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Tree assisted migration in a browsed landscape: Can we predict susceptibility to herbivores?

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A R T I C L E I N F O

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A B S T R A C T

To promote the sustainability of forest ecosystems and maintain ecosystem services to human populations in the context of climate change, forest managers are considering several adaptation tools. One of those, assisted migration, consists of displacing tree species and/or populations to locations with suitable future climate conditions. Assisted migration plantations, however, could fail to produce viable forests under high herbivory pressure from mammalian herbivores. Thus, selecting species and genotypes with low susceptibility to herbivores could be a key condition for the recruitment of translocated seedlings. We developed an approach to predict susceptibility to mammalian herbivores, based on the seedlings' chemical content (a proxy of phytochemical defence and susceptibility to herbivores). We used the approach on eight North American tree species of three climate analogues regions each (i.e. locations where the current climate is similar to the future climate at plantation site). We built chemical profiles and ranked species and climate analogue based on their potential susceptibility. To assess the reliability of our approach, we compared the chemical profiles to a systematic review of these species' chemistry and of mammalian browsing throughout their native geographic range. For most species, our chemical profiles and browse susceptibility rankings were congruent with information available in the literature, both for phytochemical defence and for browsing. Two of the eight species (*Pinus strobus* and *Thuja occidentalis*) were more susceptible than predicted based on their chemical profile. These discrepancies could be linked to specific mammalian herbivores, that were unaffected by the phytochemical defence of these species. We observed a generally higher susceptibility of broadleaf species, which could be taken into account when devising adaptive silvicultural strategies. Furthermore, we propose the chemical profiling approach as a preliminary screening tool to identify species more resistant to mammalian herbivores, but also potentially to other herbivores and pathogens. Our chemical profile approach, based on the objective assessment of multivariate analyses results, could be replicated to compare the potential susceptibility of other species. This approach could be especially useful when contending with novel plant-herbivore relationships, such as forestry and conservation assisted migration or species invasion.

1. Introduction

To sustain forest ecosystems in a changing climate, managers are considering a range of adaptive silvicultural strategies and tools. One of the tools generating substantial interest is assisted migration, which consists of displacing tree species and/or populations to locations with suitable future climate conditions. Planting options for assisted migration range from single-species enrichment planting under partial forest cover, to multi-species plantations in open conditions. Such forestry assisted migration (*sensu* Pedlar et al., 2012) could increase forest resilience to disturbance (e.g drought, insect outbreaks) and maintain ecosystem services and productivity (Aubin et al., 2011; Ste-Marie et al., 2011; Winder et al., 2011). Scientists and land managers are increasingly recognizing the role assisted migration could play in adaptation scenarios of forest ecosystems (Johnston et al., 2009; Lal et al., 2012; Government of Canada, 2019). Moreover, this approach is being tested

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in the United States, in Canada, and in Europe (Pedlar et al., 2011; Williams and Dumroese, 2013; BenitoGarzón and Fernández-Manjarrés, 2015; Nagel et al., 2017). The success of assisted migration, however, is dependent on seedlings growth and survival, which could be hindered by several abiotic and biotic factors (Winder et al., 2011; Fisichelli et al., 2013).

Tree seedlings are especially sensitive to browsing by mammalian herbivores, mostly cervids (i.e. deer species, including moose) and leporids (i.e. hares and rabbits). Deer are recognized as a potential threat to forest regeneration, particularly in areas where their populations are high or are increasing (Reimoser, 2003; Côté et al., 2004; Petersson et al., 2019). Mammalian herbivores can reduce growth and survival of seedlings and saplings found within the height stratum accessible to them (Eiberle and Nigg, 1987; Gill et al., 2006). Moose (*Alces alces* L.), for example, can browse shoots up to 2–3 m aboveground, while white-tailed deer (*Odocoileus virginianus* Zimmermann) will browse up to 1.8–2.25 m aboveground, depending on the region's maximal snow cover (Potvin, 1995; Frerker et al., 2013). Above that site-specific height, trees can escape most browsing impacts (Hester et al., 2006). The cumulative effect of browsing on tree recruitment can reduce species growth rates and survival, thereby exerting lasting changes to forest composition (Gill et al., 2006; Hidding et al., 2013; Nuttle et al., 2014). The magnitude of these effects could be amplified in assisted migration context because these plantations will, by design, introduce species or genotypes to new areas. If introduced populations originate from areas with low herbivory pressure, they may be poorly adapted to high herbivory pressure or to the herbivore community at the plantation site (Levine et al., 2004). Additionally, generalist herbivores might take advantage of new, palatable species or populations and the concentrated resources available in plantations (Averill et al., 2016). Planted seedlings could be especially attractive to mammalian herbivores, because fertilization during nursery cultivation likely increases their nutritional value (McArthur et al., 2003; Reimoser, 2003; Close et al., 2004). In this context, the success of assisted migration plantations in high-browsing pressure systems is uncertain and potentially at risk.

Considering that assisted migration is a high-investment adaptation tool, land managers with browsing issues might consider planting species and genotypes with low susceptibility to herbivores. It is difficult, however, to predict the outcome of introducing a new forage resource, especially as forage selection is known to vary among herbivore species and across populations within a species (Bergvall, 2009; Averill et al., 2016). Ideally, site-specific studies would provide information on forage selection by the local herbivore community, and on the effect of introducing a new species or genotype. Alternatively, given that foraging choices are partly driven by plant nutritional value (Swift, 1948; Pyke et al., 1977), it is possible we could predict the susceptibility and resistance of plants by assessing their nutritive and non-nutritive phytochemical composition (Champagne et al., 2020c). Chemical content varies both among plant species and within plant species, which provides a basis for choice (Moore et al., 2014). Moreover, the presence and concentration in chemical defence compounds are partially controlled by genetic variation, and high herbivory pressure can generate local adaptations (Moore et al., 2014). Local adaptations opens the way to the selection and breeding of resistant genotypes. The use of resistant species and genotypes is not a new idea, and has been applied for invertebrate herbivory, but can also be applied to resistance against mammalian herbivores (Wink, 1988; Henery, 2011; Miller et al., 2011).

In this study, we developed and assessed an approach to predict the susceptibility of seedlings to mammalian herbivores, based on the hypothesis that plant chemical composition provides an objective and reliable indicator of susceptibility to browsing. We built a chemical profile for eight tree species, each from three different climate analogue regions, using analyses of nutritive and of non-nutritive phytochemicals. A climate analogue is a location where the current climate is similar to the anticipated climate of another location, such as the site of an assisted migration plantation. We then used these profiles to rank species and climate analogues on a browse susceptibility-resistance continuum, based on known relationships between susceptibility and chemical content (Champagne et al., 2020c). We then examined the accuracy of our predictions in two ways. First, we compared the actual chemical profiles to chemical information available in the literature for those species. Second, we compared the predicted susceptibility to browsing reported in the literature for each species throughout their native geographic range. With this predictive approach, we hope to provide a tool for managers who are considering assisted migration, but that also have to contend with abundant herbivore populations.

2. Material and methods

2.1. Context and study system

This study is part of an assisted migration experiment, which will evaluate the survival and growth of seedlings potentially adapted to future climate conditions under a range of abiotic and biotic filters known to strongly influence tree species establishment. The experiment is located in Réserve faunique de Portneuf (Québec, Canada; Fig. 1). For the 1981–2010 period, the nearest weather station (Lac aux Sables) reports a mean daily temperature of 4 °C (SD = 1.3), with daily minimum in May of 4.3 °C, and mean annual precipitation and snowfall of 1133.2 mm and 230.3 cm respectively (Environment Canada, 2019). Both white-tailed deer and moose are present in the region (1.7 deer per km^2 in 2008, and 0.73 moose per km^2 in 2009; Huot and Lebel, 2012; Lefort and Massé, 2015), as well as snowshoe hares (*Lepus americanus* Erxleben).

The experimental plantation includes eight species (Table 1) selected because of their economic value, ecological functions, their variable resistance to abiotic and biotic stresses (e.g., shade tolerance), and their predicted abundance and range shifts under future climate scenarios. Six of the species are currently present in the region (*Acer saccharum* Marsh., *Picea glauca* (Moench) Voss, *Picea rubens* Sarg., *Pinus strobus* L., *Pinus resinosa* Aiton and *Thuja occidentalis* L.). Climate conditions could, however, become unfavourable for three of them (both *Picea* species and *T. occidentalis*), based on projections (Périé et al., 2014) while remaining favourable for *A. saccharum* and both *Pinus* species. The two other species (*Quercus rubra* and *Prunus serotina*) are currently absent, but climate projections suggest the study area should become favourable for them (Périé et al., 2014). For each species, seeds from three regions were used, to represent three climate zones (Fig. 1). The first region represents the current climate of the study area (hereafter current climate analogue). The other two regions present a climate analogous to the climate predicted for mid-century (2041–2070) and late century (2071–2100) for the study area (hereafter 2050 and 2080 analogues). Analogues were based on the method developed by Grenier et al. (2013) and using data from the 5th IPCC report, scaled for Québec (10 km × 10 km) for three climatic variables (mean annual precipitation, mean annual temperature and mean minimum temperature in May). All seedlings were grown from seeds (conifers sown in spring 2017, broadleaves in spring 2018) at the provincial nursery in Berthierville (Québec, Canada) and planted in 2018 at the experiment site.

2.2. Determination of potential susceptibility by chemical profiles

We developed an objective ranking of the potential susceptibility of seedlings to mammalian herbivores based on their chemical profile. We made two levels of rankings: 1) Among species, where we expected the largest differences in potential susceptibility to occur, and 2) Among climate analogues for each species.

2.2.1. Chemical analyses

To create the chemical profiles, we determined the concentration of one nutritive element (total nitrogen, hereafter nitrogen), and four non-nutritive phytochemicals : cellulose and lignin (acid detergent fibre

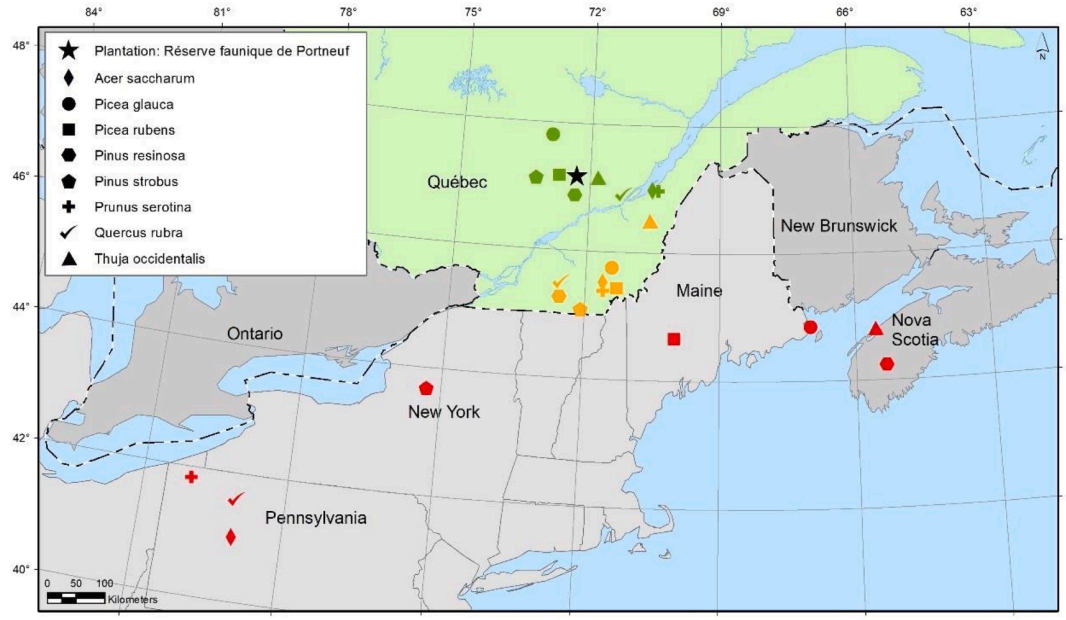

Fig. 1. Assisted migration study site (star) and approximate sites for the seed collection for the eight study species. Green points represent seed collected from a region with a climate similar (i.e. climate analogue) to the current climate at the plantation sites. Orange and red points present, respectively, a climate analogous to the climate predicted for mid-century (2041–2070) and late century (2071–2100) for the study area (hereafter 2050 and 2080 analogues). Analogues were based on the method developed by Grenier et al. (2013) and using data from the 5th IPCC report, scaled for Québec (10 km × 10 km) for three climatic variables (mean annual precipitation, mean annual temperature and mean minimum temperature in May). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Characteristics of the species included in the assessment of potential susceptibility to mammalian herbivores.

Scientific name	Type	Current status in study area	Potential effect of climate change on habitat at study site[1]	Sample sizes for chemical analyses per climate analogue	Total number of references in systematic review[2]
Acer saccharum	Broadleaf	Present	Favourable	2018 = 38, 2050 = 44, 2080 = 18	142
Picea glauca	Conifer	Present	Unfavourable	2018 = 30, 2050 = 30, 2080 = 30	132
Picea rubens	Conifer	Present	Unfavourable	2018 = 30, 2050 = 30, 2080 = 30	24
Pinus resinosa	Conifer	Present	Favourable	2018 = 29, 2050 = 30, 2080 = 29	47
Pinus strobus	Conifer	Present	Favourable	2018 = 30, 2050 = 30, 2080 = 30	112
Prunus serotina	Broadleaf	Absent	Favourable	2018 = 30, 2050 = 46, 2080 = 48	94
Quercus rubra	Broadleaf	Absent	Favourable	2018 = 41, 2050 = 41, 2080 = 42	131
Thuja occidentalis	Conifer	Present	Unfavourable	2018 = 30, 2050 = 30, 2080 = 30	86

[1] Based on Périé et al. (2014).
[2] Including chemical content and herbivore damage. Further information on systematic review available in Appendix B.

method; Goering and Van Soest, 1970), total phenolics (Folin-Ciocalteu reagent; Sauvesty et al, 1992) and flavonoids (Aluminium complexation reaction; Pękal and Pyrzynska, 2014). We realized the analyses on a subset of seedlings and a detailed account of sample size, sampling methods and chemical analyses is available in Appendix A. For conifers, we analyzed an additional prevalent group of phytochemical, terpenes (gas chromatography of non-polar extracts with methyl octanoate internal standard; Cachet et al, 2016). We selected total phenolics, flavonoids and terpenes based on a systematic review of phytochemicals involved in plant susceptibility (Champagne et al., 2020c). Because of logistical constraints (available expertise and resources), we also quantified total nitrogen and fibre content rather than available nitrogen; available nitrogen is an estimate of nitrogen that accounts for the effect of tannins, a phenolic compounds class that reduces nitrogen digestibility (Wallis et al., 2012). Nitrogen concentration is a proxy of protein content, and is sought after by herbivores. Cellulose is a fibre type digestible by hares, rabbits and deer, and a high potential source of energy, but its digestion is time-consuming (Hanley, 1982). Lignin, another fibre type, is not digestible and a high content reduces forage digestibility (Hanley, 1982). Champagne et al. (2020c) found the effect of fibres on plant susceptibility to herbivores are variable, but generally negative. Phenolics (including flavonoids) and terpenes are phytochemicals mostly avoided by both deer, hares and rabbits (Champagne et al., 2020c). Based on that study, we made the assumption that phenolics (total and flavonoids), terpenes and lignin are indicators of resistance to herbivores, while nitrogen and cellulose indicate susceptibility.

We sampled seedlings from the batch produced for planting in the assisted migration project for each combination of species and climate analogues (sample sizes in Table 1). Because the majority of deer herbivory on seedlings occurs in winter, we sampled after winter bud formation (Fall 2018), and excluded the leaves of the broadleaf species. For some chemistry analyses (i.e. terpenes, fibres), we could not analyze all samples because of limited resources. We thus used Near Infrared (NIR) spectroscopy to create calibrations between NIR spectra and concentrations, and subsequently predict concentration values (Champagne et al., 2020a; Appendix A). In all statistical analyses, we used laboratory values over predicted values, when available.

2.2.2. Creation of chemical profiles

We first statistically analyzed the chemical composition among species, and second among climate analogues for each species. At each step, we created chemical profiles using principal component analyses (PCA), with the princomp function of the vegan package using a correlation matrix (Oksanen et al., 2019) in R 3.6.0 (ReimoserR Core Team, 2019). For comparison among species, we used all chemical analyses available for the eight species (nitrogen, lignin, cellulose, flavonoids) with the exception of total phenolics content; this measure is not reliable for comparison among species because of the differences in phenolic content composition (Appel et al., 2001); species differ in the phenolic compound they produce. For within species comparisons among climate analogues (one PCA per species), we used all analyses available (nitrogen, lignin, cellulose, flavonoids, total phenolics and total terpenes for conifers). We evaluated the statistical significance of PCA axes using randomized observations (1000 randomizations) and the computation of eigen values (Peres-Neto et al., 2005). For axis interpretation (susceptibility versus resistance to herbivores based on compound classification), we used the significant eigenvectors (loadings), as evaluated by a bootstrap of eigenvectors (1000 randomizations; Peres-Neto et al., 2003). For these analyses and subsequent ones, we used a significance level α of 0.05. We used this conservative approach, rather than interpreting PCA axis based on all loading values, to create a repeatable and objective ranking of species browse susceptibility.

We used significant axis scores as a response variable in an ANOVA. For comparisons among species, we used a mixed model with species as an explanatory variable, and a random nested effect of climate analogues within species (function lmer, Bates et al., 2014). We used the package lmerTest for type III ANOVA table with degrees of freedom adjustment with Satterthwaite's method (Kuznetsova et al., 2017). For comparison among climate analogues, we did not include random effects and used the function *aov*, with analogues as the explanatory variable. For each ANOVA with statistically significant fixed effects, we used least standard mean differences with a Tukey adjustment to rank species and analogues (Lenth, 2020). All analyses respected assumptions of residual homogeneity and normality.

The PCA including all species did not allow distinctions among certain conifers species, as their values on the first axis overlapped (Fig. 2). We used a mixed model with the same structure as above to evaluated differences in total terpene concentration among conifers, with a square root transformation to respect model assumptions. All the data for these analyses and for the following analyses is available on figshare (Champagne et al., 2021).

2.3. Comparison of chemical profiles to systematic review of defence phytochemicals

We qualitatively assessed the accuracy of our profiles by comparing them to a systematic review of defence phytochemicals for these species. The systematic review process is fully described in Appendix B. Briefly, we aimed to identify references reporting the presence (qualitative information) and/or concentration (quantitative information) in plant secondary metabolites and fibres for the eight studied species. We searched two databases in June 2018 (ISI Web of Science and Pubmed), using past and current species names, and a set of 34 keywords and expression related to plant nutritional value and defence (Appendix B for complete list). We evaluated references using a systematic, PRISMA inspired protocol (Moher et al., 2009; Koricheva et al., 2013), and extracted the information regarding chemical content of 339 references. We synthesize information regarding the presence/absence of compounds in a table, using 19 groups and subgroups of plant phytochemicals linked with defence (Table B.3, Appendix B).

2.4. Comparison of potential susceptibility ranking to reported browsing across Species' range

To evaluate the efficiency of our approach, we compared the potential susceptibility ranking to actual browsing levels reported across the geographic range of the eight species. While we conducted the systematic review of chemical content, we performed a systematic review of herbivore browsing, using the same databases and species names, but replacing keywords of chemical content by herbivor* and brows* (the * allows search for different word declinations). The search for chemical content and herbivore browsing references were independent but merged after the screening phase (evaluation of relevance by title and abstract; see Appendix B). We removed duplicates and selected 240 references with herbivore browsing information. We synthesized the information in a table, under the following categories: mammalian herbivore responsible for the browsing, intensity of the browsing, and impacts on seedlings growth, height, survival and abundance (Table B.4, Appendix B). We also noted the number of references with or without herbivore browsing, and the source of information, i.e. direct evidence of herbivory (e.g. browse measurement, herbivore observations) vs indirect evidence (e.g. effects on growth or abundance). We summarized this information on the geographic range of the species, using maps (Appendix B). We compared the synthesis table and maps to the ranking generated with chemical profiles.

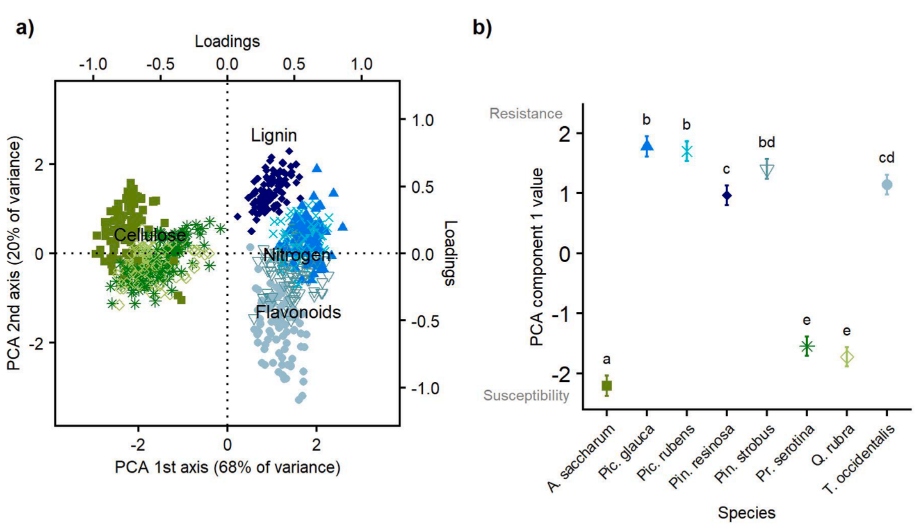

Fig. 2. Chemical profile and discrimination among species: a) Biplot for the Principal Component Analysis (PCA) based on the concentration of four compounds or group of compounds (cellulose, lignin, nitrogen and flavonoids) including all species. The broadleaves are presented in green and conifers in blue. Compound name represents loading values. Based on a), we made the assumption that higher values on this axis indicate resistance to mammalian herbivores, while low values could be associated with susceptibility; b) Mean value and 95% confidence intervals (model estimates) of 1st axis value per species. Different letters indicate different means as evaluated by least standard mean difference, with $\alpha < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Determination of potential susceptibility by chemical profiles

3.1.1. Interspecific browse susceptibility ranking

The PCA including values for all species allowed for a clear distinction between the chemical profiles of conifer and broadleaf species (Fig. 2). Conifers had positive values on the only statistically significant PCA axis (explaining 68% of the variation), and these values were associated with higher nitrogen, lignin and flavonoids concentrations, while broadleaves had negative values, which were linked to higher cellulose concentration (Fig. 2; Table 2). The association of nitrogen (susceptibility indicator) with flavonoids and lignin (resistance indicators) complicates the interpretation of this axis along a susceptibility-resistance continuum. However, the negative association with cellulose, another susceptibility indicator, suggests that positive scores on the first axis could be indicators of resistance. This interpretation is also supported by the association of positive values with conifers, that are typically less browsed than broadleaves.

Using first axis values in an ANOVA, we were able to discriminate five non-exclusive groups of species, again with a clear separation between the relatively more resistant conifers and relatively more susceptible broadleaves (Table 2; Fig. 2b). Most conifer species had similar values on this susceptibility-resistance continuum, but they differed in their total terpene content ($F_{4,10.1} = 58.68$, $p < 0.00001$), which allow for further differentiation. We identified two groups with *a posteriori* testing: more resistant conifers with high terpene content (back-transformed model estimates and SE: *Pic. glauca* = 11.6 ± 0.5 mg/g, *Pic. rubens* = 11.7 ± 0.5 mg/g and *T. occidentalis* = 9.7 ± 0.5 mg/g) and more susceptible conifers with low terpene content (*Pin. resinosa* = 3.4 ± 0.3 mg/g and *Pin. strobus* = 5.5 ± 0.4 mg/g). Based on the values of the first axis, statistical differences among these values, and differences in terpene content, we ranked species from least to most susceptible to herbivores (Table 3): *Pic. glauca* and *rubens*, *Pin. strobus* and *T. occidentalis*, *Pin. resinosa*, *Pr. serotina* and *Q. rubra,* and *A. saccharum*. Summarized means and standard deviations of individual compounds, for species and species*analogues combinations can be found in Appendix A, Table A.2.

3.1.2. Intraspecific browse susceptibility rankings

Based on the PCA and ANOVAs, we classified climate analogues along the resistance-susceptibility continuum for four species: *Pic. rubens*, *Pin. resinosa*, *Pr. serotina* and *T. occidentalis* (Table 2; Fig. 3). The only common trend among climate analogue regions is that the 2080 climate analogues were the most or among the most susceptible, at the exception of *Pr. serotina*. The statistically significant PCA loadings indicates that the differences among analogues were driven by different compounds, depending on the species (Table 2). Nitrogen and phenolics (total phenolics and flavonoids) varied among climate analogues in three out of four species and fibres (lignin and cellulose) in two out of four species. For the remaining species, we either could not interpret PCA values on a susceptibility-resistance continuum and/or

Table 2

Results of Principal Component Analyses (PCA), interpretation of significant axes and ANOVA results for each chemical profiles. We used PCA to generate chemical profiles integrating the values of four (all species PCA) and six chemical analyses (species-specific PCA), used as resistance (lignin, total phenolics, flavonoids, total terpenes) or susceptibility (cellulose, nitrogen) indicators for eight North American tree species considered for assisted migration. Each species sample include individuals from three climate analogues, i.e. locations where the current climate is similar to the future climate at plantation site (here current, mid-century (2041–2070) and late century (2071–2100) climates). The interpretation of the axis is based on significant loadings and assumptions regarding the effect of each compound on susceptibility and resistance. Values of PCA statistically significant axis were used in ANOVAs to discriminate among species or among climate analogues within species. Loadings and ANOVA results in bold are statistically significant (α < 0.05 for all analyses).

	PCA results									ANOVA Results
	Axis	Variance explained	Loadings						Interpretation of positive values based on loadings	
			Lignin	*Cellulose*	*Nitrogen*	*Total phenolics*	*Flavonoids*	*Total terpenes*		
All species	1st	68%	**0.35**	**−0.58**	**0.52**		**0.53**		Resistance	**$F_{7,17.02}$ = 474.22 p = < 0.0001**
Acer saccharum	1st	44%	**0.49**	0.06	**−0.59**	**0.33**	**−0.54**		–	**$F_{2,95}$ = 6.52 p = 0.002**
Picea glauca	1st	31%	0.19	−0.42	−0.59	0.63	−0.03	−0.22	–	**$F_{2,87}$ = 5.09 p = 0.008**
	2nd	30%	0.52	0.35	0.18	0.04	−0.55	−0.53	–	**$F_{2,87}$ = 18.59 p = < 0.0001**
Picea rubens	1st	29%	0.31	0.18	**−0.54**	**0.62**	**0.43**	0.10	Resistance	**$F_{2,84}$ = 9.67 p = 0.0002**
Pinus resinosa	1st	32%	0.10	**−0.45**	**−0.60**	**0.59**	**0.27**	−0.12	Resistance	**$F_{2,81}$ = 4.91 p = 0.010**
Pinus strobus	1st	29%	0.15	**0.55**	**0.55**	**−0.57**	−0.21	−0.11	Susceptibility	$F_{2,85}$ = 1.41 p = 0.249
	2nd	25%	**0.50**	−0.16	−0.35	−0.09	−0.39	**−0.66**	–	**$F_{2,85}$ = 14.05 p = < 0.0001**
Prunus serotina	1st	35%	**0.55**	**−0.50**	**0.50**	−0.36	−0.27		–	**$F_{2,121}$ = 13.19 p = < 0.0001**
	2nd	29%	**0.40**	−0.30	0.03	**0.60**	**0.62**		Resistance	**$F_{2,121}$ = 4.07 p = 0.020**
Quercus rubra	1st	32%	**0.43**	**−0.41**	**0.48**	**−0.47**	**0.44**		–	$F_{2,120}$ = 2.12 p = 0.125
	2nd	26%	0.44	**−0.52**	**−0.53**	**0.48**	0.18		Resistance	$F_{2,120}$ = 1.10 p = 0.337
Thuja occidentalis	1st	36%	**0.40**	−0.30	−0.01	**−0.52**	**−0.57**	**0.40**	–	**$F_{2,87}$ = 23.20 p = < 0.0001**
	2nd	30%	**0.48**	**0.35**	**−0.66**	0.37	0.03	0.28	Resistance	**$F_{2,87}$ = 8.16 p = 0.0006**

Table 3
Potential and reported susceptibility to mammalian browsing of the eight North American tree species considered for assisted migration. We based potential susceptibility on chemical profiles (results of PCA and ANOVA) taking into account the concentration in two susceptibility indicators (nitrogen and cellulose) and four resistance indicators (lignin, total phenolics, flavonoids and total terpenes). We adjusted our ranking with a systematic review of chemical content for those species. Reported browsing across species range is based on a review of 240 references (see Appendix B), and on the frequency (# of reference with browsing/ Total # of references) and intensity of reported herbivore damage (synthesis of qualitative information).

Species	Potential susceptibility From least susceptible to most susceptible		Reported browsing across species range[2]	
	Based on chemical profiles	With systematic review of chemical content	Frequency	Intensity
Picea glauca	1	1	44/68 (65%)	Low
Picea rubens	1	1	3/6 (50%)	Low
Pinus strobus	2	2	52/57 (91%)	Low to high
Thuja occidentalis	2	2	44/46 (96%)	High
Pinus resinosa	3	3	18/19 (95%)	Low
Prunus serotina	4	4	45/57 (79%)	Low
Quercus rubra	4	5	69/71 (97%)	Moderate to high
Acer saccharum	5	6	64/70 (91%)	Moderate to high

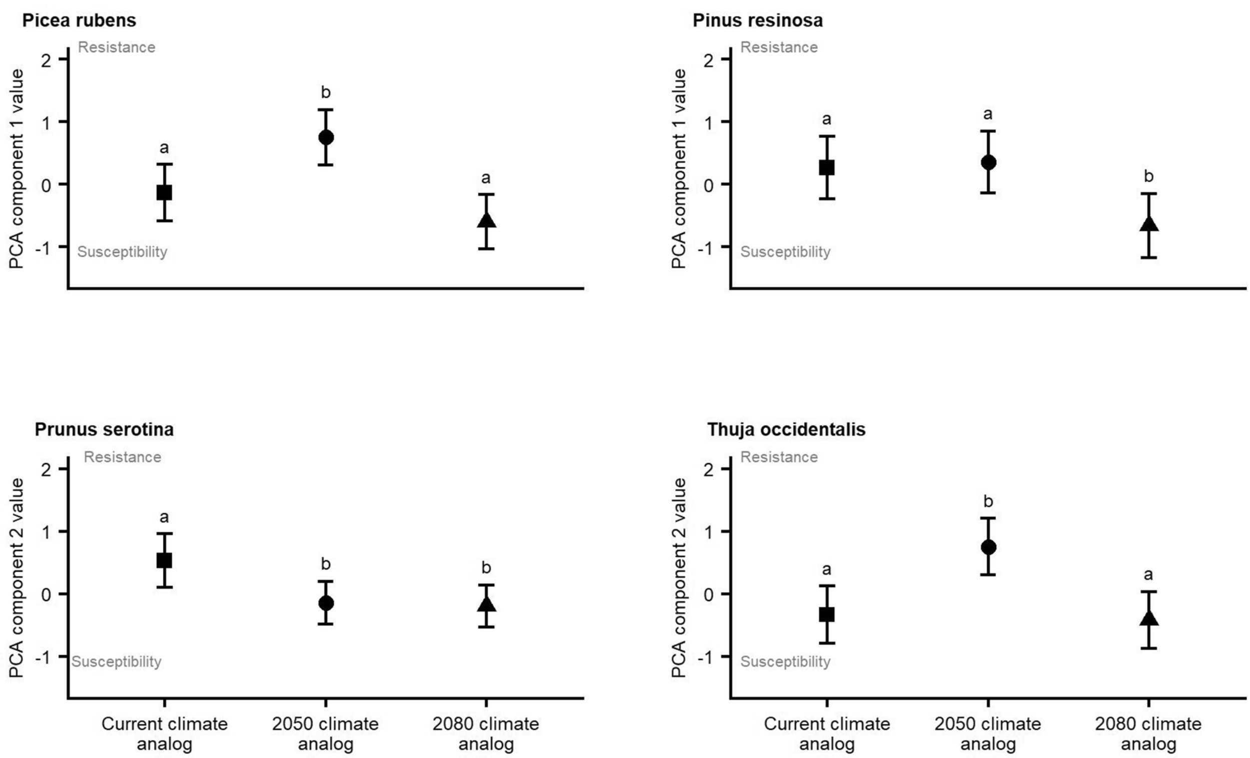

Fig. 3. Discrimination among climate analogues based on PCA results for four North American tree species considered in assisted migration. We used ANOVA to discriminate among climates analogues for species with statistically significant and interpretable PCA axis. We based interpretation of axis values on indicators of susceptibility (nitrogen, cellulose) and resistance (lignin, total phenolics, flavonoids and total terpenes for conifers). Interpretation of PCA axis values on the resistance-susceptibility continuum is indicated along the y-axes. Climates analogues are locations where the current climate is similar to the future climate at plantation site (here current, mid-century (2041–2070) and late century (2071–2100) climates, respectively current, 2050 and 2080 climate analogues). Seedlings were produced from seeds collected in these climate analogues. Model estimated means and 95% confidence intervals for PCA axis value from mixed models testing variation among climate analogues for selected species. Different letters indicate different means as evaluated by least standard mean difference, with $\alpha < 0.05$.

susceptibility did not vary among climate analogues (Table 2).

3.2. Comparison of chemical profiles to systematic review of phytochemicals

The ranking produced at this step is highly congruent with the composition and concentration of phytochemicals associated with resistance reported in the literature for these species across their range (see Appendix B, Table B.3). For example, we ranked *Pic. glauca* as one of the two most resistant species. The literature confirms that this species has a high concentration and a wide diversity of phytochemicals linked to resistance, including alkaloids, tannins, flavonoids, stilbenoids and terpenes (Appendix B, Table B.3). On the other end of the continuum, the literature reports that the phytochemical composition of *A. saccharum* mostly consists of tannins, and that their concentration is relatively low, especially when compared to *Q. rubra* (Appendix B, Table B.3). This is again consistent with our ranking *A. saccharum* as potentially more susceptible than *Q. rubra*.

The main difference between the profiles and the review is the presence of terpenes and the toxic hydrogen cyanide in *Pr. serotina*. We consequently adjusted the ranking, by separating *Pr. serotina* and *Q. rubra*, with the former being less susceptible to herbivores than the latter (Table 3).

3.3. Comparison of potential susceptibility ranking to reported browsing across Species' range

Browsing was reported for each species in almost all articles, throughout their range (Table 3, Appendix B). For example, *Pic. glauca* is browsed throughout its range, at the exception of two Canadian provinces (Nova Scotia, and Newfoundland and Labrador; Fig. 4); Browsing distribution maps for each species are included in Appendix B. The high occurence of browsing for all species was probably a bias from our review protocol; studies without observations of browsing would not have necessarily been included in our search because of the herbivory-related keywords.

For each species, reports of browsing intensity ranged from low to high, but in general, trends (i.e. most frequent intensity of browsing) were identifiable (Table 3). As predicted by chemical profiles, *Pic. glauca* and *Pic. rubens*, and *Pin. resinosa* mostly suffered low-browsing intensity, although cases of heavy browsing by small mammals were reported for *Pic. glauca* and *Pin. resinosa* (Appendix B, Table B.4, Figs. B.3–5). Similarly, we predicted high susceptibility to browsing for *A. saccharum* and *Q. rubra* and those species are frequently browsed, at moderate-high intensity and with negative impacts on their growth, survival and abundance (Table 3, Appendix B, Figs. B.2 & B.8).

On the other hand, *Pin. strobus* and *T. occidentalis* are reported to be severely browsed in multiple instances, especially by white-tailed deer, with negative impacts on their growth, survival and abundance (Table 3, Appendix B, Figs. B.6 & B.9). This is in contradiction with their chemical profile, both considering the analyses we performed and the chemical defence measured in the literature. The low browsing reported on *Pr. serotina* in the literature (Appendix B, Table B.4, Fig. B.7) also is in contradiction with its chemical profile, but congruent with the presence of a potent defence compound, hydrogen cyanide. However, *Pr. serotina* is browsed, sometimes heavily, by some white-tailed deer populations, which is in agreement with our initial ranking.

4. Discussion

By creating chemical profiles for eight North American tree species, we aimed to predict their relative susceptibility to browsing by mammalian herbivores. Although we analyzed a limited number of compounds and groups of compounds, the profiles were congruent with the current knowledge regarding these species' chemistry, based on a systematic review of the literature. The predicted susceptibility also matched levels of mammalian browsing reported in the literature for six of the eight species, suggesting that our approach efficiently identifies general trends in browsing. The *Picea* species deemed most resistant to browsing by our chemical profiles were the least browsed in the review. Similarly, chemical profiles correctly identified the two species most susceptible to browsing among the set, *A. saccharum* and *Q. rubra*. This qualitative assessment supports our previous work, where we proposed that the analysis of key compounds or groups of compounds could be used to predict species susceptibility to deer, hares and rabbits(Champagne et al., 2020c). We also identified chemical differences among climate analogues that could generate variation in susceptibility among analogues for four species (*Pic. rubens*, *Pin. resinosa*, *Pr. serotina* and *T. occidentalis*). Although we cannot determine if these differences arose from local adaptation to high herbivory pressure, they could be exploited by selecting resistant genotypes for assisted migration (Wink, 1988; Miller et al., 2011). Our chemical profile approach, based on the

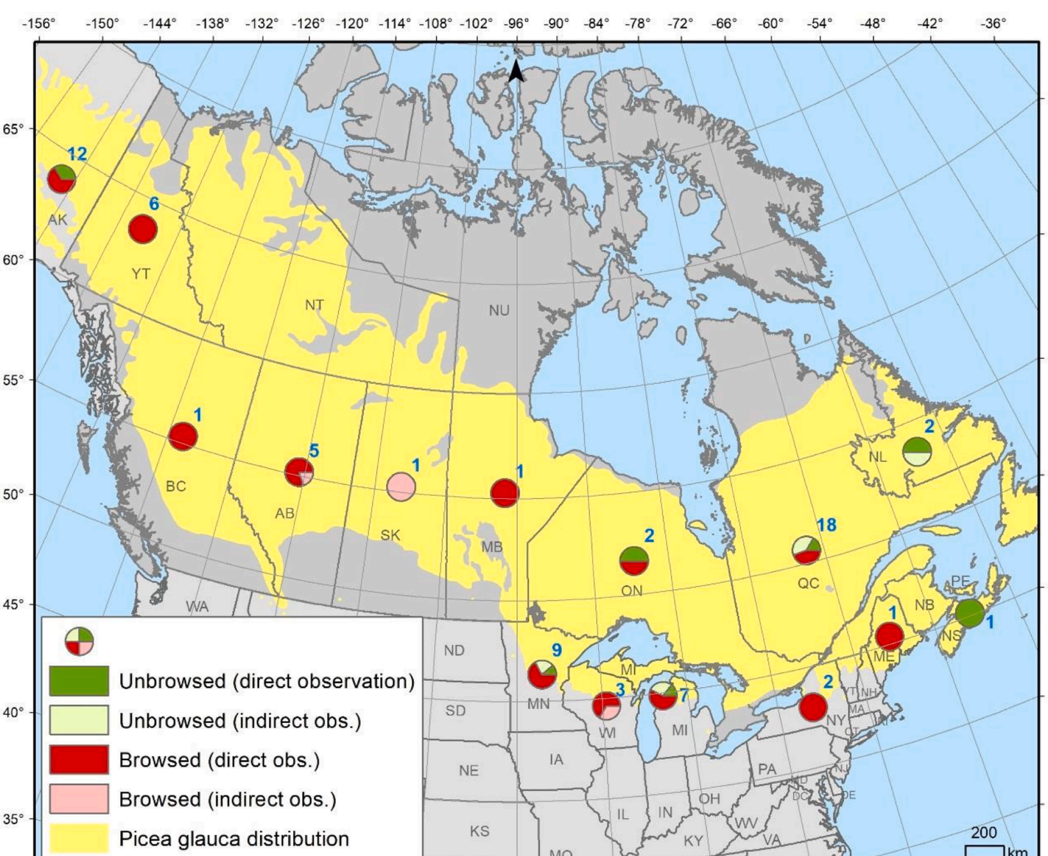

Fig. 4. *Picea glauca* browsing distribution including all herbivore species and direct (e.g. browse measurement, herbivore observations) and indirect (e.g. effects on growth or abundance) observations. Pie charts describe distribution of observations for each province (Canada) and state (USA) with a reference available. The total number of references per province and state is indicated in blue. Browsing distribution maps for each species are included in Appendix B. Species distribution from Prasad and Iverson (2003). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

objective assessment of multivariate analyses results, could be replicated to compare the potential susceptibility of other species and/or genotypes. This approach could be especially useful when contending with novel plant-herbivore relationships, such as forestry and conservation assisted migration or species invasion.

The approach, however, is not infallible as it incorrectly predicted the susceptibility of *Pin. strobus* and *T. occidentalis*; these species are more often and more intensely browsed than predicted by their chemical profiles, throughout their range. This could be explained by our analyses of broad chemical groups (total phenolics and terpenes), rather than specific bioactive compounds (Felton et al., 2018). Indeed, the specific phenolics and terpenes present in both species could be ineffective or attractive for some mammalian herbivores. This is corroborated by the fact that herbivory on both *Pin. strobus* and *T. occidentalis* is linked to a subset of herbivores (Systematic review, Appendix B). For *T. occidentalis*, white-tailed deer are recognized as a major threat to their regeneration (Cornett et al., 2000; Larouche et al., 2010). Similarly, *Pin. strobus* is browsed by deer but also by small mammals. Planted *Pin. strobus* especially are known to be browsed, sometimes heavily, by *Microtus pennsylvanicus* Ord and *Lepus americanus* (Aldous and Aldous, 1944; Rudolf, 1950; Krefting, 1975; Bergeron and Jodoin, 1989; Bucyanayandi et al., 1990). The phenolic or terpene composition of these species might be better suited for defence against other herbivores or are involved in other functions. *T. occidentalis* has a quite distinctly different terpene composition from *Pinus* and *Picea*, dominated by α-thujone, which in absent in the other conifers (detailed terpene analysis available in Champagne et al., 2020a). Thujone can reduce consumption by Sitka deer (*Odocoileus hemionus sitkensis* Merriam), roe deer (*Capreolus capreolus* L.) and Javan rusa (*Rusa timorensis* Blainville), and pygmy rabbits (*Brachylagus idahoensis* Merriam; White et al., 1982; Vourc'h et al., 2002). To our knowledge, however, its effect on moose, white-tailed deer or snowshoe hare is not documented. As for *Pin. strobus*, phenolic extracts from this species can reduce food intake by *Microtus pennsylvanicus* (Roy and Bergeron, 1990). Although browse pressure on *Pin. strobus* and *T. occidentalis* could be influenced by their abundance and the presence of alternative resources (Champagne et al. 2020b), the consistently high frequency of reported browsing throughout their range suggest a fundamentally higher susceptibility. Identifying the effect of specific phenolics and terpenes on mammalian herbivores could refine our assessment of potential susceptibility. Moreover, the example of *T. occidentalis* and *Pin. strobus* highlights the importance of considering the herbivore community composition when evaluating the potential susceptibility for a specific site.

In addition to herbivore community composition, an assessment of susceptibility to browsing should consider the ontogenic development of defence in woody plants. We evaluated chemical composition at an early growth stage of seedlings (end of first and second growing seedlings for broadleaves and conifers respectively), but phytochemical defence evolves during plant development. In their earliest growth stage, seedlings do not have enough resources to invest in costly phytochemical defence (Boege and Marquis, 2005). Consequently, phytochemical defence, and especially phenolic and terpene content, increases during the seedling stage of woody plants (Boege and Marquis, 2005; Barton and Koricheva, 2010). The development of defence could be compared among species and genotypes, to obtain a complete portrait of their susceptibility to browsing while they are accessible to mammalian browsers. A temporal assessment could also be useful to evaluate the effect of environment at the plantation site on composition, as resource availability and herbivores attacks can modify investment in phytochemical defence (Koricheva et al., 1998; Agrawal et al., 1999; Gayler et al., 2008).

A complete assessment of susceptibility to herbivores should also integrate the ability to tolerate browsing, through growth and reproduction, as it is a prevalent plant strategy to resist herbivores (Rosenthal and Kotanen, 1994; Hester et al., 2006). Saplings of *Pinus sylvestris* L., for example, can easily recover from one-time browsing events by compensatory growth, an ability that varies within species and thus that could be used for plant selection in plantations (O'Reilly-Wapstra et al., 2014). Higher tolerance capacity is also connected to faster growth rates, which could reduce the time spent in the height-stratum accessible to herbivores and positively influence the economic value of plantations (Hester et al., 2006). Higher growth rates, however, can come at the expense of phytochemical defence (Coley et al., 1985; Moreira et al., 2014). Moreover, tolerance to browsing in woody plants is linked to the release of apical dominance and the development of dormant/lateral meristems, which could affect the economic value of the stems (Haukioja and Koricheva, 2000; Hawkes and Sullivan, 2001). Even low browsing intensity can lead to trunk defects because of this release: low browsing by white-tailed deer lead to the development of multiple leader stems on *Pic. rubens*, which has been related to multi-trunk individuals in other species (Welch et al., 1992; Reyes and Vasseur, 2003). More information on the tolerance capacity and impact of browsing events on stem quality are required to make an informed selection of species and genotypes in a plantation context.

5. Management implications

Results from our chemical profiling approach can be transposed to other silvicultural contexts, especially the clear trend of higher susceptibility for broadleaf species compared to conifer species. Natural and artificial regeneration of broadleaves is currently recommended in forest adaptation frameworks, because of broadleaf suitability to warmer and drier climate conditions (e.g. Mirschel et al., 2011; Krasnow and Stephens, 2015; Lodin et al., 2017). Promoting susceptible broadleaves in regions with high herbivory pressure might entail protection against herbivores (e.g. fences, individual tree shelters) or intensified herbivore management. Protections, however, are costly, limiting their large-scale use, and the impacts of herbivore populations on highly selected species can persist after decades of herbivore population control (Tanentzap et al., 2009). Managers considering broadleaves in their adaptation strategy could evaluate this choice in light of herbivore population size and community composition. They could, for example, assess the presence of herbivore-specific defence phytochemicals in the broadleaves species of interest. Conifer species known for their high susceptibility to herbivores should also be subjected to the same evaluation. This would be the case for *Pinus strobus* and *Thuja occidentalis* in Eastern North America, but also *Abies alba* in Europe, for example. While this species favoured for its suitability to warmer climate, it is highly susceptible to ungulates and its regeneration requires adequate wildlife management or protection (Vitasse et al., 2019).

The entire chemical profile approach could also be replicated for other species to inform managers of potential susceptibility to herbivores. For example, we propose the use of the chemical profile approach for assisted migration planning as a preliminary screening tool to identify species suited for regions with moderate or high-browsing pressure. As phytochemical defence is used against most herbivores and pathogens, including invertebrates, chemical profiling could contribute to the consideration of other threats (Levin, 1976). To adequately consider pathogens and invertebrates, however, a careful selection of chemical analyses would be required to choose compounds affecting those organisms (Levin, 1976; Barton and Koricheva, 2010). Chemical profiling could also be used in the selection of appropriate genotypes, and be an additional factor considered when matching source populations to assisted migration plantation sites. In our assessment, differences among species dominated, but seven of eight species presented differences in chemical profiles among climate analogues; deer, hares and rabbits can select forage based on intraspecific variations in nutritional value, with the result of affecting long-term (cumulative) browsing risk (Bergvall et al., 2006; Champagne et al., 2020b; Champagne et al., 2020c). Current recommendations for assisted migration plantations are to fit seed source to site conditions, and herbivory pressure or herbivore community composition could be an additional condition (Vitt et al., 2010; Gray and Hamann, 2013), added to existing seed selection tools such as the seedlot selection tool and the Eastern Seed Zone Forum (Howe et al., 2017; Luther et al., 2020). Additionally, potentially resistant genotypes could be identified based on their chemical characteristics. Analyses of resistance based on chemical content could be realized across wide areas (i.e. North America) using tools streamlining analyses, such as the near infrared spectroscopy used in our study (see also Champagne et al. 2020a). In summary, the consideration of mammalian herbivore populations could be integrated in current management-decision tools, using the chemical characteristics of species and genotypes. Such integration would be beneficial for managers that are willing to invest their resources in assisted migration, but are contending with mammalian herbivore populations.

CRediT authorship contribution statement

Emilie Champagne: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Alejandro A. Royo:** Conceptualization, Writing – review & editing, Funding acquisition. **Jean-Pierre Tremblay:** Conceptualization, Writing – review & editing, Funding acquisition. **Patricia Raymond:** Conceptualization, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119576.

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