



Clear-cutting of temperate forests in late successional stages triggers successional setbacks extending compositional recovery by an additional century

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ABSTRACT

Clear-cutting is used by foresters worldwide to harvest timber from forest ecosystems. Clear-cutting of cool-wet boreal forests in late successional stages can maintain successional trajectories pointed toward the composition of a late successional stages. However, clear-cutting of warm-dry boreal forests in late successional stages can trigger reversion of successional trajectories back toward forests of earlier stages because early-successional shade-intolerant species are more abundant than in cool-wet boreal forests, a process that is referred to as a successional setback. Such successional setbacks can generate sustainability issues by extending the expected time to compositional recovery after clear-cutting. This can lead to an overestimation of allowable cuts of economically important late-successional species and subsequently to a temporary forest composition conversion if the occurrence of successional setbacks remains unassessed. Temperate forests in late successional stages are warmer and drier than boreal forests and consequently include more early-successional shade-intolerant species susceptible to encroach clear-cut areas. Even if current ecological knowledge suggests that temperate forests could be susceptible to post-clearcut successional setbacks, a comprehensive assessment has yet to be undertaken. The objective of the present study was to assess whether clear-cutting has triggered successional setbacks in temperate forests. Therefore, we studied post-clearcut successional trajectories by using forest inventory data covering the entire temperate forest of the province of Québec, eastern Canada (209 000 km²). Clear-cutting triggered successional setbacks in both ecological regions forming the temperate forest. After clear-cutting, successional trajectories of trees pointed toward the composition of an early successional stage. To address this sustainable management issue in a comprehensive manner with clear-cutting, foresters could use partial cut approaches.

1. Introduction

Clear-cutting is used by foresters worldwide to harvest timber from forest ecosystems (Lundmark et al., 2013; Boucher et al., 2021). Clear-cutting of cool-wet boreal forests in late successional stages can maintain successional trajectories pointed toward the composition of a late successional stages (Barrette et al., 2022). However, clear-cutting of warm-dry boreal forests in late successional stages can trigger reversion of successional trajectories back toward forests of earlier stages because early-successional shade-intolerant species are more abundant than in cool-wet boreal forests, a process that is referred to as a successional

setback (Cyr et al., 2009; Kuuluvainen and Gauthier, 2018; Barrette et al., 2022). By removing almost all the mature forest cover, clear-cutting can favor the development of early-successional shade-intolerant species to the detriment of advance late-successional shade-tolerant species (Boucher et al., 2009; 2017; 2021). Such successional setbacks can generate sustainability issues by extending the expected time to compositional recovery after clear-cutting. This can lead to an overestimation of allowable cuts of economically important late-successional species and subsequently to a temporary forest composition conversion if the occurrence of successional setbacks remains unassessed (Barrette et al., 2022). Temperate forests in late

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successional stages are warmer and drier than boreal forests and consequently include more early-successional shade-intolerant species susceptible to encroach clear-cut areas (Hébert, 2003; Raymond and Bédard, 2017; Boulanger and Pascual Puigdevall, 2021). Even if current ecological knowledge suggests that temperate forests could be susceptible to post-clearcut successional setbacks, a comprehensive assessment has yet to be undertaken.

Forest inventory data, which are usually available in most countries to monitor long-term forest development and composition, can be used for identifying the occurrence post-clearcut successional setbacks (Heym et al., 2021; Barrette et al., 2022). Yet, these data do not include pre-clearcut conditions, making it difficult to identify successional setbacks directly (de Bello et al., 2020). To circumvent this problem, inventory data can be studied in light of conceptual successional dynamics models that have been developed for predicting compositions of all successional stages, according to the potential natural vegetation type (van der Veen et al., 1997; Barrette et al., 2020, 2022). Potential natural vegetation is a land classification unit that is determined from superficial deposits, slope, soil texture, climate, drainage, tree species and understory indicator plant 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). Conceptual successional dynamics models, predicting stand compositions of all successional stages, can help determine the post-clearcut successional trajectory (Keane et al., 2020; Barrette et al., 2022). If this successional trajectory generally points toward early successional stages (i.e., early successional shade-intolerant species predominate over late-successional shade-tolerant species), this suggests that successional setbacks indeed occur (Cyr et al., 2009; Barrette et al., 2022).

Since the early 20th century, clear-cutting has been the most widespread forestry practice that is used in temperate forests of Quebec, eastern Canada (209 000 km²) (Barrette and Bélanger, 2007; Boucher et al., 2021; MRNF, 2022). Clearcuts in this region have always been dedicated to supplying the pulp and paper industry in addition to the sawmill industry. Both industries target all commercial trees (i.e., DBH

≥ 9.1 cm) in mature and old growth forests that are dominated by late-successional shade-tolerant species (Barrette and Bélanger, 2007; Alvarez et al., 2011; Boucher et al., 2021). The objective of the present study was to assess whether clear-cutting has triggered successional setbacks in temperate forests. Therefore, we studied post-clearcut successional trajectories (1- to 87-years-old) by using forest inventory data ($n = 3\,932$ plots) covering the Province of Québec (Canada), in light of conceptual successional dynamics models that have been elaborated for this forest region (Barrette et al., 2020; 2022).

2. Materials and methods

2.1. Study area

Our study area encompasses the actively managed temperate forest region of Quebec, eastern Canada, which is classified into two ecological regions, i.e., the sugar maple (*Acer saccharum* Marsh.) region and the balsam fir (*Abies balsamea* (L.) Mill.)–yellow birch (*Betula alleghaniensis* Britt.) region (Grondin et al., 2007; Fig. 1). Climatic conditions are warmer in the southernmost region, i.e., the sugar maple region, but precipitation is similar between the two regions (Table 1). To the north, the balsam fir–yellow birch ecological region is mainly occupied by mixedwood stands where balsam fir, yellow birch, and red spruce (*Picea rubens* Sarg.) are the main components (Barrette and Bélanger, 2007; Raymond and Dumais 2023). To the south, the sugar maple ecological

Table 1
Climatic conditions in the ecological regions.

Ecological region	Mean annual temperature (°C)	Mean annual precipitation (mm)	Mean annual number of frost-free days
Balsam fir–yellow birch	1.5	1100	180
Sugar maple	3.0	1100	200

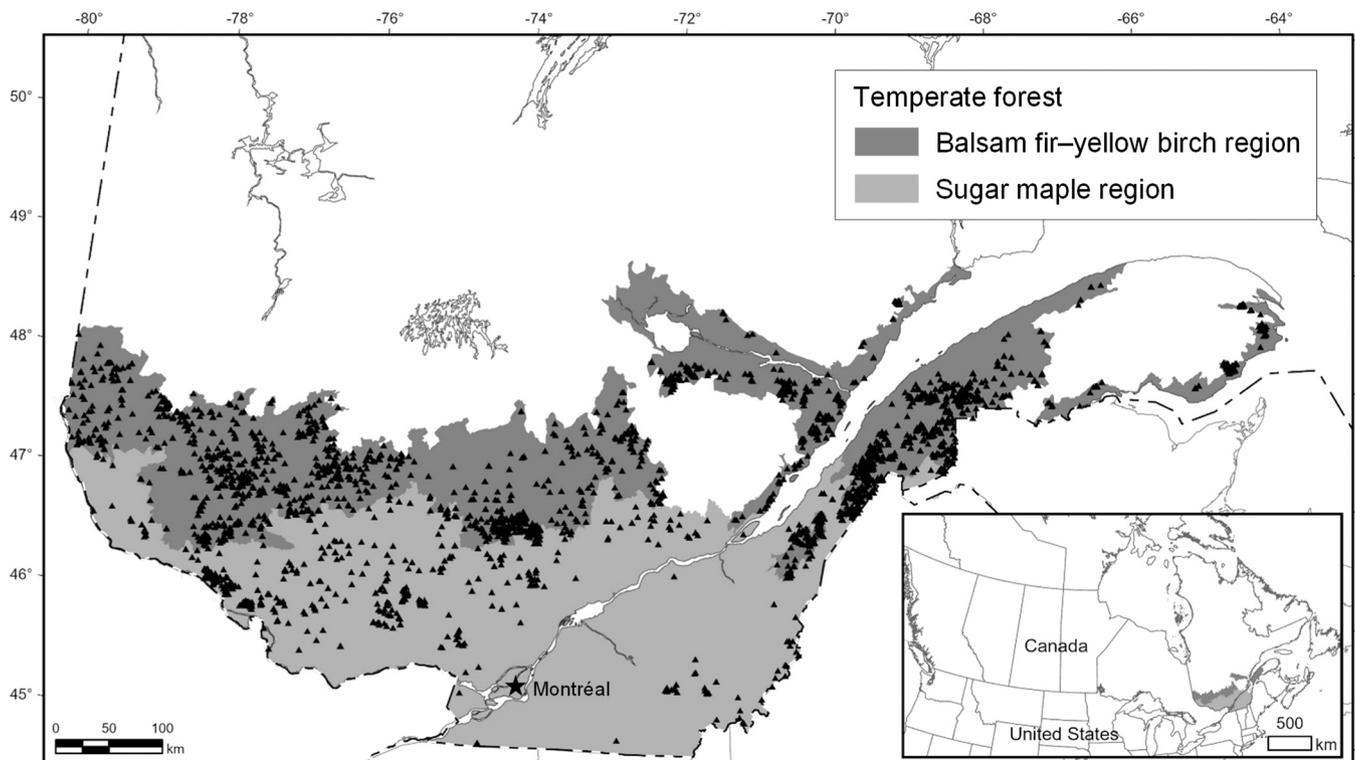


Fig. 1. Location of the sample plots (black triangles; $n = 3\,932$) of the forest inventory data for the province of Quebec, eastern Canada, used in our study.

region is mainly occupied by hardwood stands where sugar maple and yellow birch are the most abundant species.

Depending on the ecological region, main species are found in mixtures with varying densities of companion species, such as American beech (*Fagus grandifolia* Ehrh.), white or paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), black ash (*F. nigra* Marsh.), basswood (*Tilia americana* L.), white elm (*Ulmus americana* L.), red oak (*Quercus rubra* L.), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), black cherry (*Prunus serotina* Ehrh.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Miller) B.S.P.), jack pine (*Pinus banksiana* Lambert), red pine (*P. resinosa* L.), white pine (*P. strobus* L.), eastern hemlock (*Tsuga canadensis*), 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 (*P. tremuloides* Michaux) (MRN, 2013).

2.2. Data

We used sample plots ($n = 3\,932$; Fig. 1) of the forest inventory data of Quebec, Canada (MRNF 2006a, 2006b). To monitor forest growth, plots were distributed across the forest area in a stratified random sampling design. We selected all plots that were established after clear-cutting, which were located in the balsam fir–yellow birch ($n = 3\,226$) and sugar maple ($n = 666$) ecological regions. Stand conditions

before clear-cutting and disturbance history were not available. To be selected, plots also had to be located on the typical potential natural vegetation of the ecological region according to the forest inventory data, i.e., on sugar maple potential natural vegetation in the sugar maple ecological region or on balsam fir–yellow birch potential natural vegetation in the balsam fir–yellow birch ecological region (MRNF, 2009). Trees (diameter at breast height, DBH ≥ 9.1 cm) were counted by species and by 2-cm DBH classes in either 400-m² circular plots (forest height ≥ 7 m) or 100-m² 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-m² circular subplots. All clearcuts were performed by removing 75 % or more of the mature forest cover. We removed from the data set all plots in which natural (e.g., insect outbreak, fire, windthrow) or other anthropogenic (e.g., thinning modalities, plantation scenario) disturbances occurred to isolate clear-cut effects.

2.3. Data analysis

To assess whether 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 dynamic models (Barrette et al., 2020). Models were developed for the two main types of potential natural vegetation that are found in temperate forests of eastern Canada, i.e., balsam fir–yellow birch and sugar maple forests (Figs. 2 and 3,

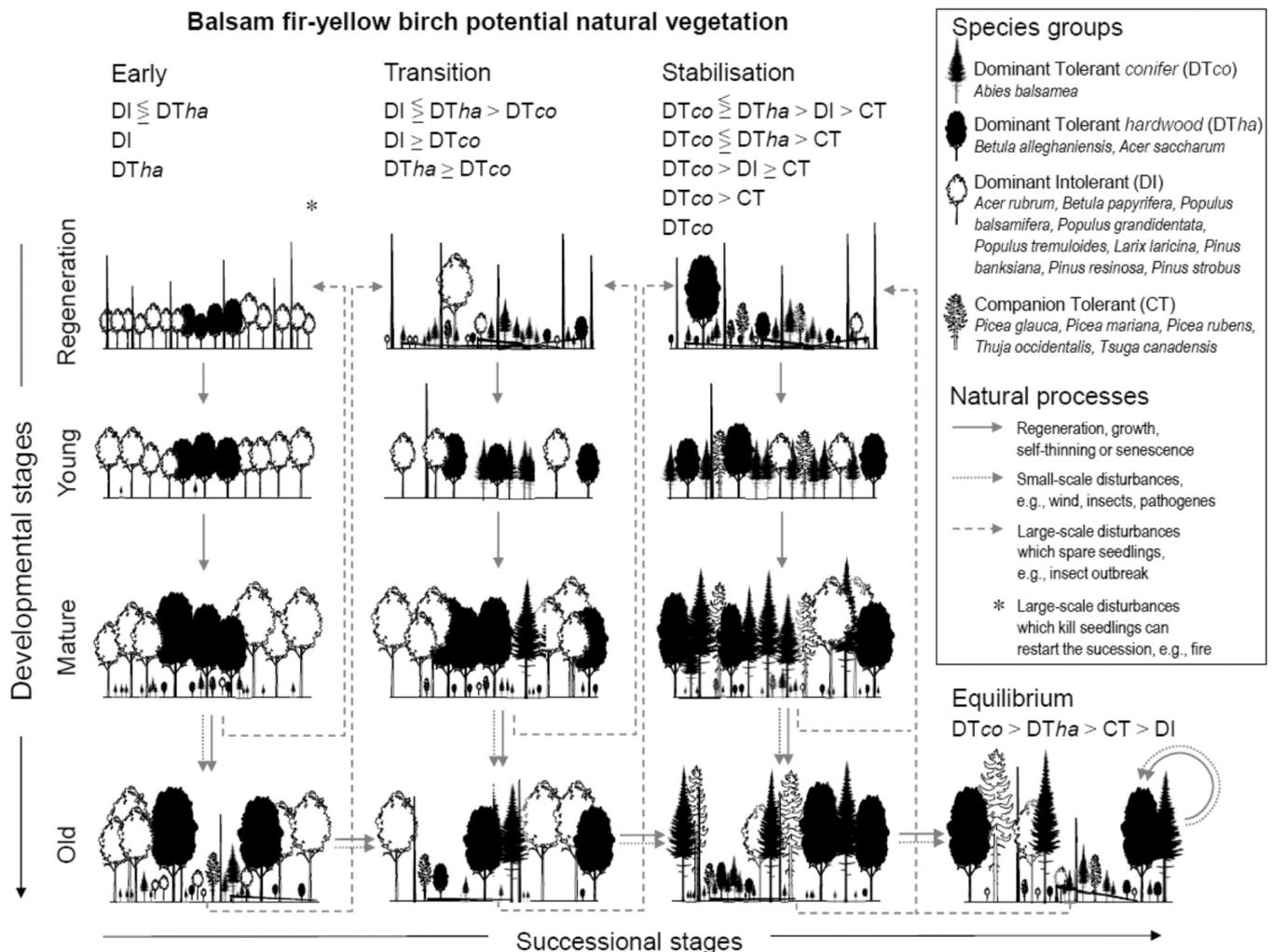


Fig. 2. Conceptual successional dynamics model from Barrette et al. (2020) predicting stand compositions of the different successional stages of the balsam fir–yellow birch potential natural vegetation.

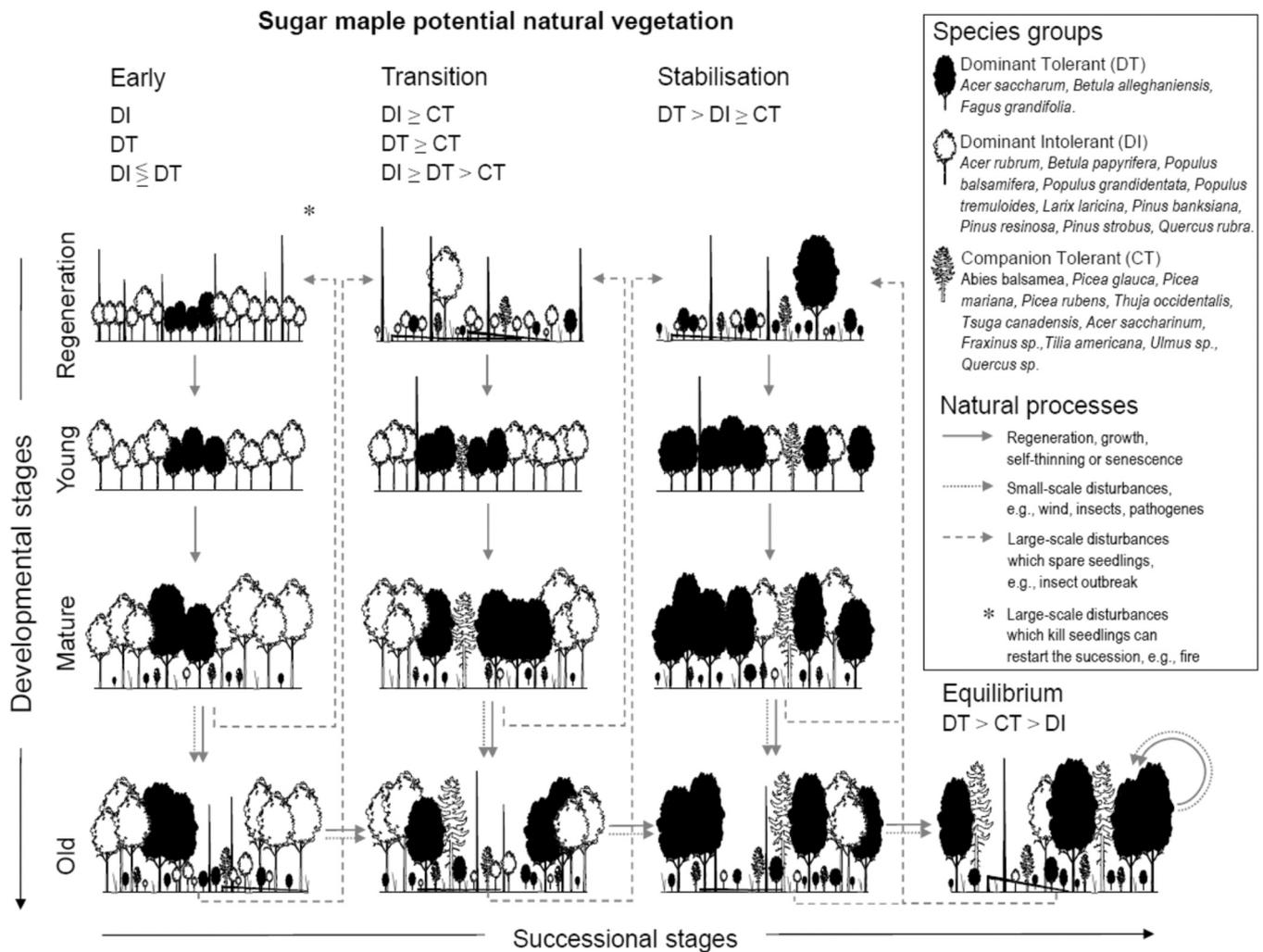


Fig. 3. Conceptual successional dynamics model from Barrette et al. (2020) predicting stand compositions of the different successional stages of the sugar maple potential natural vegetation.

respectively). Conceptual model development was based on a synthesis of available knowledge regarding successional dynamics occurring in the forests of eastern Canada (Archambault et al., 1997; Bergeron, 2000; Chen and Popadiouk, 2002; Hébert, 2003; Lorimer and Halpin, 2014; MRN, 2013; Grondin et al., 2013; Maleki et al., 2020). To allow development of comprehensive models and reduce complexity, species were aggregated according to their capacity to dominate the forest cover (i.e., dominant or companion species) and their shade tolerance (i.e., tolerant or intolerant species). Species groups were classified as dominant intolerant (DI), dominant tolerant hardwood (DTha), dominant tolerant conifer (DTco) and companion tolerant (CT) species. Natural processes drove the models (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). Developmental stage refers to the time since the last stand replacing disturbance while successional stage refers to the stand species composition (Raymond and Dumais, 2024). Early and transition stages are considered to be early successional stages while stabilization and equilibrium stages are considered to be late successional stages (Kuuluvainen and Gauthier, 2018; Barrette et al., 2020; Maleki et al., 2020).

In the early successional stage of the balsam fir–yellow birch potential natural vegetation model, DI and DTha species can occur alone or co-dominate stand composition, given that both species groups can return after stand-replacing fires (Fig. 2). In the transition successional

stage, DTco 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. The sugar maple potential natural vegetation model follows the same succession of species groups, apart from the fact that this model does not include DTco species (Fig. 3). Hence, in the sugar maple model, dominant tolerant species were simply named DT species. In the analysis of data from the plots that were located in the sugar maple ecological region, *Fagus grandifolia* was considered apart (DTfa) from the other dominant tolerant species given its strong capacity to steer succession (Bose et al., 2017; Dumont et al., 2023).

We analyzed the evolution of the composition of sapling density and tree basal area in post-clearcut stands separately for each of the ecological regions with two-way analysis of variance (ANOVA), which was implemented through linear mixed-effects models (PROC MIXED; SAS/STAT 15.1 (2018) of SAS software 9.4). Stand age groups (10-year classes), species groups, and their interaction, was used in the model as fixed effects, and plots were considered a random effect. We tested mean sapling density and tree basal area differences using a simulation method of adjustment for multiple comparisons (LSMESTIMATE statement, option adjust=simulate) 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 shade-intolerant species predominate over

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 $\alpha = 0.05$ as a significance threshold. We log-transformed the data to meet normality assumptions, but we present data in their original scales, for the sake of clarity.

3. Results

3.1. Balsam fir-yellow 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: $DI \geq DTco$; Figs. 2 and 4a). After an increase over more than 40

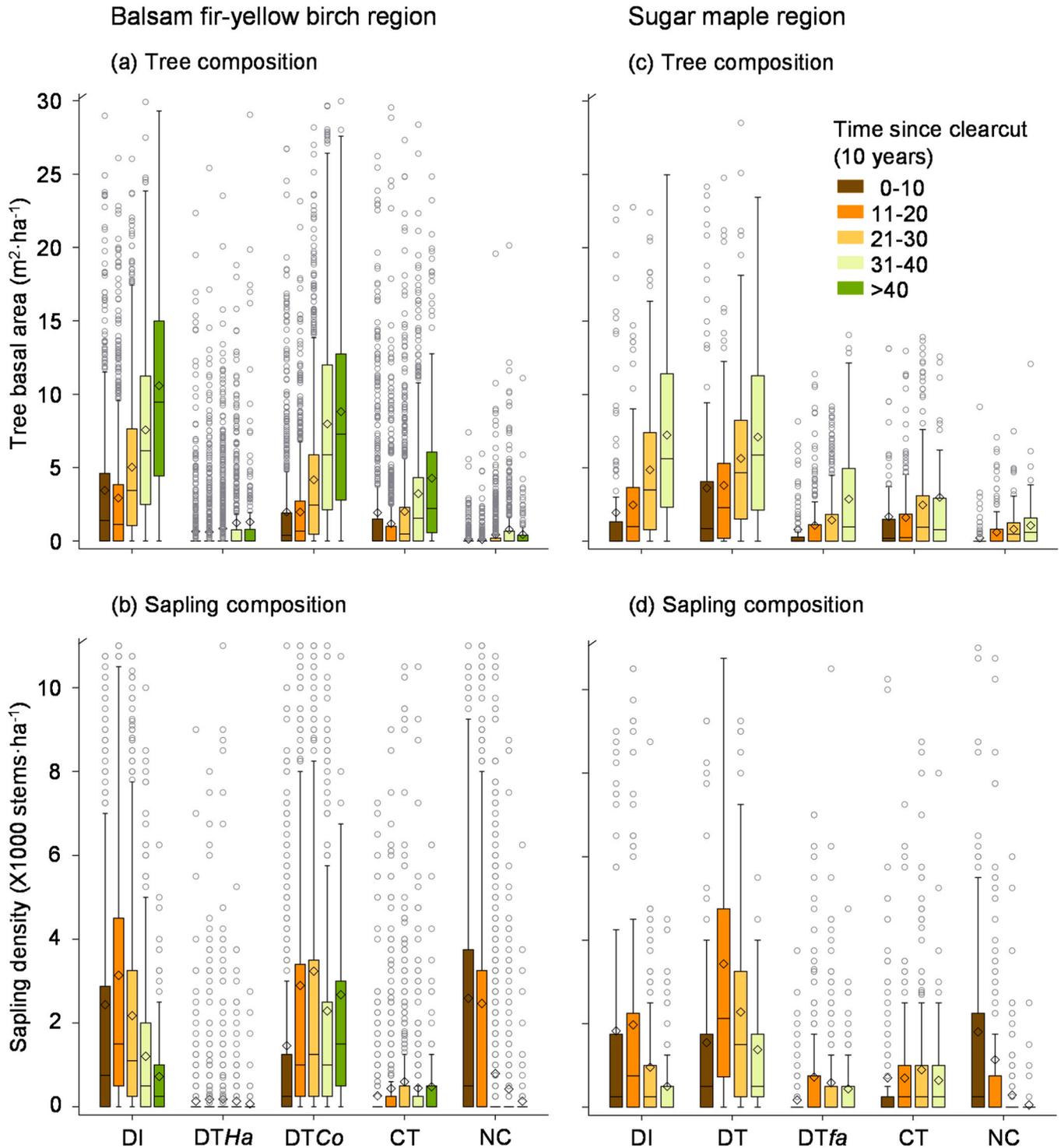


Fig. 4. Distribution of tree basal area (a, c; diameter at breast height [DBH] ≥ 9.1 cm) and sapling density (b, d; DBH: 1.1–9.0 cm) by species groups in sample plots in post-clearcut stands located in the balsam fir–yellow birch ecological region on balsam fir–yellow birch potential natural vegetation (a, b) and in the sugar maple ecological region on sugar maple potential natural vegetation (c, d). 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 $1.5 \times$ IQR; open circles enclose $>1.5 \times$ IQR).

years (Table 2; $t \geq 13.07$, $p < 0.001$), mean basal area of DI species was similar to the basal area of DTco species ($t = -1.24$, $p = 0.847$), while basal area of DTco species was two-fold higher than the basal area of CT species ($t = -6.40$, $p < 0.001$). Finally, mean basal area of DT θ a species always remained low.

Conversely, the successional trajectory of saplings in post-clearcut stands pointed toward the composition of a late successional stage (i. e., stabilization stage: DTco > DI \geq CT; Figs. 2 and 4b). After an increase over more than 40 years ($t \geq 9.11$,

$p < 0.001$) mean density of DTco species was 3.7 times higher than density of DI species ($t = 8.20$, $p < 0.001$), while density of DI species was 1.5 times higher than density of CT species ($t = -3.58$, $p = 0.005$). Finally, density of non-commercial species (NC) was abundant only in the first 20 years.

3.2. Sugar maple 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 \geq DT > CT; Figs. 3 and 4c). After an increase over more than 30 years (Table 2; $t \geq 12.45$, $p < 0.001$), mean basal area of DI species was similar to the basal area of DT species ($t = 0.928$, $p = 1.000$), while basal area of DT species was two times higher than the basal area of CT species ($t = -8.00$, $p < 0.001$). Mean basal area of DI species was still similar to the basal area of DT species, when DT *Fagus grandifolia* was included in the larger group of DT species ($t = 1.88$, $p = 0.348$). After an increase over more than 30 years ($t = 6.63$, $p < 0.001$), mean basal area of DT *Fagus grandifolia* was 2.5 times lower than the basal area of DT species ($t = -7.89$, $p < 0.001$). Basal area of NC species increased over more than 30 years ($t = 6.31$, $p < 0.001$).

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 \geq CT; Figs. 3 and 4d). After more than 30 years of stand development, mean density of DT species was three times higher than the density of DI species ($t = 5.09$, $p < 0.001$), while density of DI species was similar to the density of CT species ($t = 1.48$, $p = 0.728$). When DT *Fagus grandifolia* was included in the larger group of DT species, the density of this latter group was evidently still higher than the density of DI species ($t = 7.44$, $p < 0.001$). Mean density of DT *Fagus grandifolia* remained stable for more than 30 years ($t = 2.70$, $p = 0.083$), and then was three times lower than the density of DT species ($t = -5.19$, $p < 0.001$). Finally, density of NC species was abundant only during the first 20 years.

Table 2

ANOVA summaries and associated probabilities (*p-values*) for tree basal area and 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
Balsam fir-yellow birch region				
Age group	4	12 884	307; 52	< 0.001
Species group	4	12 884	1464; 796	< 0.001
Age group \times Species group	16	12 884	23; 32	< 0.001
Sugar maple region				
Age group	3	2 648	104; 27	< 0.001
Species group	4	2 648	160; 110	< 0.001
Age group \times Species group	12	2 648	6; 14	< 0.001

4. Discussion

Clear-cutting triggered successional setbacks in both ecological regions. After clear-cutting, successional trajectories of trees pointed toward the composition of an early successional stage in the balsam fir-yellow birch and in the sugar maple ecological regions. Even if pre-clearcut condition were not available, we are confident that these clearcuts have generally occurred in mature and old growth forests that are dominated by late-successional shade-tolerant species (Bergeron, 2000; Cyr et al., 2009; Boucher et al., 2017; Kuuluvainen and Gauthier, 2018). First, all plots were on potential natural vegetation where successional trajectories led to stands that were dominated by late-successional shade-tolerant species (Grondin et al., 2013; Robitaille et al., 2015; Prach et al., 2016). In addition, temperate forests in Quebec have been largely dedicated to supplying the pulp and paper and sawmill industries, both of which target mature and old growth forests that are dominated by late-successional shade-tolerant species (Barrette and Bélanger, 2007; Alvarez et al., 2011; Boucher et al., 2021). Also, successional trajectories of saplings in the two ecological 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 present in the understory of an early stage stand (Chen and Popadiouk, 2002; Hébert, 2003; Raymond and Dumais, 2024). Finally, the presence of companion tolerant species in early stage stands suggests that the stands under study were for the most part, in a late stage before clear-cutting, given that these species generally do not regenerate rapidly after natural disturbances akin to clear-cutting (i.e., fire; Bergeron, 2000; Barrette et al., 2019; Maleki et al., 2020). These are all indications that stands, which are now in an early stage, were in a late stage before clear-cutting; hence, clear-cutting did indeed trigger a successional setback.

Successional setbacks occurred following clear-cutting probably because this treatment is generally more beneficial to dominant shade-intolerant species (e.g., *Betula papyrifera*, *Acer rubrum*, *Populus* sp., *Pinus* sp.) and non-commercial competing species, e.g., mountain maple (*Acer spicatum* Lamb.), pin cherry (*Prunus pensylvanica* L. f.), and raspberry (*Rubus idaeus* L.), than to dominant shade-tolerant species (e.g., *Acer saccharum*, *Betula alleghaniensis*, *Abies balsamea*, *Picea rubens*) (Raymond and Dumais, 2024). By removing large part of the mature forest cover, clear-cutting puts regeneration under full sunlight conditions, which is beneficial to dominant shade-intolerant species (Carleton and MacLellan, 1994; Laquerre et al., 2009), but creates morpho-physiological stress and incurs mortality in dominant shade-tolerant species (e.g., Tucker et al., 1987; Gnojek, 1992; Dumais and Prévost, 2008). In addition, successional setbacks likely occurred because clear-cutting operations mechanically destroyed a large part of advance regeneration of dominant tolerant species (Chen and Popadiouk, 2002; Prévost, 2008). By contrast, common disturbances that preserve complex stand structure, spare and allow the acclimation of advance regeneration (e.g., moderate insect outbreaks, partial windthrows) can maintain the natural dynamics and resilience of the temperate forests toward late successional stages (Bergeron, 2000; Kneeshaw and Prévost, 2007; Kuuluvainen and Gauthier, 2018; Barrette et al., 2020; Schneider et al., 2021; Raymond and Dumais, 2024).

A major post-clearcut concern emerging from the present study for the balsam fir-yellow birch ecological region is the extirpation of the dominant shade-tolerant hardwood species, mainly represented by the loss of yellow birch. This species is an important ecological and economical component of the temperate mixedwood forest (Raymond and Dumais, 2024). Even if yellow birch can utilize moderate to high light levels to increase its subsequent growth performances at sapling stage, full-light post-cut conditions favor establishment and development of aggressive and abundant competing vegetation that is detrimental to young yellow birch seedlings (Erdmann, 1990; Bouffard et al., 2007; Gastaldello et al., 2007; Prévost et al., 2010). In temperate

mixedwood forest, yellow birch regenerates naturally under small to medium canopy gaps that are created by light due to moderate insect outbreaks, partial windthrow and individual tree senescence (Bouchard et al., 2006; Kneeshaw and Prévost, 2007; Prévost and Charette, 2015). Yet, successful regeneration of yellow birch after large to total canopy openings is also possible in temperate mixedwood forest, when mineral soil is largely exposed (e.g., after unusual catastrophic wildfire) and competing vegetation is destroyed or sparse (e.g., on less fertile soils), but such conditions are rarely reproduced by clear-cutting alone (Lafèche et al., 2000; Nguyen-Xuan et al., 2000).

In sugar maple forest, our results also highlighted compositional issues. Notably, 30–40 years after clear-cutting, the proportion of dominant shade-tolerant species is still comparable to the proportion of dominant shade-intolerant species, which runs contrary to expectation regarding natural dynamics and composition of this hardwood ecosystem (Majcen et al., 2003; Saucier et al., 2009; Nolet et al., 2014). When clear-cutting is used in this ecological forest region, this prescription likely tends to reduce the commercial value of the forest, because species such as aspen, red maple and non-commercial competing species occupy the place of more valuable hardwoods such as sugar maple and yellow birch, for an extended period. Furthermore, expansion of the problematic American beech in sugar maple stands in last few decades is a well-known phenomenon (e.g., Duchesne and Ouimet, 2009; Gravel et al., 2011; St-Jean et al., 2021). Results of the present study indicate that clear-cutting can generate such undesirable situations. Therefore, major clear-cutting disturbance could have exacerbated this problem by favoring rapid growth of saved advance American beech and development of its root suckers (Beaudet et al., 2007; Nelson and Wagner, 2014) as well as other competing vegetation (Lafèche et al., 2000; Prévost, 2008; Raymond and Bédard, 2017) at the expense of sugar maple and yellow birch seedlings and saplings. By contrast, recent results of St-Jean et al. (2021) suggest increasing harvest intensity under an irregular shelterwood scenario may favour sugar maple over beech, but only when maple constitutes less 60 % of advance seedling regeneration and the overstory contains low beech abundance (basal area < 6 m²/ha). Finally, our study confirms the status of sugar maple as a late successional species, even if its plasticity and sprouting ability allow it to establish after large canopy disturbances like fire or clearcut (Nolet et al., 2008).

5. Forest management implications

When post-clearcut successional setbacks occur in temperate forests, as was observed in the present study, the expected time to compositional recovery may be extended by at least an additional century (Hébert, 2003; Raymond and Dumais, 2024). This prolongation could lead to an overestimation of allowable cuts of economically important late-successional species and subsequently to a temporary forest composition conversion. To address this sustainable management issue in a comprehensive manner with clear-cutting, foresters could use partial cut approaches such as selection or group-selection cut and irregular shelterwood scenarios (Nolet et al., 2014; Raymond and Bédard, 2017; St-Jean et al., 2021). Such partial cut approaches gradually remove the forest cover, creating small to medium canopy gaps promoting advance regeneration of late successional species such as yellow birch, red spruce and sugar maple (Majcen et al., 2003; Dumais and Prévost, 2008; Prévost and Charette, 2015; Raymond and Bédard, 2017; St-Jean et al., 2021; Raymond and Dumais, 2024). It will be essential to improve our understanding of long-term effects of clear-cutting when used in conjunction with partial cutting on successional dynamics to promote the sustainable management of temperate forests.

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CRediT authorship contribution statement

Isabelle Auger: Formal analysis, Validation, Writing – review & editing. **Daniel Dumais:** Conceptualization, Methodology, Writing – review & editing. **Yan Boucher:** Writing – review & editing. **Martin Barrette:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Generative AI and AI-assisted technologies in the writing process

None used.

Declaration of Competing Interest

None declared.

Data availability

I have shared the link to the data in the manuscript

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