Clear-cutting without additional regeneration treatments can trigger successional setbacks prolonging the expected time to compositional recovery in boreal forests

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Abstract

Clear-cutting is one of the most widespread forestry practices used in boreal forests. Clear-cutting of boreal forests in late successional stages could trigger reversion of successional trajectories back toward forests of earlier stages. Such successional setbacks could generate sustainability issues by prolonging the expected time to compositional recovery after clear-cutting. This could lead to overestimation of allowable cuts of economically important late-successional species if the occurrence of successional setbacks remains unassessed. Our objective was to assess whether clear-cutting without additional regeneration treatments has triggered successional setbacks. We studied post-clearcut successional trajectories by using forest inventory data in post-clearcut stands, in light of conceptual successional dynamics models. These data covered the actively managed boreal forest region of Quebec, eastern Canada, which is classified into two ecological regions, themselves subdivided into eastern (cool-wet) and western (warm-dry) sub regions. Clear-cutting triggered successional setbacks in half of these regions. Such setbacks could prolong, by at least an additional century, the expected time to compositional recovery after clear-cutting. To prevent the overestimation of allowable cuts of economically important late-successional species, foresters could monitor post-clear-cut successional trajectories to assess if setbacks were triggered. Post-clear-cut successional setbacks occurred in the two western ecological regions where climatic conditions are warmer and drier than in their eastern counterpart where no setbacks occurred. Hence, sustainability issues brought on by successional setbacks may be exacerbated by climate change. Finally, furthering our understanding of the transformation of successional dynamics by anthropogenic disturbances will be essential to insure sustainable forestry practices.

Keywords: successional dynamics; forest landscapes; allowable cuts; sustainable forestry; climate change.

Introduction

Clear-cutting is one of the most widespread forestry practices used in boreal forests (Cyr et al. 2009; Kuuluvainen and Gauthier 2018; Boucher et al. 2021). It removes the entirety of the mature forest cover, which can favor the establishment of early successional light-demanding species to the detriment of pre-established late-successional, shade-tolerant species (Carleton and MacLellan 1994; Chen and Popadiouk 2002; Laquerre et al. 2009; Danneyrolles et al. 2019). Hence, clear-cutting of forests in late successional stages could trigger the reversion of successional trajectories back toward forests of earlier stages (Lieffers et al. 2008; Cyr et al. 2009; Kuuluvainen and Gauthier 2018). Such successional setbacks could generate sustainability issues by prolonging the expected time to compositional recovery after clear-cutting (van der Veen et al. 1997; Angelstam and Kuuluvainen 2004; Barrette et al. 2020). More especially, this could lead to overestimation of allowable cuts of economically important late-successional species if the occurrence of successional setbacks remains unassessed.

National forest inventory data available worldwide could be useful for identifying the occurrence of successional setbacks since they are gathered to monitor long-term forest growth and compositional change over large areas and diverse climatic conditions (de Bello et al. 2020; Barrette et al. 2021; Heym et al. 2021). However, a significant problem with these data sources is a general lack of information on pre-clearcut composition, making it difficult to identify the occurrence of post-clearcut successional setbacks in a straightforward manner (Didion et al. 2009; de Bello et al. 2020). A way to circumvent this problem could be to study national forest inventory data in light of conceptual successional dynamics models developed for predicting potential natural vegetation (van der Veen et al. 1997; Didion et al. 2009; Barrette et al. 2020). Potential natural vegetation is a land classification unit that is determined by climate, superficial deposits, soil texture, slope, drainage and understory indicator plant species, tree species, and which predicts stand composition, but only for the latest successional stage (Grondin et al. 2013; Robitaille et al. 2015; Prach et al. 2016). Since conceptual successional dynamics models predict stand compositions of all successional stages, their use can help determine the stage toward which the successional trajectory of post-clearcut stands is oriented (Barrette et al. 2020; Keane et al. 2020). If the successional trajectory of these post-clearcut stands generally points toward early successional stages (i.e. early successional light-demanding species predominate late-successional, shade-tolerant species), this suggest that successional setbacks occurs (van der Veen et al. 1997; Cyr et al. 2009; Didion et al. 2009).

The actively managed boreal forest (529 000 km^2) of the province of Quebec, eastern Canada, make up about 1% of the world's boreal forest area (National Forestry Database 2020). Since the early 20th century, clear-cutting has been the most widespread forestry practices used in boreal forests of Quebec (Barrette and Bélanger 2007; Boucher et al. 2021). These clearcuts generally have occurred in mature and old-growth forests dominated by late-successional shade-tolerant species (Bergeron 2000; Cyr et al. 2009; Boucher et al. 2017; Kuuluvainen and Gauthier 2018). Our objective was to assess whether clear-cutting without additional regeneration treatments has triggered successional setbacks in boreal forests. To do this, we studied post-clearcut successional trajectories by using Quebec's forest inventory data in post-clearcut stands, in light of conceptual successional dynamics models (Prach et al. 2016; Barrette et al. 2020; Keane et al. 2020). We studied successional trajectories by analyzing species composition in 5 935 plots located in post-clearcut stands ranging in age from 1- to 91-years-old. To determine if the trajectory of post-clearcut stands was oriented toward early successional stages, we compared the transition of their composition versus the predicted compositions of all successional stages obtained from the conceptual successional dynamics models.

Materials and methods

Study area

Our study area encompasses the actively managed boreal forest region of Quebec, eastern Canada, which is classified into two ecological regions, themselves subdivided into eastern and western sub regions (Grondin et al. 2007; Fig. 1). Climatic conditions are warmer and drier in the western part of an ecological region compared to its eastern counterpart (Table 1). The main natural disturbances include insect outbreaks (e.g. eastern spruce budworm [*Choristoneura fumiferana*]), windthrows and wildfire, which is the main ecological driver in western ecological regions (Boucher et al. 2014; Boucher et al. 2021). The most abundant native tree species are black spruce (*Picea mariana* (Miller) B.S.P.), balsam fir (*Abies balsamea* (L.) Miller) and white birch (*Betula papyrifer*a Marsh.). Depending on the ecological region, these species are found in mixtures with varying densities of companion species, such as white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lambert), eastern white cedar (*Thuja occidentalis* (L.)), eastern larch or tamarack (*Larix laricina* (Du Roi) K. Koch), balsam poplar (*Populus balsamifera* L.), bigtooth aspen (*Populus grandidentata* Michaux) and trembling aspen (*Populus tremuloides* Michaux) (MRN 2013).

Data

We used sample plots (n = 5 935; Fig. 1) of the forest inventory data of Quebec, Canada (MRNF 2006a; 2006b). To monitor forest growth, plots were spread across the forest area in a stratified random sampling design. We selected all plots that were established after clear-cutting, located in the balsam fir–white birch (western, n = 700, eastern, n = 3053) and black spruce (western, n = 1814, eastern, n = 368) ecological regions. Pre-clearcut stand conditions or disturbance history were not available. To be selected, plots also had to be located on the typical potential natural vegetation of the ecological region (e.g. on black spruce potential natural vegetation in the black spruce ecological region) according to the forest inventory data (MRNF 2009). Five percent of the plots were permanent sample plots measured up to 4 times while the other 95% were temporary sample plots measured only once. Trees (diameter at breast height, DBH ≥ 9.1 cm) were counted by species and by 2-cm DBH classes in either 400-m^2 circular plots (forest height ≥ 7 m) or 100-m^2 circular plots (forest height < 7 m). Saplings (DBH 1.1–9.0 cm) were counted by species and by 2-cm DBH classes in concentric 40-m^2 circular subplots. Clearcuts were performed, between 1919 and 2016, by removing the entirety of the mature forest cover. Clearcuts in the ecological regions covered by our study have always been dedicated to supply to pulp and paper industry in addition to the sawmill industry both of which target all commercial trees (i.e. DBH ≥ 9.1 cm) in mature and old-growth forests dominated by late-successional shade-tolerant species (Barrette and Bélanger 2007; Alvarez et al. 2011; Boucher et al. 2021). Clearcutting without any particular modalities (82% of plots) and clearcutting with modalities to protect pre-established regeneration (17%) occurred during the complete period of the study while clearcutting with modalities to protect pre-established regeneration and soils (< 1%) occurred only in the last ten years. Moreover, the three modalities can be considered similar for analysis purposes also because the majority of clearcuts without any particular modalities most probably have been done in winter (MFFP 2020) during which the snow cover offered a protection to pre-established regeneration and soils (Archambault et al. 2006; Wolf et al. 2008). We removed, from the data set, all plots in which natural (e.g. fire, insect outbreak, windthrow) or anthropogenic (e.g. thinning modalities, plantation scenario) disturbances other than clearcutting occurred.

Data analysis

To determine if the trajectory of post-clearcut stands was oriented toward early successional stages we compared the transition of their composition to the predicted compositions of all successional stages obtained from the conceptual successional dynamics models. Models were developed by Barrette et al. (2020) for the two main types of potential natural vegetation that are found in the boreal forest of eastern Canada, i.e. balsam fir–white birch forests (Fig. 2) and black spruce forests (Fig. 3). Development of the conceptual models was based on a synthesis of available knowledge regarding successional dynamics occurring in the boreal forest of eastern Canada (Bergeron 2000; Chen and Popadiouk 2002; MRN 2013; Grondin et al. 2013; Maleki et al. 2020). In order to allow the development of comprehensive models, model complexity was reduced by grouping species according to their capacity to dominate the forest cover (i.e. dominant or companion species) and shade tolerance (i.e. tolerant or intolerant species). Species groups were classified as dominant intolerant (DI), dominant tolerant (DT), and companion tolerant (CT) species. The models were driven by five natural processes (i.e. regeneration, growth, self-thinning, senescence and natural disturbances) within four developmental stages (i.e., regeneration, young, mature, old) and four successional stages (i.e. early, transition, stabilization and equilibrium). Early and transition stages are considered early successional stages while stabilization and equilibrium stages are considered late successional stages (Kuuluvainen and Gauthier 2018; Barrette et al. 2020; Maleki et al. 2020). In the early successional stage of the balsam fir–white birch potential natural vegetation model, DI species are the only ones present. In the transition successional stage, DT species appear and can come to co-dominate stand composition. In the stabilization successional stage, CT species can appear, but they remain subdominant while they are more abundant than DI species in the equilibrium successional stage. In the early successional stage of the black spruce potential natural vegetation model, DI and DT species can occur alone or co-dominate stand composition, because both species groups can come back after stand replacing fires. Moreover, CT can now occur in the transition stage.

We analyzed the transition of the composition of sapling density and tree basal area in post-clearcut stands separately for each of the four ecological regions with two-way analysis of variance, which was implemented through linear mixed-effects models (PROC MIXED; SAS/STAT 15.1 (2018) of SAS software 9.4) with stand age groups (10-year classes) and species groups, and their interaction, as fixed effects, and plots as a random effect. We tested mean sapling density and tree basal area differences using a simulation method (LSMESTIMATE statement) between the youngest and oldest age groups within each species group and between species groups (pairwise) within the oldest age group. A species group predominated composition (e.g. early successional light-demanding species predominate late-successional, shade-tolerant species late-successional, shade-tolerant species) if its basal area or density was statistically significantly higher than the basal area or density of any other species group. We used α = 0.05 as a significance threshold. We log-transformed the data to meet normality assumptions. We present data back-transformed to their original scales, for the sake of clarity.

Results

Western balsam fir–white birch ecological region

The successional trajectory of trees in post-clearcut stands pointed toward the composition of an early successional stage (i.e. transition stage: DI ≥ DT; Fig. 2 and 4a). After an increase over more than 40 years (Table 2; $t = 5.2$, $p < 0.001$), mean basal area of DI species was two times higher than the basal area of DT species ($t = 3.16$, $p = 0.002$).

The successional trajectory of saplings in post-clearcut stands also pointed toward the composition of a late successional stage (i.e. stabilization stage: DT > DI ≥ CT; Fig. 2 and 4b). Mean density of DT species remained stable over the 40 year-period (Table 2; $t = 0.65$, $p = 0.513$), and then was three times higher than density of DI species ($t = 2.34$, $p = 0.019$) while density of DI species was similar to the density of CT species ($t = 1.55$, $p = 0.122$). Finally, mean density of non-commercial species (NC) was abundant only in the first 20 years.

Eastern balsam fir–white birch ecological region

The successional trajectory of trees in post-clearcut stands pointed toward the composition of a late successional stage (i.e. stabilization stage: DT > DI ≥ CT; Fig. 2 and 4c). After an increase over more than 60 years (Table 2; $t = 26.4$, $p < 0.001$), mean basal area of DT species was five times higher than the basal area of DI species ($t = 15.0$, $p < 0.001$) while basal area of DI species was similar to the basal area of CT species ($t = 1.33$, $p = 0.182$)

The successional trajectory of saplings in post-clearcut stands also pointed toward the composition of a late successional stage (i.e. stabilization stage: DT > DI ≥ CT; Fig. 2 and 4d). Mean density of DT species remained stable over the 60-year-period ($t = -1.11$, $p = 0.269$), but was then eight times higher than the density of DI species ($t = 11.2$, $p < 0.001$) while density of DI species was two times higher than the density of CT species ($t = 3.06$, $p = 0.002$).

Western black spruce ecological region

The successional trajectory of trees in post-clearcut stands pointed toward the composition of an early successional stage (i.e. transition stage: DI ≥ DT > CT; Fig. 3 and 5a). After an increase over more than 30 years (Table 2; $t = 19.5$, $p < 0.001$), mean basal area of DI species was similar to the basal area of DT species ($t = 0.94$, $p = 0.349$) while DT species was two times higher than CT species ($t = 19.9$, $p < 0.001$).

Conversely, the successional trajectory of saplings in post-clearcut stands pointed toward the composition of a late successional stage (i.e. stabilization stage: DT > DI ≥

CT; Fig. 3 and 5b). After an increase over more than 30 years ($t = 6.25$, $p < 0.001$), mean density of DT species was three times higher than the density of DI species ($t = 12.27$, $p < 0.001$) while DI species were similar to CT species ($t = -0.27$, $p = 0.790$). Finally, mean density of NC species was abundant only during the first 20 years.

Eastern black spruce ecological region

The successional trajectory of trees in post-clearcut stands pointed toward the composition of a late successional stage (i.e. stabilization stage: DT ≥ CT; Fig. 3 and 5c). After an increase over more than 40 years (Table 2; $t = 12.9$, $p < 0.001$), mean basal area of DT was 1.2 times higher than the basal area of CT ($t = 2.82$, $p = 0.005$), while DI species were almost absent.

The successional trajectory of saplings in post-clearcut stands also pointed toward the composition of a late successional stage (i.e. stabilization stage: DT ≥ CT; Fig. 3 and 5d). After an increase over more than 40 years ($t = 6.49$, $p < 0.001$), mean density of DT species was similar to the density of CT species ($t = -1.6$, $p = 0.109$) while DI species were almost absent. Finally, the mean density of Non-Commercial species (NC) was abundant only during the first 20 years.

Discussion

Clear-cutting without additional regeneration treatments triggered successional setbacks in half of the ecological regions. Effectively, after clear-cutting, successional trajectories of trees pointed toward the composition of an early successional stage in the western black spruce and western balsam fir ecological regions. Clear-cutting did not trigger successional setbacks in in the eastern black spruce and eastern balsam fir ecological regions where post-clear-cut successional trajectories of trees and of saplings pointed toward the composition of a late successional stage. The main limit of our study is that we could not consider the important influence pre-clearcut stand condition has on post-clearcut species composition because information on pre-clearcut stand condition was not available. However, we are confident that these clearcuts generally have occurred in mature and old-growth forests dominated by late-successional shade-tolerant species (Bergeron 2000; Cyr et al. 2009; Boucher et al. 2017; Kuuluvainen and Gauthier 2018). Effectively, all plots were on potential natural vegetation where successional trajectories always leads to stands dominated by late-successional shade-tolerant species (Grondin et al. 2013; Robitaille et al. 2015; Prach et al. 2016). Moreover, the ecological regions covered by our study have always been dedicated to supply to pulp and paper industry in addition to the sawmill industry both of which target mature and old-growth forests dominated by late-successional shade-tolerant species (Barrette and Bélanger 2007; Alvarez et al. 2011; Boucher et al. 2021). Finally, there is evidences in our own study that pre-clearcut stand condition was dominated by late-successional shade-tolerant species. Notably, successional trajectories of saplings in the two western regions pointed toward the composition of a late successional stage. These saplings probably established themselves before clear-cutting under the canopy of a late stage stand for their trajectory to already be pointing toward the composition of a late stage while now being in the understory of an early stage stand (Chen and Popadiouk 2002; Laquerre et al. 2009). This indicates that these stands, now in an early stage, were in a late stage before clear-cutting;

hence, clear-cutting did indeed trigger a successional setback. The occurrence of companion tolerant species in early stage stands is a similar indication that these early stage stands were in a late stage before clear-cutting. Effectively, companion tolerant species are mostly found in late stage stands since they generally do not regenerate after fire (Bergeron 2000; Barrette et al. 2019; Maleki et al. 2020). Moreover, these companion tolerant species could be legacies from clear-cutting of late stage stands since clear-cutting can maintain pre-established regeneration to a certain degree (Bouchard et al. 2019; Boucher et al. 2021).

Clear-cutting without additional regeneration treatments triggered successional setbacks in the two warmer and drier regions probably because it favored dominant intolerant species (e.g. *Betula papyrifera, Acer rubrum, Populus* sp., *Pinus* sp.) to the detriment of dominant tolerant species (e.g. *Acer saccharum*, *Betula alleghaniensis, Abies Balsamea, Picea mariana*). Clear-cutting can favor the establishment of such early successional light-demanding species to the detriment of pre-established late-successional, shade-tolerant species because it removes the mature forest cover in its entirety, which puts seedlings under full sunlight (Carleton and MacLellan 1994; Laquerre et al. 2009). Successional setbacks probably occurred because clear-cutting did not spare sufficient pre-established seedlings of dominant tolerant species for them to steer succession (Wurtz and Zasada 2001; Chen and Popadiouk 2002). Effectively, natural disturbances that kill seedlings (e.g. fire) can trigger successional trajectories to revert back toward forests of earlier stages while natural disturbances that spare pre-established seedlings (e.g. insect outbreaks, windthrows) can maintain a successional trajectory oriented toward late successional stages (Bergeron 2000; Kuuluvainen and Gauthier 2018; Barrette et al. 2020).

Post-clear-cut successional setbacks occurred in the two western ecological regions where climatic conditions are warmer and drier than in their eastern counterpart where conditions are cooler and wetter and where no setbacks occurred. Warmer and drier conditions usually enables dominant intolerant species to steer successional trajectories generally more so than for dominant tolerant species or companion tolerant species (Boisvert-Marsh et al. 2014; Brecka et al. 2018; Boulanger and Pascual Puigdevall 2021). For instance, in only modestly warmer conditions (i.e. +2 °C), deciduous broadleaf trees may become more dominant to the detriment of conifers (Schaphoff et al. 2016). Such a temperature differential is generally found between warmer and drier western ecological regions where we found that successional setbacks did occur compared to cooler and wetter eastern ecological regions where they did not occur. Moreover, a higher frequency of drought even brought on by drier conditions can favor drought-tolerant species such as *Pinus spp.* (Brecka et al. 2018). More specifically, red maple, white birch and poplar species may outperform balsam fir, eastern white cedar, yellow birch as well *Picea spp*. under warmer and drier conditions (Boisvert-Marsh et al. 2014; Boulanger et al. 2019; Vaughn et al. 2021). Warmer and drier conditions also favor short fire cycles (e.g. 150 years; Boucher et al. 2017; Kuuluvainen and Gauthier 2018). Hence, clearcuts in western regions where such conditions occur could also be more susceptible to being colonized by dominant intolerant species occurring in neighboring areas, since these species are frequent in fire-prone landscapes (Bouchard et al. 2019; Brice et al. 2019). In cooler and wetter eastern regions where fire cycles are longer (e.g. 400 years), dominant intolerant species may be generally less frequent than dominant tolerant species in the landscape hence also be less available to colonize neighboring clearcuts (Boulanger et al. 2021).

Forest management implications

Post-clear-cut successional setbacks could prolong, by at least an additional century, the expected time to compositional recovery after clear-cutting without additional regeneration treatments (Bergeron 2000; Kuuluvainen and Gauthier 2018; Barrette et al 2020). To prevent the overestimation of allowable cuts of economically important late-successional species, foresters could monitor post-clear-cut successional trajectories to assess if setbacks were triggered. Moreover, to prevent successional setbacks, foresters could insure that regeneration of late-successional species prior to logging is sufficiently established to steer successional trajectories toward forests of late successional stages after clear-cutting. Furthermore, care should be taken during clear-cutting to spare enough pre-established regeneration of late-successional species to enable it to steer succession. To wait until stands reach the old-growth developmental stage would probably ensure that sufficient regeneration is established to prevent setbacks (Barrette et al. 2020).

Post-clear-cut successional setbacks occurred more frequently in warmer and drier conditions. Hence, sustainability issues brought on by post-clear-cut successional setbacks may in turn be exacerbated by climate change in the boreal forest of eastern Canada, which is believed will become warmer and drier (Flanagan and Syed 2011; Boisvert-Marsh et al. 2014; Reich et al. 2018). Finally, furthering our understanding of the transformation of successional dynamics by anthropogenic disturbances (e.g. forestry, climate change) will be essential to insure sustainable forestry practices.

Acknowledgements

We thank Jean Noël for help in figure preparation and W.F.J. Parsons for English language revision.

Funding

This work was supported by Project 142332110, Direction de la recherche forestière of the Ministère des Forêts, de la Faune et des Parcs (MFFPQ) of the provincial government of Quebec (Canada).

Conflict of interest

None declared.

Data availability

Data is available at https://mffp.gouv.qc.ca/le-ministere/acces-aux-donnees-gratuites/

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Table 1. Climatic conditions in the four ecological regions.

Ecological region	Mean annual temperature (°C)	Mean annual precipitation (mm)	Mean annual number of frost-free days
Balsam fir-white birch			
Western	1.0	1000	175
Eastern	0.5	1300	170
Black spruce			
Western	0.0	900	165
Eastern	-2.0	1100	145

Table 2. Analysis of variance and associated probabilities (*p-values*) for mean tree basal area and mean sapling density in each ecological region. Df num.: numerator degrees-of-freedom; df den.: denominator degrees-of-freedom.

Sources of variation	df num.	df den.	*F*-value (*tree; sapling)*	*p-value*
Western balsam fir-white birch				
Age group	4	2085	81; 12	< 0.001
Species group	3	2085	317; 85	< 0.001
Age group × Species group	12	2085	9; 17	< 0.001
Eastern balsam fir-white birch				
Age group	6	9138	401; 68	< 0.001
Species group	3	9138	2212; 1384	< 0.001
Age group × Species group	18	9138	50; 13	< 0.001
Western black spruce				
Age group	3	5430	228; 31	< 0.001
Species group	3	5430	576; 143	< 0.001
Age group × Species group	9	5430	23; 30	< 0.001
Eastern black spruce				
Age group	4	1089	47; 17	< 0.001
Species group	3	1089	319; 157	< 0.001
Age group × Species group	12	1089	17; 8	< 0.001

Figure captions

Fig 1 Location of sample plots (black triangles; n = 5 935) of the forest inventory data for the province of Quebec, eastern Canada. We used data from plots that were established after clear-cutting that was performed between 1919 and 2016 (white line separates the western ecological region from its eastern counterpart).

Fig 2 Conceptual successional dynamics model from Barrette et al. (2020) predicting stand compositions of the different successional stages of the balsam fir–white birch potential natural vegetation.

Fig 3 Conceptual successional dynamics model from Barrette et al. (2020) predicting stand compositions of the different successional stages of the black spruce potential natural vegetation.

Fig 4 Distribution of tree basal area (a, c; diameter at breast height [DBH] ≥ 9.1 cm) and sapling density (b, d; DBH: 1.1–9.0 cm) by species groups in sample plots in post-clearcut stands located in the balsam fir–white birch ecological region on balsam fir–white birch potential natural vegetation. Diamonds and horizontal lines in each box represent means and medians, respectively. Boxes enclose the 25th and 75th percentiles (the interquartile range (IQR); whiskers enclose 1.5 × IQR; open circles enclose >1.5 × IQR).

Fig 5 Distribution of tree basal area (a, c; diameter at breast height [DBH] ≥ 9.1 cm) and sapling density (b, d; DBH: 1.1–9.0 cm) by species groups in sample plots in post-clearcut stands located in the black spruce ecological region on black spruce potential natural vegetation. Diamonds and horizontal lines in each box represent means and medians, respectively. Boxes enclose the 25th and 75th percentiles (the interquartile range (IQR); whiskers enclose 1.5 × IQR; open circles enclose >1.5 × IQR).

Fig 1.

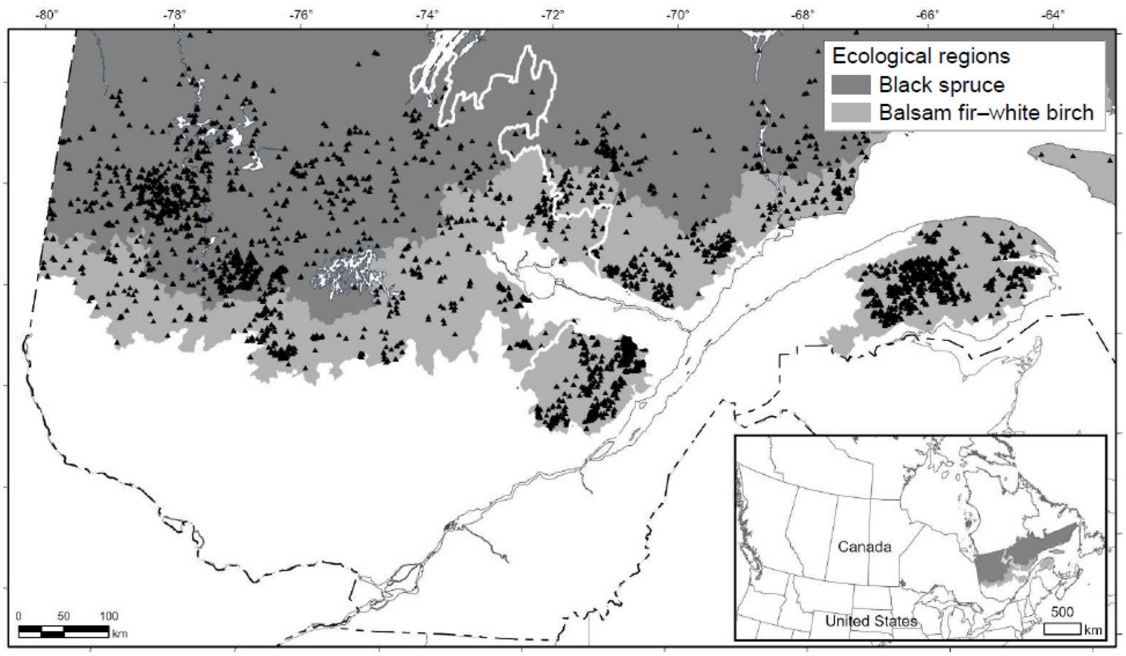
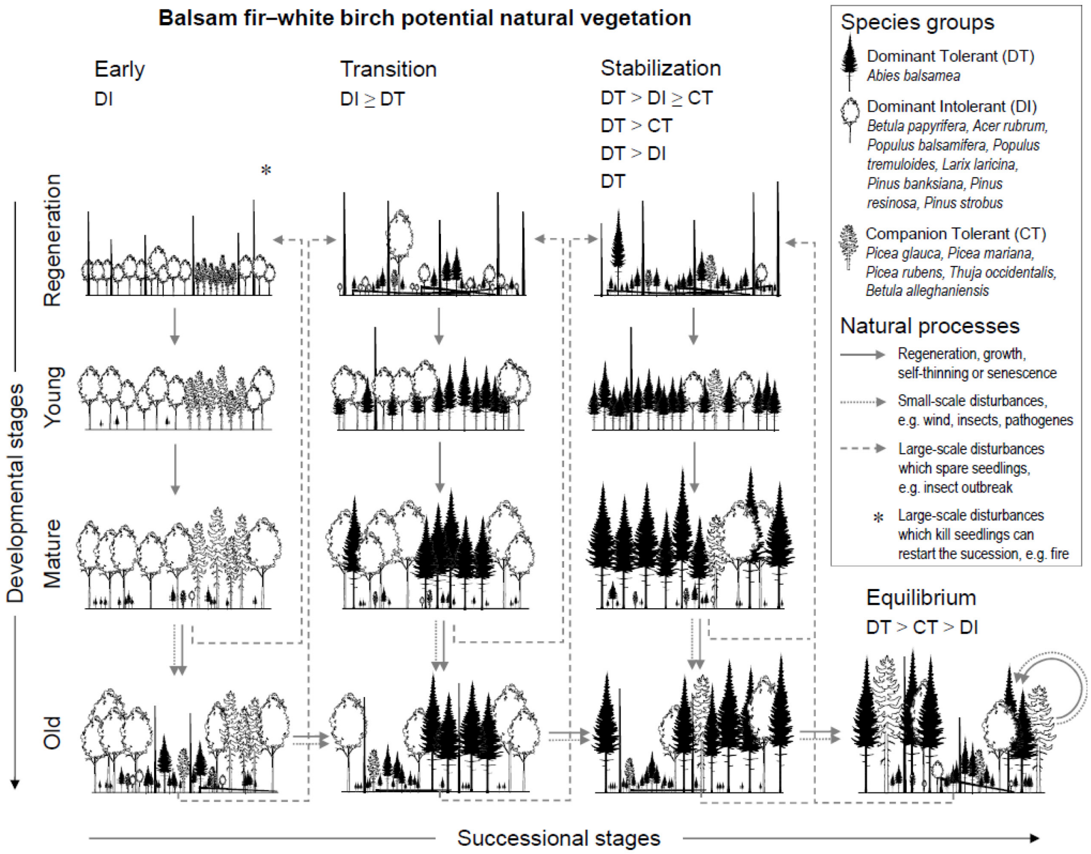
532 
-80°
-78°
-76°
-74°
-72°
-70°
-68°
-66°
-64°
50°
49°
48°
47°
46°
45°
Ecological regions
Black spruce
Balsam fir–white birch
Canada
United States
500
km
0
50
100
km

Fig 2.



Balsam fir–white birch potential natural vegetation
Early
DI
Transition
DI ≥ DT
Stabilization
DT > DI ≥ CT
DT > CT
DT > DI
DT
Equilibrium
DT > CT > DI
Regeneration
Young
Mature
Old
Developmental stages
Successional stages
Species groups
Dominant Tolerant (DT)
Abies balsamea
Dominant Intolerant (DI)
Betula papyrifera, Acer rubrum, Populus balsamifera, Populus tremuloides, Larix laricina, Pinus banksiana, Pinus resinosa, Pinus strobus
Companion Tolerant (CT)
Picea glauca, Picea mariana, Picea rubens, Thuja occidentalis, Betula alleghaniensis
Natural processes
Regeneration, growth, self-thinning or senescence
Small-scale disturbances, e.g. wind, insects, pathogenes
Large-scale disturbances which spare seedlings, e.g. insect outbreak
Large-scale disturbances which kill seedlings can restart the sucession, e.g. fire

533

Fig 3.

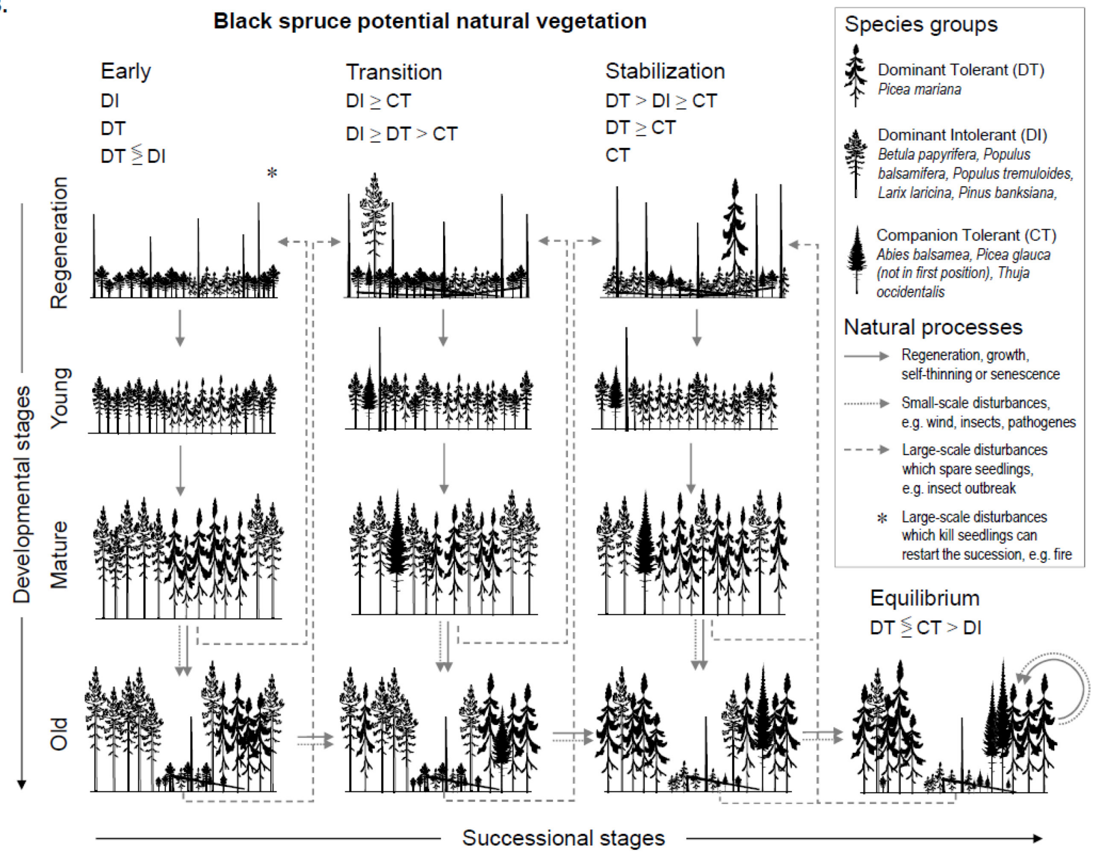
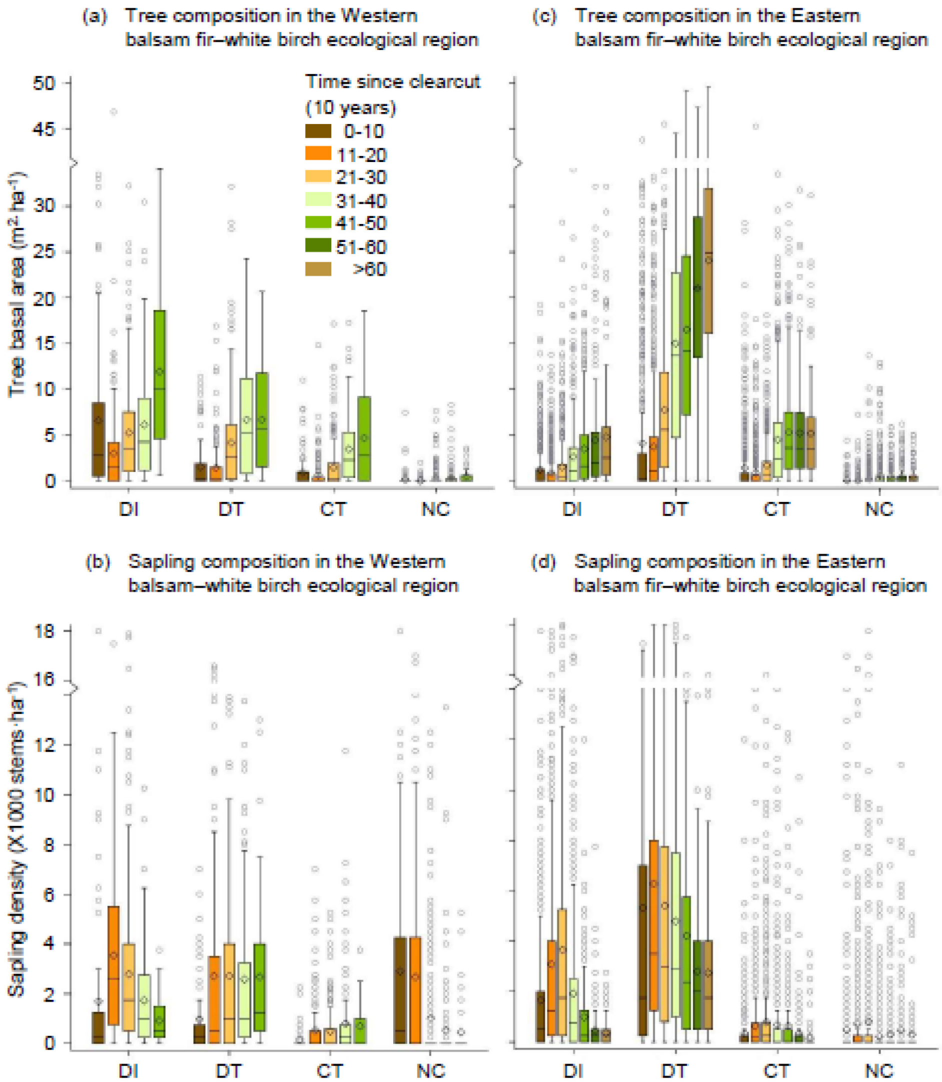

Black spruce potential natural vegetation
Early
DI
DT
DT ≶ DI
Transition
DI ≥ CT
DI ≥ DT > CT
Stabilization
DT > DI ≥ CT
DT ≥ CT
CT
Equilibrium
DT ≶ CT > DI
Regeneration
Young
Mature
Old
Developmental stages
Successional stages
Species groups
Dominant Tolerant (DT)
Picea mariana
Dominant Intolerant (DI)
Betula papyrifera, Populus balsamifera, Populus tremuloides, Larix laricina, Pinus banksiana,
Companion Tolerant (CT)
Abies balsamea, Picea glauca (not in first position), Thuja occidentalis
Natural processes
Regeneration, growth, self-thinning or senescence
Small-scale disturbances, e.g. wind, insects, pathogenes
Large-scale disturbances which spare seedlings, e.g. insect outbreak
Large-scale disturbances which kill seedlings can restart the sucession, e.g. fire

Fig 4.

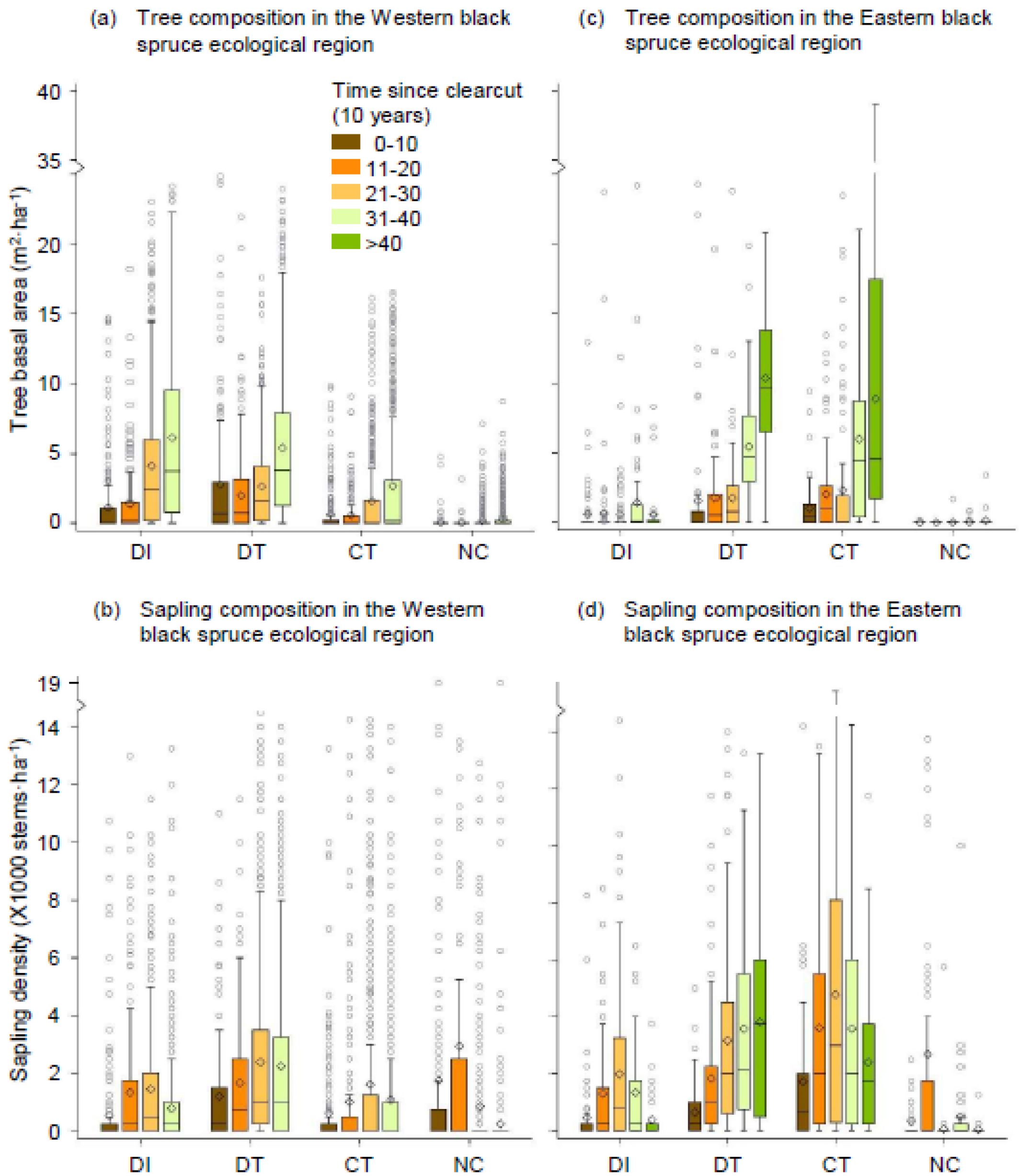


(a) Tree composition in the Western balsam fir–white birch ecological region
(c) Tree composition in the Eastern balsam fir–white birch ecological region
Time since clearcut (10 years)
0-10
11-20
21-30
31-40
41-50
51-60
>60
Tree basal area (m^2·ha^{-1})
DI
DT
CT
NC
(b) Sapling composition in the Western balsam–white birch ecological region
(d) Sapling composition in the Eastern balsam fir–white birch ecological region
Sapling density (X1000 stems·ha^{-1})

536

537

Fig 5.



(a) Tree composition in the Western black spruce ecological region
(c) Tree composition in the Eastern black spruce ecological region
Time since clearcut (10 years)
0-10
11-20
21-30
31-40
>40
Tree basal area (m²·ha⁻¹)
40
35
20
15
10
5
0
DI
DT
CT
NC
(b) Sapling composition in the Western black spruce ecological region
(d) Sapling composition in the Eastern black spruce ecological region
Sapling density (X1000 stems·ha⁻¹)
19
14
12
10
8
6
4
2
0

538