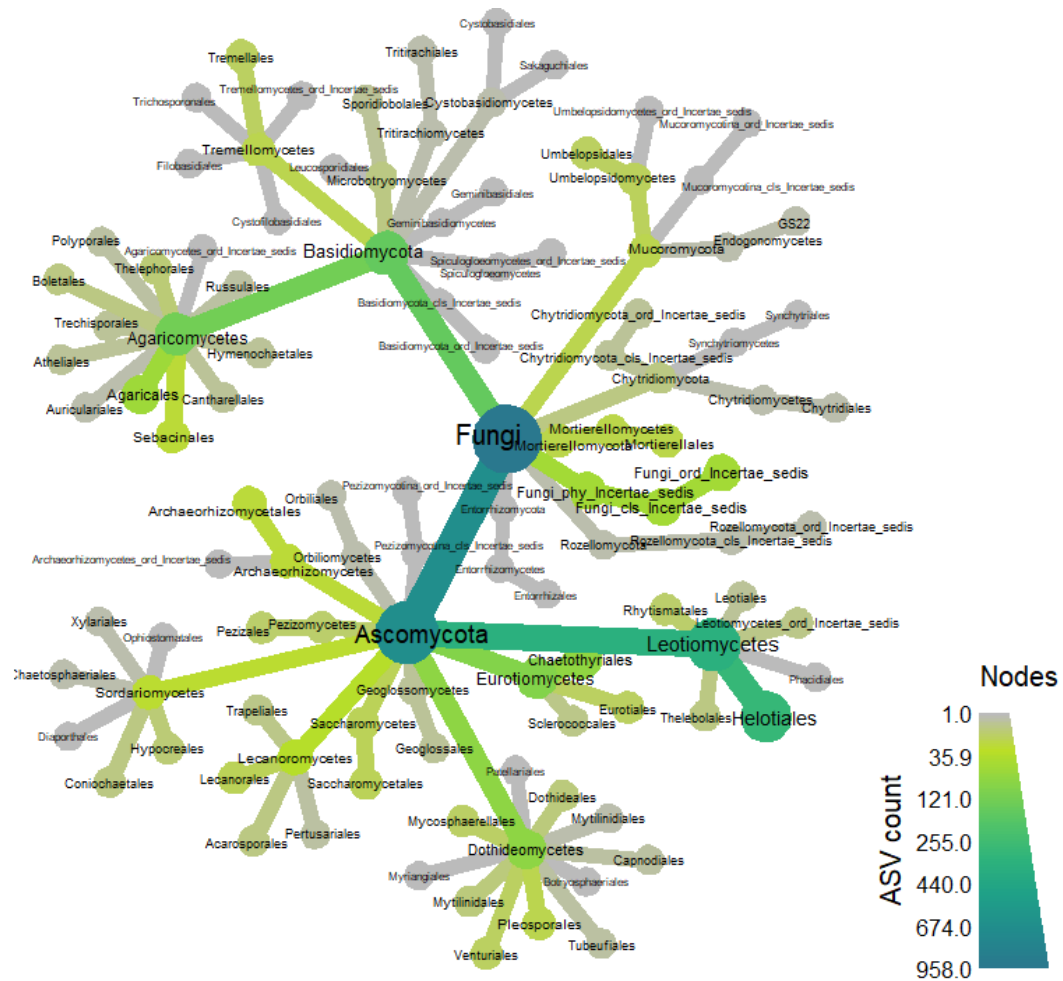


Figure S4.2 Phylogenetic heat tree of the fungal diversity and abundance across all soil samples. ASVs below the order are not shown to declutter the figure. Point size and color represent the relative abundance of each taxon.

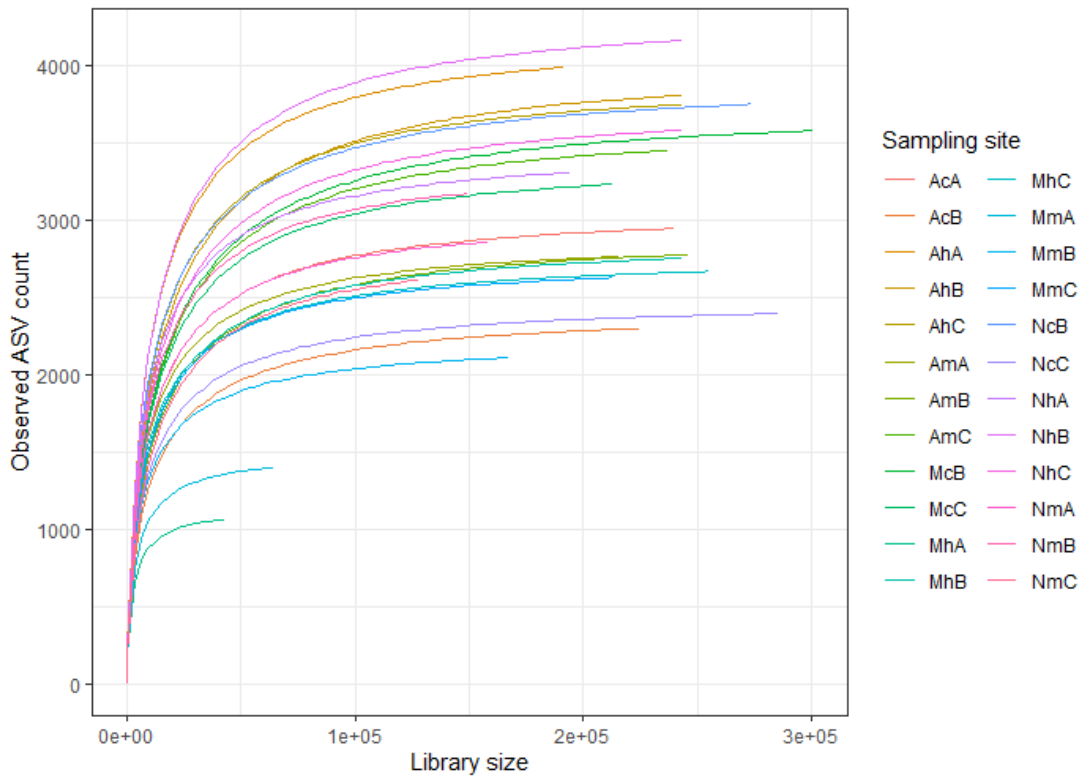


Figure S4.3 Rarefaction curves of the observed bacterial ASVs count as a function of library size for each soil samples. Different soil samples are shown in different colors.

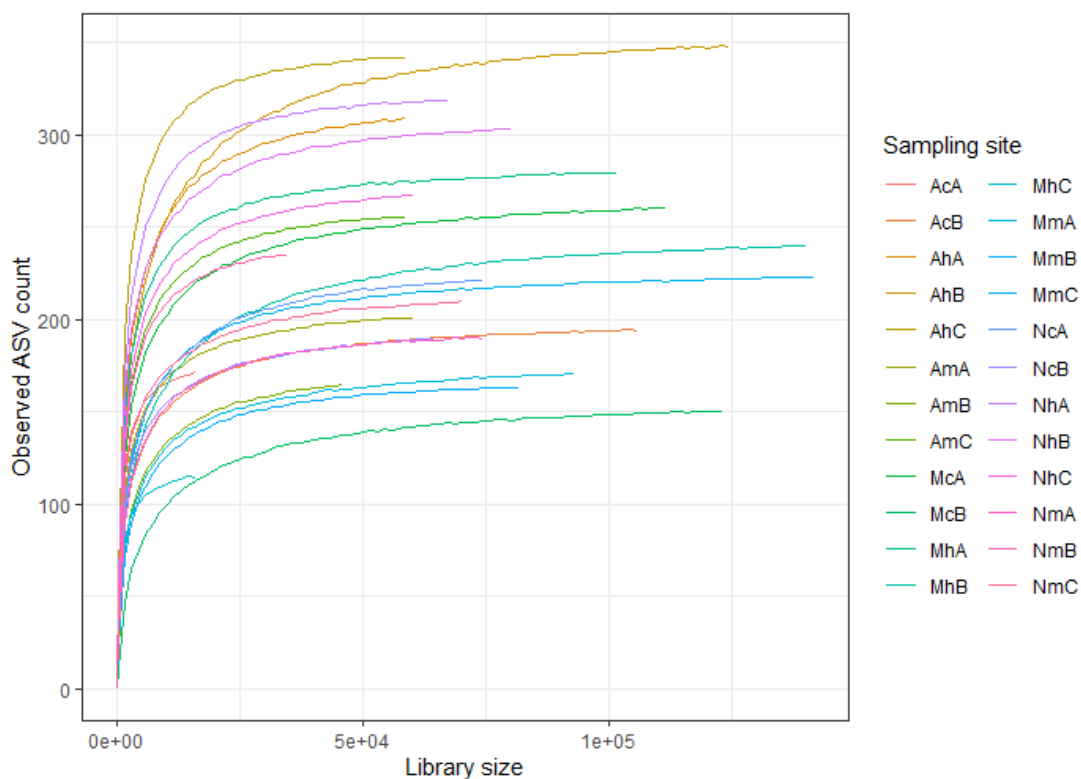


Figure S4.4 Rarefaction curves of the observed fungal ASVs count as a function of library size for each soil samples. Different soil samples are shown in different colors.

Table S4.1 PERMANOVA of the variation in the phenolic profile of the samples as a function of disturbance type, territory, and their interaction.

	Df	Sum of Squares	R ²	F	Pr(>F)
Disturbance	2	0.1056	0.0371	2.0220	0.7228
Territory	2	0.2509	0.0881	4.8068	0.0573
Disturbance:Territory	4	0.2208	0.0775	2.1152	0.7737
Residual	87	2.2708	0.7973		
Total	95	2.8481	1		

Table S4.2 Redundancy analysis (RDA) of the effect of bacteria phyla abundance on the concentration in (poly)phenolics in *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values, and significant (< 0.05) adjusted *P*-values are shown in bold. Model adjusted $R^2 = 0.57$. For the sake of brevity, only the first 4 of the 18 axes are presented in the table.

		Df	Variance	F	Pr(>F)
Global	Model	18	111618	2.6857	0.0102
	Residual	5	11544		
Axes	RDA1	1	60319	26.1244	0.2124
	RDA2	1	27533	11.9249	1
	RDA3	1	10602	4.5917	1
	RDA4	1	6061	2.6251	1
	RDA5	1	2944	1.2750	1
Terms	Proteobacteria	1	7414	3.2109	0.1144
	Acidobacteriota	1	10824	4.6882	0.0729
	Actinobacteriota	1	3469	1.5024	0.2985
	Planctomycetota	1	1778	0.7700	0.5598
	RCP2-54	1	7744	3.3539	0.1144
	WPS-2	1	6843	2.9636	0.1348
	Bacteroidota	1	7796	3.3763	0.1144
	Chloroflexi	1	10610	4.5952	0.0729
	Cyanobacteria	1	5548	2.4028	0.1753
	Verrucomicrobiota	1	777	0.3366	0.8382
	Armatimonadota	1	3516	1.5229	0.2985
	Myxococcota	1	11526	4.9919	0.0729
	Firmicutes	1	12691	5.4967	0.0729
	Bdellovibrionota	1	5204	2.2537	0.1807
	Desulfobacterota	1	2490	1.0783	0.4247
	Gemmatimonadota	1	2803	1.2141	0.3791
	Dependentiae	1	4395	1.9033	0.2372
Elusimicrobiota	1	6192	2.6817	0.1532	

Table S4.3 Redundancy analysis (RDA) of the effect of classes from Proteobacteria abundance on the concentration in (poly)phenolics in *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values. Model adjusted $R^2 = 0.02$.

		Df	Variance	F	Pr(>F)
Global	Model	2	12726	1.2100	0.2954
	Residual	21	110436		
Axes	RDA1	1	8825	1.6781	0.5343
	RDA2	1	3901	0.7419	0.5343
Terms	Alphaproteobacteria	1	8629	1.6408	0.3374
	Gammaproteobacteria	1	4098	0.7792	0.5062

Table S4.4 Redundancy analysis (RDA) of the effect of fungi phyla abundance on the concentration in (poly)phenolics in *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values. Model adjusted $R^2 = 0.12$.

		Df	Variance	F	Pr(>F)
Global	Model	5	38258	1.6222	0.1000
	Residual	18	84904		
Axes	RDA1	1	26292	5.5740	0.4955
	RDA2	1	6626	1.4048	0.9990
	RDA3	1	3669	0.7779	0.9990
	RDA4	1	1428	0.3027	0.9990
	RDA5	1	243	0.0514	0.9990
Terms	Ascomycota	1	5545	1.1756	1
	Basidiomycota	1	1502	0.3185	1
	Mucoromycota	1	10683	2.2648	0.3768
	Chytridiomycota	1	18105	3.8383	0.0835
	Mortierellomycota	1	2423	0.5137	1

Table S4.5 Redundancy analysis (RDA) of the effect of classes from Ascomycota abundance on the concentration in (poly)phenolics in *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *p*-values. Model adjusted $R^2 = 0.20$. For the sake of brevity, only the first 4 of the 9 axes are presented in the table.

		Df	Variance	F	Pr(>F)
Global	Model	9	63340	1.6470	0.0745
	Residual	14	59822		
Axes	RDA1	1	36001	8.4253	0.9963
	RDA2	1	18955	4.4361	1
	RDA3	1	3282	0.7682	1
	RDA4	1	3001	0.7023	1
Terms	Leotiomyces	1	2749	0.6434	1
	Eurotiomyces	1	1572	0.3679	1
	Dothideomyces	1	8810	2.0619	0.7278
	Geoglossomyces	1	14930	3.4941	0.2322
	Saccharomyces	1	3084	0.7218	1
	Lecanoromyces	1	11073	2.5913	0.5138
	Pezizomyces	1	1164	0.2724	1
	Archaeorhizomyces	1	6018	1.4085	1
Sordariomyces	1	13939	3.2621	0.2680	

Table S4.6 Redundancy analysis (RDA) of the effect of classes from Basidiomycota abundance on the concentration in (poly)phenolics in *V. angustifolium* fruits. Statistical significance was evaluated through a permutation test with 9999 permutations. A Benjamini-Hochberg correction was applied to *P*-values. Model adjusted $R^2 = 0.04$.

		Df	Variance	F	Pr(>F)
Global	Model	2	15461	1.5073	0.1835
	Residual	21	107701		
Axes	RDA1	1	11144	2.1728	0.4483
	RDA2	1	4317	0.4483	0.4483
Terms	Agaricomycetes	1	5728	1.1169	0.3517
	Tremellomyces	1	9733	1.8977	0.2476

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