Resilience of uneven-aged mixedwood stands altered by diameter-limit cutting and opportunities for their rehabilitation

By Patricia Raymond[1,*], Hugues Power[1], François Guillemette[1], Josianne DeBlois[1] and Daniel Dumais[1]

ABSTRACT

Repeated diameter-limit cutting in mixedwood forests often leads to altered stand composition, quality, and regeneration, hence decreasing productivity and value over time. We studied the evolution of stand characteristics after diameter-limit cutting on a 15-year period, beginning from 11 to 43 years after cutting. We used 415 sample plots (200 m²) and three criteria: (i) ≥9.0 m²/ha overstory (trees ≥9.1 cm dbh [diameter at breast height, 1.3 m above ground]) acceptable growing stock (AGS, i.e. basal area of vigorous trees with sawlog potential), (ii) ≥3.0 m²/ha pole timber AGS (9.1 cm-23.0 cm dbh) and (iii) ≥60% sapling (dbh 1.1-9.0 cm) stocking of desired species. Stand initial quality was determined in function of overstory AGS at the beginning of the monitoring period: good quality (AGS≥9.0 m²/ha), impoverished (7.0≤AGS< 9.0 m²/ha), degraded (AGS <7.0 m²/ha). After 15 years, 47% of stands satisfied at least two criteria, but most stands (65%) had insufficient sapling regeneration. Stands in good quality and impoverished categories had sufficient basal area and AGS to support a new partial cutting cycle, contrary to stands in the degraded category. A conceptual model based on these three criteria is presented to guide silvicultural rehabilitation of uneven-aged mixedwood stands altered by past cutting practices.

Keywords: yellow birch, red spruce, balsam fir, diameter-limit cutting, anthropogenic disturbances, resilience, silvicultural rehabilitation

RÉSUMÉ

L'utilisation répétée des coupes à diamètre limite en forêt mixte peut altérer la composition, la qualité et la régénération des peuplements à long terme. Nous avons étudié l'évolution des caractéristiques de peuplements récoltés en coupe à diamètre-limite sur une période de 15 ans, débutant de 11 à 43 ans après coupe. Nous avons utilisé 415 placettes-échantillons (200 m²) et trois critères : (i) ≥9,0 m²/ha de capital forestier en croissance (CFC, i.e. surface terrière des arbres vigoureux avec potentiel sciage) du peuplement (arbres ≥9.1 cm au dhp [diamètre à hauteur de poitrine, 1,3 m du sol]), (ii) ≥3,0 m²/ha de CFC des perches (dhp 9,1 cm-23,0 cm) et (iii) un coefficient de distribution des gaules (dhp 1,1-9,0 cm) en essences désirées ≥60 %. La qualité initiale des peuplements a été déterminée en fonction du CFC du peuplement au début de l'étude : bonne qualité (CFC≥9,0 m²/ha), appauvrie (7,0≤CFC<9,0 m²/ha), dégradée (CFC<7,0 m²/ha). Après 15 ans, 47 % des peuplements satisfaisaient au moins deux critères, mais la majorité (65 %) avaient une régénération insuffisante en gaules. Les peuplements des catégories de bonne qualité et appauvrie ont suffisamment récupéré en surface terrière et en CFC du peuplement pour permettre un nouveau cycle de coupes partielles, contrairement aux peuplements de la catégorie dégradée. Un modèle conceptuel basé sur ces trois critères est présenté pour guider la réhabilitation sylvicole de peuplements mixtes de structure inéquienne altérés par les pratiques passées.

Mots-clés : bouleau jaune, épinette rouge, sapin baumier, coupe à diamètre limite, perturbation anthropique, résilience, réhabilitation sylvicole

Introduction

Rehabilitation of forests altered by anthropogenic or natural disturbances is recommended for mitigating effects of global change through enhanced carbon storage capacity (Roxburgh *et al.* 2006; Krug 2019; Thom and Keeton 2019). Forest rehabilitation is also an opportunity to improve adaptive capacity by promoting resilience to disturbances through functional diversity, the components of biodiversity that influence how an ecosystem operates and responds to environmental change (Messier *et al.* 2019). Structural and compositional diversity have been identified as major drivers of functional diversity represented by plant traits (Thom *et al.* 2021). Hence, mixedwoods (i.e., mixed-species forests made of conifer and deciduous species), which naturally occur through complementary niche use, possess high functional diversity and inherent resilience (Raymond *et al.* 2020; Pardos *et al.* 2021; Urgoiti *et al.* 2022). In the North American temperate-boreal ecotone, light and moderate disturbances between long fire intervals generate a variety of ecological niches suitable to a diversity of species, thereby facilitating spatio-temporal coexistence (Kneeshaw and Prévost 2007; Kern *et al.* 2021).

In managed forests, anthropogenic disturbances are superposed on natural disturbances and interfere with their natural dynamics (Danneyrolles *et al.* 2019; Kenefic *et al.* 2021). When anthropogenic disturbances alter key ecosystem

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[1]Direction de la recherche forestière, Ministère des Ressources naturelles et des Forêts du Québec, 2700 rue Einstein, Québec (Québec), Canada G1P 3W8. *Corresponding author: patricia.raymond@mrnf.gouv.qc.ca

functions, resilience and successional trajectories can be affected (Ghazoul *et al.* 2015; Webster *et al.* 2018). One common anthropogenic disturbance in managed forests is diameter-limit cutting (Kenefic and Nyland 2005; Belair and Ducey 2018). This exploitative cutting method removes all quality trees of desired commercial species above fixed diameter thresholds (Prévost and Charette 2019). The repeated use of this method can lead to the alteration of stand composition, quality, and regeneration over time (Vásquez-Grandón *et al.* 2018; Power *et al.* 2019; Curtze *et al.* 2022), hence decreasing productivity and value (Sokol *et al.* 2004; Kenefic *et al.* 2005; Rogers *et al.* 2017). In certain cases, cumulative effects can result in resilience losses and push stands to alternative stable states, where they are maintained in suboptimal states from both ecological and economic points of views (Ghazoul *et al.* 2015; Vásquez-Grandón *et al.* 2018; Webster *et al.* 2018). More effort is then required to recover natural successional trajectories and productivity; rehabilitation actions are necessary to provoke significant changes in stand dynamics (Ghazoul *et al.* 2015; Webster *et al.* 2018).

Nyland (2016) defines silvicultural rehabilitation as the process of re-establishing functionality in stands compromised by a disturbance. Silvicultural actions for rehabilitation include treatments designed to improve or restore missing components of functionality. For instance, silvicultural rehabilitation restores desired species composition, structure, or processes to an altered ecosystem (Stanturf *et al.* 2014). In the specific case of natural uneven-aged stands, we pose that productive healthy stands have enough vigorous high-quality trees and regeneration of desired species at all stages (seedling, sapling, poles) to ensure functionality and sustainability over time. In this perspective, silvicultural actions to rehabilitate functionality in natural uneven-aged mixedwood stands could aim to improve tree regeneration, as well as pole and mature tree composition, quality, and structure to help stands recover natural trajectories (Vásquez-Grandón *et al.* 2018).

In practice however, we know little about the extent of alteration after diameter-limit cutting in mixedwood stands, how they recover naturally, and in which situations a rehabilitation would be necessary. Recent work indicates that stands harvested with this method can recover their production in absence of intervention, but some components can be missing (such stands are considered as "impoverished") (Power *et al.* 2019; Raymond *et al.* 2020). There is also a need for identifying stand-scale regional thresholds to define the degree of alteration and possible silvicultural actions for rehabilitation (Vásquez-Grandón *et al.* 2018). In addition, certain forest types could be more vulnerable to loss of functional components than others after diameter-limit cutting, but very few studies have documented the long-term effects with regards to ecological site conditions.

Acceptable growing stock (AGS), the basal area of vigorous trees with sawlog potential, is one criterion commonly used in forest management to define stand vigor and quality (Majcen *et al.* 1990; Leak *et al.* 2014; Nyland 2016). For example, in a former study (Power *et al.* 2019), we used overstory AGS (trees with a dbh >9.0 cm [diameter at breast height, 1.3 m above ground]) to assess stands harvested by diameter-limit cutting but left to grow without intervention. Based on stand vigor and quality, we found that the proportion of stands classified as degraded or impoverished decreased by 37% in 15 years, based on the reconstitution of overstory AGS, especially that of conifers. Nevertheless, 45% of stands still had suboptimal production and required improvement to various degrees, 26 to 58 years after diameter-limit cutting. These results based on overstory AGS, however, do not inform about the potential stand structure and composition. For this reason, the present study further analyzed, in addition to overstory AGS, how future lumber sawlog trees, e.g., pole-size trees with potential sawlog production (i.e., 9.1–23.0 cm dbh, hereafter "pole AGS") and regeneration (i.e., sapling stocking, 1.1–9.0 cm dbh) have evolved over the last 15 years, with the goal of identifying shortfalls and making recommendations for silvicultural rehabilitation. We also aim to detect forest types where mixedwood stands grow that could be more vulnerable to loss of functional components and for which rehabilitation could be prioritized. Given the contribution of conifers to the reconstitution of overstory AGS observed in former studies in mixedwood forests (Power *et al.* 2019; Raymond *et al.* 2020), we predict that forest types with lower conifer proportions (<25% BA in conifer, i.e., deciduous forest types) will have lower overstory AGS, pole AGS and sapling stocking, and thus require more rehabilitation treatments than those with higher conifer proportions (i.e., mixedwood and conifer types). We then verify if stands categorized as degraded and impoverished at the beginning of the study have lower sapling stocking in desired species than those classified as good quality. Finally, we propose a general framework of rehabilitation silviculture based on our observations.

Material and methods

Data collection

The study was conducted in the province of Québec, Canada, in both the sugar maple (*Acer saccharum* Marsh., SM)–yellow birch (*Betula alleghaniensis* Britt., YB) and the balsam fir (*Abies balsamea* (L.) Mill., BF)-yellow birch bioclimatic domains (Saucier *et al.* 2009). We used the Québec 3rd forest inventory program (1991–2003) to identify potentially altered mixedwood stands, searching for stands with mixed composition of yellow birch and conifers, a cover density between 25% and 60%, and a partial cut disturbance code, with or without light epidemic defoliation, occurring between 1970 and 1990. Within the 259 710 ha that corresponded to this situation, we initially identified 598 mapped forest stands. Then, we randomly selected 102 of these mapped stands located on public lands and accessible from the main road network in three administrative regions (Mauricie, Capitale-Nationale and Bas-Saint-Laurent) (Fig. 1). A group of 533 circular sample plots, each with an area of 200 m^2, were established in 2000 and 2001 using transects with cluster of four to 10 sample plots. The transects within the same mapped stand were positioned perpendicularly to the slope and were located 100 m from each other. Most of the plots (75%) were in mixed yellow birch–balsam fir stands, and a smaller proportion (25%) in stands largely dominated by yellow birch. Stands also contained red maple (*Acer rubrum* L.), sugar maple, red spruce (*Picea rubens* Sarg.) and other less abundant species (Power *et al.* 2019). The year of the partial cut was retrieved from archived forest cover maps and tree cores (see Power *et al.* 2019 for details). For each plot, drainage and soil texture were identified

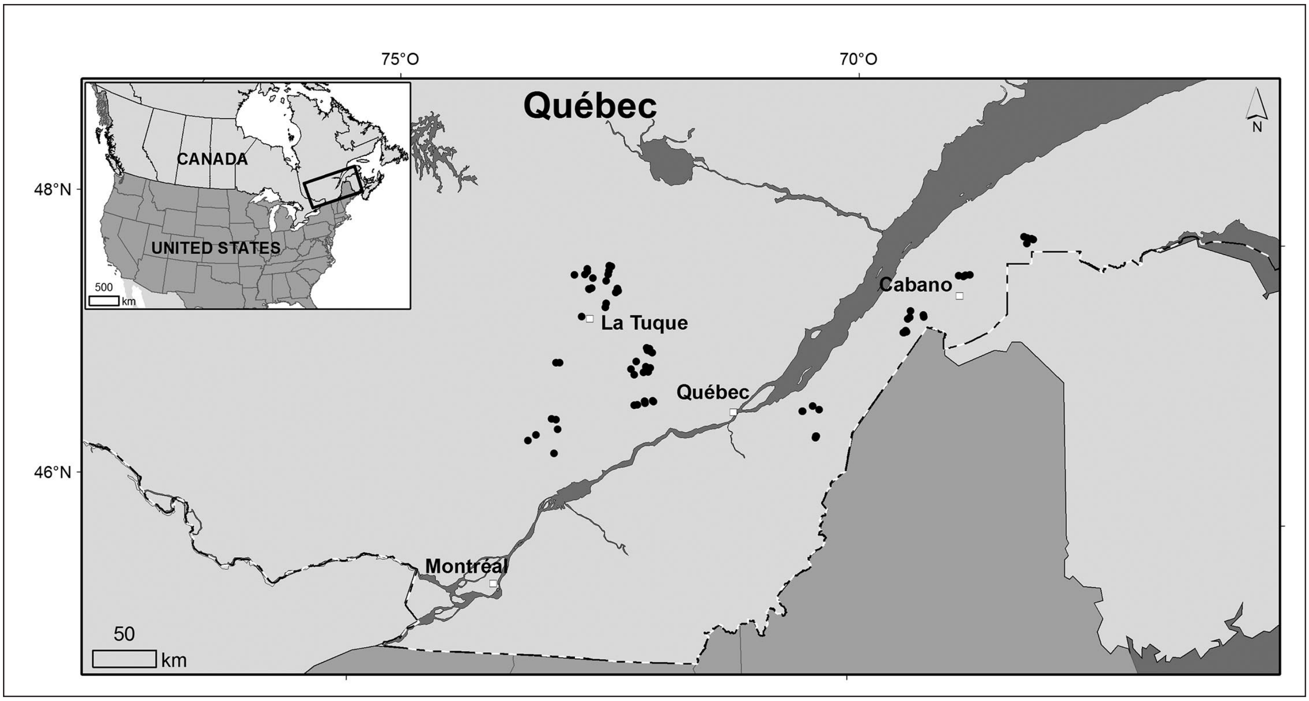

Fig. 1 Geographical distribution of the 102 mapped stands selected in southern Quebec to assess stand characteristics after diameter-limit cutting.

according to Québec's forest inventories method (MFFP 2015). Each plot was measured four times at 5-year intervals. A total of 415 plots of the 533 initial plots were monitored over the 15-year period. The other plots were abandoned due to harvesting or loss of accessibility (51 after five years and 66 after 10 years of monitoring). The assessment after 15 years represents stand characteristics 26 to 58 years after diameter-limit cutting.

Forest type, based on Quebec's ecological classification (Gosselin 2002) was initially assessed in each plot. The plots represented six forest types: sugar maple–yellow birch (SM–YB, corresponding to "FE3" in the provincial classification), yellow birch–balsam fir–sugar maple (YB–BF–SM; MJ1), yellow birch–balsam fir (YB–BF; MJ2), balsam fir–yellow birch (BF–YB; MS1), balsam fir–white birch (*Betula papyrifera* Marsh., WB) (BF–WB; MS2), and balsam fir–eastern white cedar (*Thuja occidentalis* L., WC) (BF–WC; RS1). At each measurement, living trees with a dbh greater than 9.0 cm were measured with a diameter tape. In addition, tree vigour and sawlog potential were estimated based on the Majcen *et al.* (1990) classification system to calculate the basal area (BA, m^2/ha) in AGS. This system comprises six tree vigor classes: I) vigorous deciduous tree with sawlog potential; II) vigorous deciduous tree without sawlog potential; III) nonvigorous deciduous tree with sawlog potential (if dbh >23.0 cm only); IV) nonvigorous deciduous tree without sawlog potential; V) vigorous conifer tree and VI) nonvigorous conifer tree (conifers are considered as always having sawlog potential). A tree is deemed as sawlog potential when it has at least one 2.5 m log of lumber or could produce one over the next cutting cycle. Minimal dbh for a sawlog potential in conifers is 9.1 cm and 23.1 cm in hardwoods in the region. Trees that grew above the 9.1 cm threshold between two measurements were added to the database as recruits. Dbh, species, and tree vigour were also recorded for each recruited tree. Each 200 m^2 plot comprised five subsampling points (9 m^2 subplots), where saplings (woody stems including shrubs >1.0 cm and <9.0 cm at dbh) were tallied by species and 2 cm dbh classes.

Data analysis

Criteria used for the functionality assessment

Overstory AGS was computed by summing the BA of trees of desired species belonging to either vigor class I (hardwood vigorous trees with sawlog production potential) or V (softwood tree with sawlog production potential) according to the Majcen *et al.* (1990) system. Desired species included those with commercial value: yellow birch, white birch, sugar maple, red spruce, white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea Mariana* [Mill.] BSP.), balsam fir, eastern white cedar, and eastern hemlock (*Tsuga canadensis* [L.] Carr). We excluded balsam fir larger than 19 cm from the calculus, given the rapid vigor decline and higher mortality risk after trees of that species reach that size in temperate mixedwood stands (Fortin *et al.* 2008; Raymond *et al.* 2016; Guillemette 2019). We did not include red maple as desired species, because the study area is located at the northern edge of its range, it has poor form and value (Gunn *et al.* 2019), and generally outcompetes the desired species after heavy cuttings (Abrams 1998). Stand initial quality was rated according to three categories, based on overstory AGS at the beginning of the measurement period (MRN 2013): good quality ($AGS \geq 9.0$ m^2/ha, >40% of BA in AGS, after Leak *et al.* 1987), impoverished ($7.0 \leq AGS < 9.0$ m^2/ha, 30 to 40% of BA in AGS) or degraded ($AGS < 7.0$ m^2/ha, less than 30% in BA in AGS). Stand values were first computed at each measurement by grouping plots on the same transects found in the same forest type (thereafter called "stands") and used for all analyses. The overstory AGS criterion was considered as fulfilled with at least 9.0 m^2/ha in trees >9.0 cm dbh of desired species (MRN 2013) and the pole AGS criterion with a minimum of 3.0 m^2/ha in trees of desired species between 9.1 and 23.0 cm dbh (Majcen *et al.* 1990). We used a 60% stocking (i.e., the percentage of occurrence in subplots) in saplings (1.1–9.0 cm dbh) of desired species as regeneration criterion threshold. At year 15, we calculated the number of stands that met each overstory, pole and regeneration criteria, and their combination.

We used linear mixed models with repeated measurements (MIXED procedure; SAS statistical software version 9.4, SAS Institute Inc., Cary, North Carolina, USA) to determine the effect of time, forest type and stand quality at the start of the measurement period (hereafter "stand initial quality") on the variables merchantable-size basal area (hereafter "overstory BA"), overstory AGS, pole AGS and sapling stocking (variables analyzed separately). Analyses were performed on stand values at each measurement (0, 5, 10 and 15 years) using year, forest type and stand initial quality as fixed effect factors, as well as the three double-interactions and the three-way interaction between these factors. The time elapsed since partial cutting at year 0 (between 11 and 43 years) was also tested as a covariate to account for differences at the beginning of the study period. We started with the complete model and used a backward elimination process to sequentially remove nonsignificant effects until all the remaining effects in the model were significant ($p<0.05$). Interactions between the covariate and the other factors in the reduced model were tested, but they were never retained in the model. A transect random effect was also tested but the models did not converge, so it was not included. We used Kenward-Roger's method to approximate the denominator degrees of freedom and a variance-covariance matrix to consider the correlation between measurements made on the same stands. This matrix was chosen to minimize the likelihood value of the model, while involving as few parameters as possible and considering consistency across sets of analyses. The heterogenous Toeplitz matrix (TOEPH) was used for all analyses, considering different residual variances for each stand initial quality to take unequal variances into account for overstory and pole AGS analyses only. In the resulting models, a simulation-based approach was used on significant factors and interactions to make pairwise comparisons and to assess differences while considering test multiplicity (Edwards and Berry 1987; Westfall *et al.* 2011). For significant interactions between main factors, all mean values that related to the levels of one factor were compared at a fixed level of the other factors. The 0.05 error rate was applied within each fixed level of the main factors, as a separate-family approach (Westfall *et al.* 2011). Although tests were done on least squares means, all mean values presented in the results section are those calculated on the original data (observed means). For all models, the normality and the homogeneity of residuals variance and the presence of outliers were verified graphically.

Results

Assessment of functionality criteria after 15 years of monitoring

At the fourth measurement (15 years), 21% of sampled stands met all three criteria (i.e., overstory AGS, pole AGS and sapling stocking) (Fig. 2). Almost half of stands (47%) met two criteria; the most frequent situation was satisfactory overstory and pole AGS with poor regeneration of desired species (35%). The remainder of sampled stands (32%) had only one (25%) or no (7%) criterion met. Our results also indicated that approximately two-third of stands could require silvicultural treatments to establish regeneration (65%), a third would need improvement of overstory AGS (33%), and a fifth (21%) an increase of pole AGS.

When considering the forest type, all had overstory and pole AGS exceeding our minimum levels of 9.0 m^2/ha and 3.0 m^2/ha, respectively, after 15 years (Table 1). Note that the forest type BF–YB had only 26.7% conifer basal area, while this mixedwood forest type would be expected to be dominated by conifers (i.e., percent BA >50%). Regeneration wise, only BF–WB met the 60% stocking of desired species threshold after 15 years. The two other conifer-dominated forest types, BF–YB and BF–WC, had the poorest regeneration

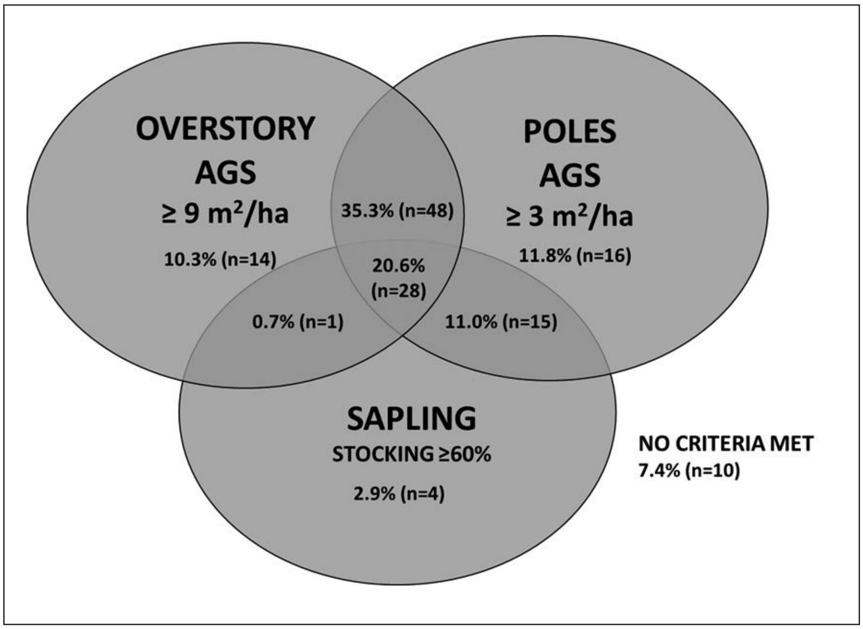

Fig. 2 Proportion of stands meeting the criteria of overstory AGS (acceptable growing stock), pole AGS and sapling stocking after 15 years of observation (n=136). The overstory AGS criterion was satisfied with at least 9.0 m^2/ha in vigorous trees >9.0 cm dbh of desired species (MRN 2013) and poles AGS with a minimum of 3.0 m^2/ha in vigorous trees 9.1–23.0 cm dbh of desired species (Majcen *et al.* 1990). The regeneration criterion was met with a sapling (1.1–9.0 cm dbh) stocking of at least 60% in desired species.

Table 1. Average stand conditions (mean ± standard error) in terms of merchantable-size basal area (overstory BA), stand acceptable growing stock (overstory AGS), pole-size AGS and regeneration (saplings 1.1–9.0 cm dbh) by forest type after 15 years of observation (26 to 58 years after cutting).

Forest type	n	Overstory BA (m^2/ha)	% BA in conifers	Overstory AGS (m^2/ha)	Pole AGS (m^2/ha)	Saplings (% stocking)
SM–YB	28	26.6 ± 1.6	16.1 ± 3.5	11.9 ± 1.1	4.1 ± 0.4	44.6 ± 4.1
YB–BF–SM	15	29.3 ± 2.7	27.7 ± 4.7	10.0 ± 1.5	5.7 ± 0.7	44.3 ± 7.1
YB–BF	50	25.2 ± 1.0	41.1 ± 2.7	11.1 ± 0.6	5.7 ± 0.4	42.3 ± 3.2
BF–YB	18	23.6 ± 2.1	26.7 ± 3.6	11.7 ± 1.2	3.9 ± 0.7	31.8 ± 5.7
BF–WB	16	23.0 ± 1.7	53.3 ± 8.0	12.6 ± 1.6	9.8 ± 1.7	62.1 ± 7.0
BF–WC	9	30.7 ± 3.5	72.2 ± 5.6	19.0 ± 3.5	3.4 ± 0.8	35.6 ± 10.9

Note: SM=sugar maple; YB=yellow birch; BF=balsam fir; WB=white birch; WC=eastern white cedar. In this table, n refers to the number of plot clusters on the same forest type within a same transect. Overstory basal area (BA) includes merchantable trees >9.0 cm dbh of all commercial tree species. Overstory AGS is the BA of vigorous trees of desired species with potential sawlogs (>9.0 cm dbh) and pole AGS is the BA of vigorous trees of desired species with potential sawlogs between 9.1 and 23.0 cm. Regeneration is the stocking of desired species in saplings (1.1–9.0 cm dbh).

Table 2. Number of stands satisfying the criteria of overstory acceptable growing stock (AGS), pole AGS and regeneration by forest type after 15 years of observation (26 to 58 years after diameter-limit cutting). The proportion (%) of stands of the same forest type that meet a criterion is presented in parentheses.

		Criteria satisfied							
Forest type	n	Overstory Pole Regen	Overstory Pole	Overstory Regen	Pole Regen	Overstory	Pole	Regen	None
SM-YB	28	5 (18)	6 (21)	0 (0)	5 (18)	6 (21)	4 (14)	2 (7)	0 (0)
YB–BF–SM	15	3 (20)	6 (40)	0 (0)	2 (13)	0 (0)	1 (7)	1 (7)	2 (13)
YB–BF	50	10 (20)	24 (48)	1 (2)	3 (6)	1 (2)	8 (16)	0 (0)	3 (6)
BF–YB	18	2 (11)	8 (44)	0 (0)	1 (6)	3 (17)	0 (0)	0 (0)	4 (22)
BF–WB	16	7 (44)	2 (13)	0 (0)	3 (19)	1 (6)	3 (19)	0 (0)	0 (0)
BF–WC	9	1 (11)	2 (22)	0 (0)	1 (11)	3 (33)	0 (0)	1 (11)	1 (11)
Total	**136**	**28 (21)**	**48 (35)**	**1 (<1)**	**15 (11)**	**14 (10)**	**16 (12)**	**4 (3)**	**10 (7)**

Note: SM=sugar maple; YB=yellow birch; BF=balsam fir; WB=white birch; WC=eastern white cedar. In this table, n refers to the number of plot clusters on the same forest type within a same transect. We used the same overstory BA, overstory AGS, pole AGS and regeneration criteria as for Table 1.

with 31.8% and 35.6% sapling stocking of desired species, respectively. Else, BF–WC, SM–YB and BF–YB had the highest proportion of stands with only one or no criterion met (56%, 43% and 39%, respectively) (Table 2). This proportion of poor results was lower for the three other mixedwood forest types: 26% for YB–BF–SM, 24% for YB–BF, and 25% for BF–WB. The latter three mixedwood types had the highest functionality satisfaction criteria, with nearly three-quarters of stands meeting two or three criteria.

The satisfaction of functionality criteria slightly varied with the stand quality at the start of the measurement period. The percentage of stands with initial good quality (76%) that met two or three criteria after 15 years was higher than that of stands initially categorized as impoverished (65%) or degraded (64%) (Table 3). Good and impoverished stands tended to have more similar trends in functionality satisfaction criteria than those in the degraded category. Moreover, most of the initially good quality and impoverished stands could need an action to establish regeneration (70% and 85%, respectively). A lower percentage (24%) of initially good quality stands met only one or no criterion after 15 years relative to initially impoverished and degraded categories (35% and 36%, respectively). Finally, 40% of stands in the degraded category satisfied either pole AGS only or pole AGS and regeneration criteria.

Dynamics of overstory BA, overstory AGS, pole AGS and sapling stocking

Time elapsed since partial cutting was significant for overstory BA, overstory AGS and sapling stocking (Table 4). All other things being equal, the more time elapsed since the partial cut, the greater the increase in overstory BA and AGS (the covariate parameter estimate, and its standard error are 0.2781 ± 0.0877 and 0.0334 ± 0.0154, respectively). In contrast, the more time elapsed since the partial cut, the greater the decrease in sapling stocking (-0.0087 ± 0.0028 for the covariate).

Analyses with repeated measurements revealed significant variation of overstory BA and AGS and sapling stocking with year ($p<0.001$), and with the interaction of year and stand initial quality for pole AGS ($p=0.002$) (Table 4). Overstory BA and AGS gradually increased at each measurement for an overall gain of 36% and 54% over 15 years of observation, respectively (Fig. 3a, b). The corresponding overstory BA periodic annual increment was 0.45 m^2/ha/year. The year × stand initial quality interaction shows three distinct trajecto-

Table 3. Number of stands satisfying the criteria of overstory acceptable growing stock (AGS), pole AGS and regeneration by stand initial quality after 15 years of observation (26 to 58 years after diameter-limit cutting). The proportion (%) of stands of the same initial quality that meet a functional criterion is presented in parentheses.

		Criteria satisfied							
Stand initial quality	**n**	**Overstory Pole Regen**	**Overstory Pole**	**Overstory Regen**	**Pole Regen**	**Overstory**	**Pole**	**Regen**	**None**
Good	37	9 (24)	18 (49)	0 (0)	1 (3)	6 (16)	0 (0)	1 (3)	2 (5)
Impoverished	26	4 (15)	13 (50)	0 (0)	0 (0)	6 (23)	1 (4)	0 (0)	2 (8)
Degraded	73	15 (21)	17 (23)	1 (1)	14 (19)	2 (3)	15 (21)	3 (4)	6 (8)

Note: In this table, n refers to the number of plot clusters on the same forest type within a same transect. We used the same overstory BA, overstory AGS, pole AGS and regeneration criteria as for Table 1.

Table 4. Resulting model for each variable.

Variable	Effect	ndf	ddf	F Value	*Pr>F*
Overstory BA	Year	3	189.8	67.28	<0.001
	Forest type	5	136.1	4.76	<0.001
	Stand initial quality	2	136.1	12.91	<0.001
	Time since partial cutting	1	136.1	10.05	0.002
Overstory AGS	Year	3	149.2	63.87	<0.001
	Stand initial quality	2	74.7	135.47	<0.001
	Time since partial cutting	1	33.8	4.67	0.0378
Pole AGS	Year	3	112.2	13.14	<0.001
	Forest type	5	97.7	3.82	0.003
	Stand initial quality	2	51.5	2.88	0.065
	Year × Stand initial quality	6	101.4	3.79	0.002
Sapling stocking	Year	3	203.2	24.30	<0.001
	Forest type	5	128.3	4.07	0.002
	Time since partial cutting	1	128.3	9.72	0.002

Note: ndf = numerator degrees of freedom; ddf = denominator degrees of freedom; BA = basal area; AGS = acceptable growing stock. The heterogenous Toeplitz matrix (TOEPH) was retained for all variables, considering different residual variances for each stand initial quality for overstory and pole AGS only.

ries for pole AGS: (i) remained constantly high in good quality, (ii) increased during the first 5-year period and then remained high in impoverish, and (iii) steadily increased significantly at each measurement in the degraded category (Fig. 3c). Sapling stocking decreased with time after year 5, dropping from 53% to 44% in ten years (Fig. 3d).

Analyses detected effects of stand quality at the start of measurement period on overstory BA (p<0.001) and AGS (p<0.001). Overall overstory BA and AGS after 15 years were significantly lower with poorer stand initial quality (Fig. 4a,b). Overstory BA averaged 28.2 m^2/ha in good quality, 23.5 m^2/ha in impoverished and 19.5 m^2/ha in the degraded category. AGS in good quality (15.8 m^2/ha) was more than twice the value observed in degraded (6.8 m^2/ha), while impoverished fell between these two (11.2 m^2/ha). Thus, AGS represented 56%, 48% and 35% of the growing stock, respectively for stands initially categorized as good, impoverished, and degraded.

When considering the forest type, differences were observed for overstory BA (p<0.001), pole AGS (p=0.003) and sapling stocking (p=0.002). These revealed that BF–WB differed slightly from other forest types: 1) overstory BA was lower in BF–WB (18.8 m^2/ha) than in SM–YB (24.6 m^2/ha) and YB–BF–SM (26.1 m^2/ha), 2) pole AGS was higher in BF-WB (7.8 m^2/ha) than SM–YB (3.6 m^2/ha), BF–YB (3.6 m^2/ha) and BF–WC (3.3 m^2/ha), and 3) sapling stocking was higher in BF–WB (68%) than in BF-YB (36%) and BF–WC (38%) (Fig. 5). The absence of significant difference in overstory BA between BF–WC and BF–WB may seem surprising, but their least squares means (BF–WC = 21.4 m^2/ha and BF–WB = 19.2 m^2/ha) were closer than their observed means presented in the Fig. 5a (BF–WC = 25.8 m^2/ha and BF–WB = 18.8 m^2/ha).

Discussion

Given their capacity to recover their growth and vigor in the long term, mixedwood stands altered by diameter-limit cutting have proven to exhibit some resilience (Power *et al.* 2019; Raymond *et al.* 2020). In fact, for stands that have undergone high grading, the majority of which were considered

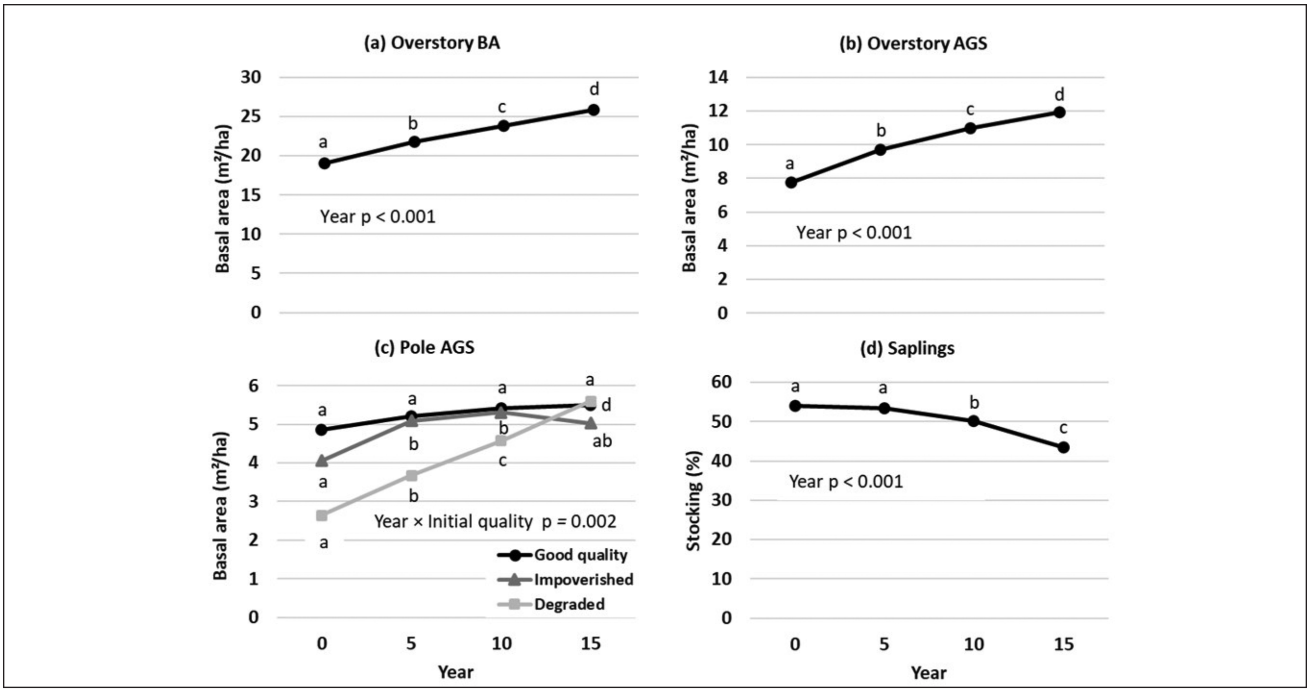

Fig. 3 Significant effects of year on overstory merchantable BA **(a)**, overstory acceptable growing stock (AGS) **(b)**, pole AGS **(c)** and sapling stocking **(d)**. Different letters indicate a significant difference ($p<0.05$, simulation-based adjusted *p* values) among years for overstory BA, overstory AGS and saplings (a, b, d), and among years within a stand initial quality category for pole AGS (c).

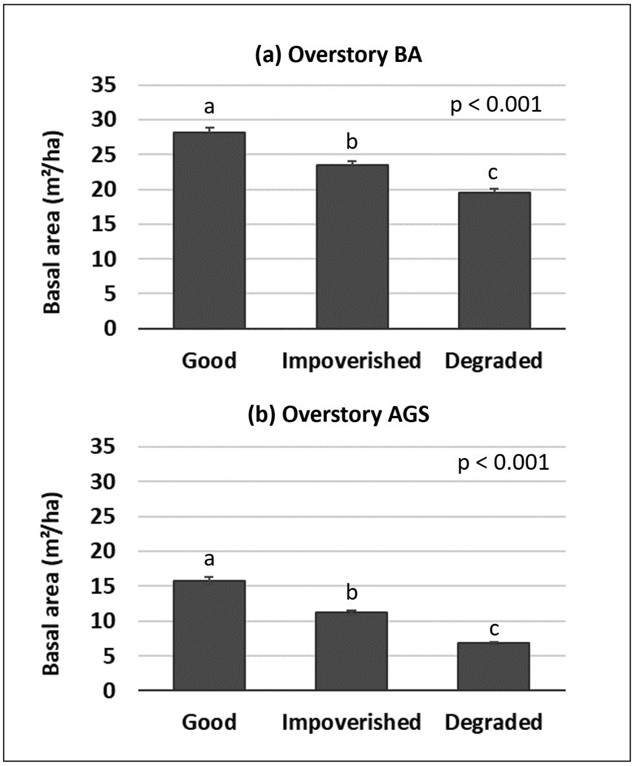

Fig. 4 Significant effects of stand initial quality on overstory merchantable BA **(a)** and overstory acceptable growing stock (AGS) **(b)** over 15 years. Different letters indicate a significant difference among stand initial quality categories ($p<0.05$, simulation-based adjusted *p* values). Error bars represent the standard error of means.

degraded or impoverished at the beginning of the study (Table 3), rare are those that did not meet any of our three functional criteria after 15 years of growth (7.4%, Fig. 2). Overall, the BA of overstory and pole AGS met or exceeded the thresholds we established (i.e., 9 and 3 m^2/ha, Fig. 3b and 3c). Most of these stands still show good resilience based on the criteria used here. This can be partly explained by the fact that these natural stands experienced a limited number of diameter-limit cuts (one or two), as this harvest method was banned on public land in Quebec since 1990. Outcomes could have been quite different if this exploitative cutting method would have been conducted repeatedly on a longer period (Belair and Ducey 2018; Gunn *et al.* 2019). In the present study, we assessed three criteria based on forest stand metrics. It is possible that other components have been altered, with potential impacts from both economic (e.g., species composition, stem quality, log grades) and ecological perspectives (e.g., species and structural diversity, rare species seed trees, standing and downed woody debris, wildlife trees, carbon sequestration, resilience). Other studies have demonstrated that a silvicultural intervention might be necessary to recover silvicultural functionality as defined by stand composition, tree quality, or regeneration (Kenefic *et al.* 2014; Rogers *et al.* 2017; Raymond *et al.* 2020). Yet, effects of diameter-limit cutting depend in large part on initial stand conditions, harvest intensity, and operating season. For example, studies tend to show that light to moderate intensity harvests are generally less damaging to the regeneration process than severe cuts in mixedwood stands (e.g., <40% harvest; Archambault *et al.* 2003, 2009 vs. >50% harvest; Fortin *et al.* 2003; Archambault *et al.* 2006).

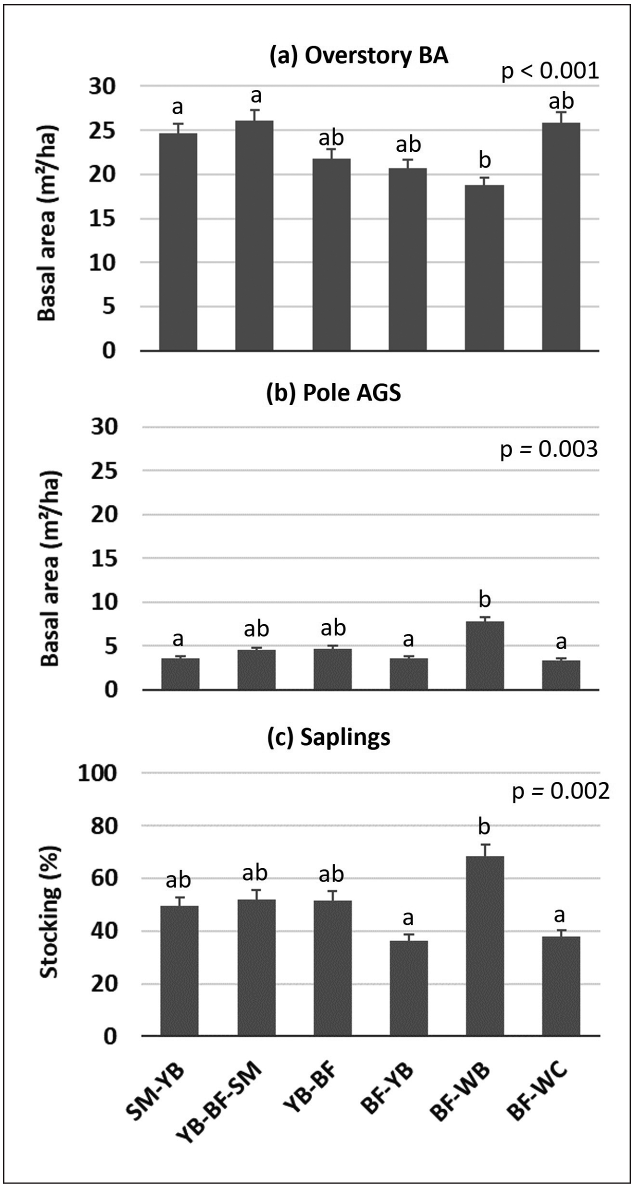

Fig. 5 Significant effects of forest type on overstory merchantable BA **(a)**, pole acceptable growing stock (AGS) **(b)** and sapling stocking **(c)** over 15 years. SM=sugar maple; YB=yellow birch; BF=balsam fir; WB=white birch; WC=eastern white cedar. Different letters indicate a significant difference among forest types ($p<0.05$, simulation-based adjusted *p* values). Error bars represent the standard error of means.

Assessment of criteria by forest type

Contrary to our first prediction, forest types with the lowest conifer proportion did not necessarily experience more problems as defined by the criteria used for this study. In fact, two conifer-dominated forest types had more problems (balsam fir–yellow birch and balsam fir–eastern white cedar), while a third one (balsam fir–white birch) did well. Diameter-limit cutting is based on prescribed diameters that set the minimum dbh size to harvest trees. This is generally lower for conifers (especially balsam fir) than for deciduous species in eastern Canadian forests, implying more intense harvests in stands with high conifer proportions (Fortin *et al.* 2003; Archambault *et al.* 2009). Conifer-dominated stands are known to experience regeneration difficulties after intense harvesting when the advance regeneration is not established before canopy removal, because of reduced seed tree abundance and increased interspecific competition (Archambault *et al.* 1998; Laflèche *et al.* 2000; Raymond and Bédard 2017). This is likely what happened in the balsam fir–yellow birch forest type in the present study. This is especially worrisome, knowing that impacts of severe diameter-limit cutting on compositional trajectories, e.g., persistent increase of deciduous tree species in conifer-dominated stands, can last for several decades (Fortin *et al.* 2003; Archambault *et al.* 2006). However, if deciduous species have good value, such as yellow birch, and allow conifers to establish under the main canopy (Dumais and Prévost 2008), then stands could still be economically valuable and slowly return to a more natural composition. In the balsam fir–eastern white cedar type, results could be explained by high stand density, as reflected in the overstory basal area (30.7 m²/ha) and acceptable growing stock (19.0 m²/ha) (Table 1), which could transmit little light to the understory to the expense of the regeneration survival and growth. As for the balsam fir–white birch type, this one did well overall in terms of overstory BA, pole AGS and sapling stocking. This forest type grows on slightly poorer sites compared to yellow birch fir–balsam fir type (Saucier *et al.* 2009), where the interspecific competition can be less intense, and where balsam fir regenerates well (Doucet 1988; Côté and Bélanger 1991; Larouche *et al.* 2015). This might be also due to the greater light transmission through the foliage of shade-intolerant hardwoods in the canopy (Canham *et al.* 1994), compared to shade-tolerant hardwoods that are more abundant in other forest types.

Assessment of criteria by stand initial quality

The majority of stands with good initial quality at the beginning of study (73%) had sufficient overstory and pole AGS after 15 years, but only a minority (30%) reached the 60% sapling threshold in desired species. That was also a major problem for impoverished stands (15%). These two categories had higher initial overstory BA and AGS and have probably closed their canopy since diameter-limit cut, leaving little light to facilitate an establishment phase for regeneration. Our results did not support our second prediction stating that stands categorized as degraded and impoverished have more regeneration problems than ones with good quality, since we observed no significant difference in terms of total sapling stocking in desired species. It is possible, however, that repeated high grading harvests leads to stand impoverishment in rare and high-value species such as shade-tolerant conifers (Kenefic *et al.* 2021), and to an increase in lower-value species such as balsam fir, red maple and non-commercial shrubs (Fig. S1) (Gunn *et al.* 2019). The interacting effect of year with stand initial quality showed a constant increase of pole AGS in the degraded category (Fig. 3). This could be related to an important establishment and growth of hardwoods like yellow birch, red maple, and others (Fig. S1) typically observed after severe diameter-limit cut (e.g., Robitaille and Boivin 1987). Low to moderate post -cut densities and ground disturbance are favorable conditions to establish yellow birch (Perala and Alm 1990; Lorenzetti *et al.* 2008; Prévost 2008). Otherwise, hardwood species like red maple may resprout after logging, and thus benefit of increased resources availability to grow (Laflèche *et al.* 2000;

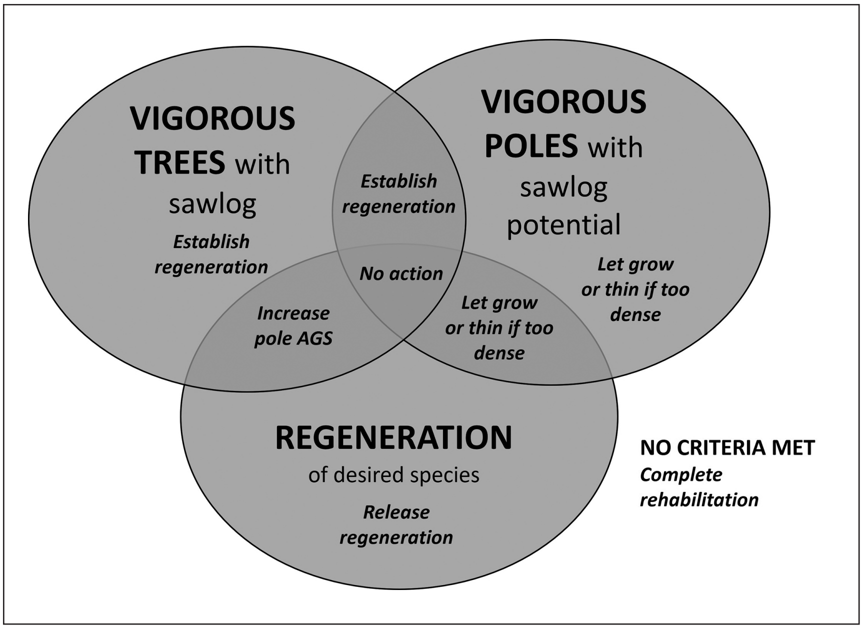

Fig. 6 Conceptual framework of silvicultural actions required to rehabilitate uneven-aged mixedwood stands.

Prévost and Charette 2019). Nevertheless, our results show that stands categorized as degraded at the beginning of the study can remain in that condition for a long time, while those considered as impoverished and good quality recovered sufficient basal area and acceptable growing stock to bare a new partial cutting cycle (Fig. 4). Stand composition might be less diverse over time in impoverished and degraded categories, especially the conifer component that has been depleted of red spruce and other conifers than balsam fir (Fig. S1). Red spruce regeneration, generally preestablished in temperate mixedwood forests, is sensitive to severe stand disturbance, and new seedling establishment after canopy opening is correlated with density of large seed trees (Dumais and Prévost 2007). A greater abundance of competing vegetation such as red maple and non-commercial shrubs (e.g., *Rubus* spp. and mountain maple) in lower density cuts (Fig. S1) may also have interfered with the regeneration process of slow-growing shade-tolerant conifers (Raymond and Bédard 2017; Raymond *et al.* 2020).

Finally, diameter-limit cutting as a harvest method to maximise immediate profit has proven not to be the best to optimize forest value over time (Rogers *et al.* 2017; Curtze *et al.* 2022; Granstrom *et al.* 2022). A more cautious approach focusing on silvicultural goals rather than solely on harvest criteria would be preferable to avoid stand quality alteration and understory competition problems (Gunn *et al.* 2019). This type of cutting is no longer permitted in public forests in Quebec and Ontario, for instance.

Conceptual framework to rehabilitate uneven-aged mixedwood forests

Although this approach does not replace stand decision-making tools finely adapted to local conditions, the conceptual framework of silvicultural actions required to rehabilitate multi-aged mixedwood stands we propose (Fig. 6) can be used to detect problems and guide actions. When the three criteria are met, e.g., overstory AGS, pole AGS and regeneration stocking, no action is needed. When stands have high-quality and vigorous sawtimber mature and pole trees, but insufficient regeneration, a silvicultural system tailored to the current stand conditions could be used to establish a new cohort of regeneration. In temperate mixedwood stands for example, this can be achieved with continuous cover irregular shelterwood, or hybrid small group and single-tree selection cutting (e.g., Raymond and Bédard 2017; Raymond *et al.* 2018) with passive or active scarification and enrichment planting (Dumais *et al.* 2020; Bourque *et al.* 2022), if needed. If stands have high-quality and vigorous sawtimber mature trees, but insufficient regeneration and poles, extended irregular shelterwood or regular shelterwood methods would be more indicated for establishing regeneration, depending on long-term structural goals (Raymond *et al.* 2020). Again, scarification during a good seed crop or enrichment planting can be included, if needed.

If solely the pole AGS criterion is met, the stand can be let grown or commercially thinned if too dense because of a high density of small stems (e.g., converting an even-aged stand, Nyland 2003) and/or to promote spruce over fir (Moores *et al.* 2007). If stands have sufficient overstory AGS and regeneration, but not enough poles, the development of pole AGS could be encouraged with crop-tree release of understory saplings. When only the regeneration criterion is met, while the other AGS criteria are not, a major rehabilitation effort is needed because there are important deficiencies in terms of vigor and/or tree quality. Overstory removal can be considered where site invasion by understory shrubby species is not an issue or if they can be controlled efficiently. Given the rapid expansion of interspecific competition after overstory removal in temperate mixedwood stands (Laflèche *et al.* 2000; Prévost *et al.* 2010; Raymond and Bédard 2017), it would be recommended to gradually open it to release the natural regeneration, especially in places where herbicides cannot be used . In highly heterogeneous, yet patchy stands, a multi-treatment approach (*sensu* Lussier and Meek 2014) could prove useful to harvest the overstory, while tending denser pole patches and creating new seedbeds for future regeneration. Finally, when no criteria are met, the stand can remain for a long time in a highly altered, yet alternative stable state (Ghazoul *et al.* 2015; Webster *et al.* 2018). A full rehabilitation scenario would be then needed, including different site preparation methods and/or tree planting (e.g., Gastaldello *et al.* 2007; Kenefic *et al.* 2014; Dumais and Prévost 2019). To maximise stand productivity and carbon sequestration, it would be judicious to prioritize the rehabilitation efforts in highly productive but poorly functional stands (Messier *et al.* 2019; Thom and Keeton 2019). Areas requiring complete rehabilitation could be also used to implement climate change adaptation strategies, such as assisted migration (Champagne *et al.* 2021; Royo *et al.* 2023). In addition to rehabilitating highly altered stands, these investments could facilitate transition and foster stand resilience and adaptability in a context of uncertain future conditions driven by climate change (Millar *et al.* 2007; Messier *et al.* 2019).

Implications for management

This long-term study has shown that, in absence of treatment, only about 20% of stands harvested by diameter-limit cutting 26 to 58 years in the past fully satisfied the functionality criteria defined in this assessment in terms of acceptable growing stock (mature trees and poles) and sapling regeneration stocking. Among these criteria, regeneration was the least achieved. This result could be explained, at least partly, by the canopy closure occurring in stands left with higher density after diameter-limit cutting. However, the increased abundance of hardwoods and non-commercial species in the understory can have also hindered the regeneration process, especially in more heavily cut stands. This study also highlights the fact that forest quality assessments and silvicultural decisions should not be based solely on standing tree data, but also on those from the regenerating layers. Yet, in forest management, regeneration is often the data that requires the greatest effort to collect and that is most often neglected (Guillemette *et al.* 2023), even if regeneration, particularly saplings, contributes substantially to the recovery of stand and pole tree merchantable basal area after partial cutting (Power *et al.* 2022). Poor attention to regenerating layers during and after diameter-limit cutting or high grading is one of the factors that lead to stand degradation over time (Kenefic *et al.* 2005; Rogers *et al.* 2017). Nevertheless, stands that did not meet any of our three functional criteria were rare (7%). These stands could remain in alternative stable states for a long time if no intervention is done (Ghazoul *et al.* 2015; Vásquez-Grandón *et al.* 2018; Webster *et al.* 2018). Our study also pointed out that stands growing on balsam fir–yellow birch forest types appear especially sensitive to loss of functional components after diameter-limit cutting and should be more carefully managed to sustain their productivity and resilience. Using a rehabilitation framework based on components of functionality can help to detect problems and guide silvicultural actions to restore functionality in uneven-aged mixedwood stands altered by past cutting practices.

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