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Key ecosystem attributes and productivity of boreal stands 20 years after the onset of silviculture scenarios of increasing intensity

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A B S T R A C T

Ecosystem-based management, now a dominant forestry paradigm, implies reducing the gap between variability of natural and managed forests (i.e. ecological distance) to reconcile ecological issues with production of socioeconomic services. Here, we tested whether a trade-off exists between conserving key ecosystem attributes of natural forests and maintaining and/or increasing merchantable wood production at the stand scale in humid boreal stands. Using 20-y data from an experimental design comparing silviculture scenarios of increasing intensity, (i) careful logging around advance growth (CLAAG); (ii) CLAAG followed by pre-commercial thinning; (iii) plantation followed by mechanical release; and (iv) plantation followed by chemical release, we examined plant community composition, stand structure and the quantity and the quality of snags. We also assessed timber productivity by comparing scenarios in terms of conifer and merchantable (diameter at breast height > 9 cm) tree dimensions. We used data from stands originating from a spruce budworm outbreak as a baseline to understand scenario impacts on variability of key attributes and productivity. Our results showed increasing differences in these attributes between natural and managed stands with increasing silviculture intensity: the diameter structure became more homogenized, light demanding species richness and abundance increased and the quantity and the quality of snags decreased. Therefore, our results showed that the ecological distance from naturally disturbed stands was lower after CLAAG than after the other silviculture scenarios. However, CLAAG favored an increase in the density of deciduous trees and a decrease of conifer snag density that have the potential to affect resilience of mature stands. Pre-commercial thinning resulted in crop trees reaching larger diameter than following CLAAG only and in the decrease of birch tree density, with no effect on deciduous regeneration density $\geqslant 60$ cm in height. We measured higher basal area of merchantable trees in plantations than in stands originating from natural regeneration scenarios, with mechanical and chemical release scenarios resulting in similar crop tree productivity. Globally, our study confirmed a general antagonism between the impacts of silviculture on key ecosystem attributes and forest productivity, posing a challenge for reconciling ecological issues with the production of socioeconomic services. At the stand level, results support that retention forestry could emulate natural disturbances by conserving biological legacies during harvest in humid boreal forests. Further research is needed to determine retention parameters to achieve expected wood production while maintaining variability of key attributes in humid boreal forests.

1. Introduction

While conservation of intact areas is necessary to deal with some biodiversity issues (e.g. Ray et al., 2015), adapting the management of the remaining forest matrix is essential to maintain ecosystem diversity and processes (Seiferling et al., 2012; Kareiva and Marvier, 2012). Over the past two decades, ecosystem-based management has thus become the dominant forestry paradigm in many countries (e.g. Butler and Koontz, 2005). Under this paradigm, forest managers aim at reducing the gap between variability of natural and managed forests (i.e. ecological distance) to reconcile ecological issues with production of socioeconomic services

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(Cardinall et al., 2004). Efforts to increase fiber production are, however, generally coincident with an increase in the intensity of silviculture, mainly due to plantations (Fu et al., 2007; Park and Wilson, 2007), which has a significant potential of conversion of natural forests to artificial ecosystems (Brockerhoff et al., 2008; Barrette et al., 2014). Hence, there is an apparent antagonism between maintaining variability of natural forests and increasing management intensity to favor merchantable wood production of desired species.

Extending over approximately 12.1 million km^2, the boreal biome is widely used for industrial forestry (Saucier et al., 2015). In terms of timber resources only, boreal forests worldwide support more than one million direct jobs in the forestry sector (Burton et al., 2010). This pressure has inevitable effects on boreal forest ecosystems; ecosystem-based management have thus been implemented in northeastern Canada (Gauthier et al., 2008). While many studies have shown a positive link between diversity and forest productivity (Forrester and Bauhus, 2016; Liang et al., 2016), production is often considered from an ecosystem perspective (e.g. aboveground biomass; Paquette and Messier, 2011) rather than from a forest management perspective. Many studies have reported on the short-term impacts of silviculture treatments on crop tree growth or plant community diversity after harvesting in temperate and boreal ecosystems (see review by Wagner et al., 2004). To our knowledge, few have assessed the effects of forest management on both the production from a forest management perspective and the ecological distance between managed and natural forests (but see Bell, 2015). To support the successful implementation of ecosystem-based management, there is a need to investigate the combined mid-term effects of silviculture scenarios of increasing intensity on merchantable wood production and variability of key ecosystem attributes at the stand level.

Humid boreal forests typical of northeastern America offer a particular challenge regarding ecosystem-based management of regenerating second growth stands. Balsam fir (*Abies balsamea* (L.) Mill.) is the dominant tree species of this ecosystem. It establishes understory seedling banks that survive decades under low light conditions until the opening of the canopy that typically follows cyclic insect outbreaks (Leblanc and Bélanger, 2000; Parent and Ruel, 2002). This natural disturbance dynamics supports the use of careful logging around advance growth (Thiffault et al., 2015). When fir advance growth is deficient, regenerating sites can, however, become dominated by northern hardwoods (e.g. white birch; *Betula papyrifera* Marsh.), a dynamic that favors the development of deciduous stands at the expense of conifer dominated stands (Déry et al., 2000). For such stands, reducing intra- and interspecific competition through pre-commercial thinning (PCT) became one of the most frequently applied silviculture treatments in the province of Quebec (Canada) during the 1990s (Thompson and Pitt, 2003). Although it may or may not enhance merchantable volume per hectare (depending on initial stand density), this treatment enables redistributing the site growth potential to a limited number of desired crop trees (Pothier, 2002; Pitt and Lanteigne, 2008). PCT generally increases species richness of ground vegetation cover and understory layers as it decreases canopy closure (Lindgren et al., 2006; Bataineh et al., 2014), but nonlinear responses to site fertility and light availability make it hard to predict understory responses to the treatment (Thomas et al., 1999). Thinning can also homogenize stand structure and composition (Puettmann et al., 2012). Furthermore, the establishment of spruce plantations (mainly black spruce; *Picea mariana* (Mill.) BSP) involving site preparation and one or more vegetation management treatments (either mechanical or chemical) is also common in this ecosystem. This practice raises concerns regarding variability of key attributes compatible with ecosystem-based management of fir-dominated forests (Hartley, 2002).

In this context, there is a need to assess silviculture scenarios along a gradient of intensity and balance their potential impacts on variability of key ecosystem attributes of natural forests with the benefits they can produce regarding productivity of desired crop species. It is crucial to test whether a trade-off exists between conserving key ecosystem attributes of natural forests and maintaining and/or increasing merchantable wood production at the stand scale. We thus report on a 20-y study assessing the impacts of silviculture scenarios of increasing intensity on stand productivity as well as on stand composition, structure and snags, i.e. three key ecosystem attributes of natural forests. We compared the variability of stand productivity, composition, structure and snags between managed stands and control stands. With globally distributed emissions of CO_2 and land use, we can nowadays consider that forests untouched by human activities no longer exist anywhere (Winter et al., 2010). We therefore used second growth stands with the maximum time past since management was abandoned (Winter, 2012) as a control baseline to assess the ecological distance between managed and 'natural' forests. These natural stands are regularly affected by spruce budworm outbreaks (*Choristoneura fumiferana* (Clem.)), the dominant natural disturbance that has driven forest species composition in this region over the last century (Boucher et al., 2016). We hypothesized that an increase in intensity of management (defined by the number of treatments and their objectives; Bell et al., 2008) concentrates environmental resources to desired crop species. Based on this hypothesis, we predicted that more intense scenarios would result (i) in a modification in plant community composition with an increase in heliophilous species at the expense of sciaphilous species, (ii) in a more homogenized stand structure, (iii) a decrease in snag density and quality and (iv) an increase of merchantable conifer wood production than less intense scenarios. Globally, we therefore predicted that at the stand scale, the ecological distance between managed and natural forests and the merchantable wood production would both increase with increasing silviculture intensity.

2. Materials and methods

2.1. Study area

We conducted this experiment on sites located in *Forêt Montmorency* and *Parc de la Jacques-Cartier* (47°16′–47°21′N; 71°01′–71°19′W), both located about 80 km North of Québec City (Québec, Canada) (Fig. 1). Vegetation in this region is typical of the balsam fir–white birch bioclimatic domain described by Saucier et al. (2009). Mature forests growing on mesic sites are typically dominated by balsam fir, black spruce and white birch. The region presents a boreal per humid climate with a mean annual temperature of 0.5 °C and mean annual precipitation of 1583 mm, of which about two-thirds fall as snow (weather station n° 7042388 located at 47°19′N; 71°09′W, Environnement Canada, 2015). The region is also characterized by a hilly landscape with an elevation ranging from 600 to 1100 m, and by soils covered by acidic glacial tills. Spruce budworm outbreaks constitute the main natural disturbances in our study area whereas wildfires are not frequent because of the high precipitation regime (Leblanc and Bélanger, 2000).

Only natural disturbances shape the forest landscape within *Parc de la Jacques-Cartier* since the last historical clear-cut harvests that occurred during the 1940s. Indeed, the *Parc* was classified as a conservation zone in the early 1980s and hence, forest stands within its limits have not been submitted to silviculture activities since then. Stands we selected within the *Parc* experienced a single spruce budworm outbreak between 1974 and 1986 (Fig. 2).

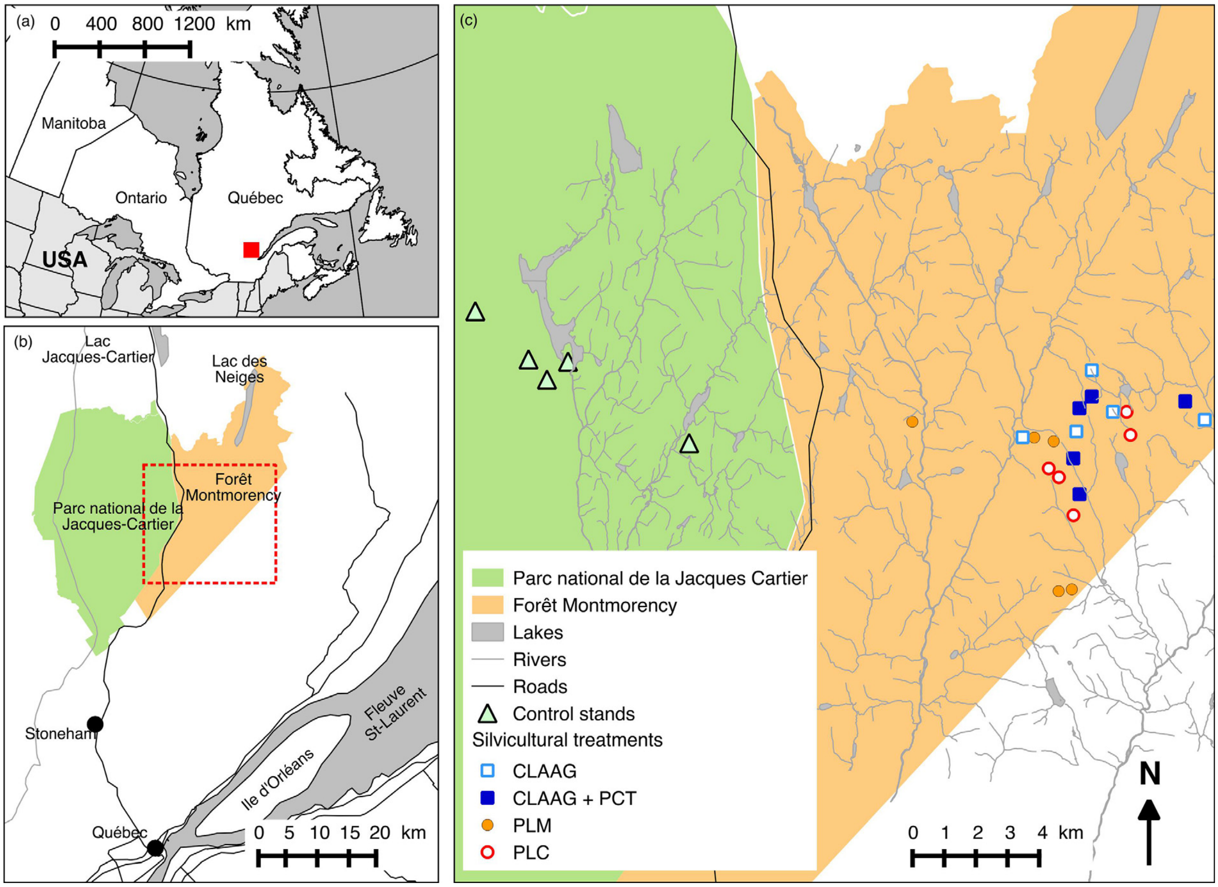

Fig. 1. Location of the study region and sites. (a) Map of northeastern America showing the study region (red square) in Québec, Canada. (b) Details of the study region showing the study area within which the study sites are located (dashed red box). (c) Location of the 5 naturally disturbed sites (Control, light-green triangles) within *Parc de la Jacques-Cartier* and 20 managed sites representing an increasing gradient of silviculture intensity within *Forêt Montmorency*: CLAAG (light-blue squares), CLAAG + PCT (dark-blue squares), PLM (orange dots) and PLC (red circles). CLAAG = careful logging around advance growth; PCT = pre-commercial thinning; PLM = plantation followed by mechanical release from competing vegetation; PLC = plantation followed by chemical release from competing vegetation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Both natural and anthropogenic disturbances shape the forest landscape within *Forêt Montmorency*. Stands located within *Forêt Montmorency* were clear-cut harvested between 1941 and 1944. They naturally regenerated before being harvested through careful logging around advance growth between 1987 and 1989. Therefore, the landscape of the *Forêt Montmorency* is characterized by recent clearcuts of maximum 250 ha separated by blocks of residual forest (3–10 ha), riparian forests about 20-m wide and roads. After the application of CLAAG (see below), densities of balsam fir and white birch in stands selected for this study were over 25,000 stems ha^{-1} and density of black spruce was less than 100 stems ha^{-1} (de Bellefeuille et al., 2001). Stands within *Forêt Montmorency* were less affected by the spruce budworm outbreak than stands in the *Parc* as they were sprayed with insecticides (Fig. 2).

2.2. Experimental design and measurements

The experimental design is partially based on the experimental setup established by de Bellefeuille et al. (2001). We selected 25 sites, ranging from 6 to 9 ha each: 20 stands originated from harvesting between 1987 and 1989 within the *Forêt Montmorency* (hereafter 'managed') and five stands originated from the spruce budworm outbreak within the *Parc de la Jacques-Cartier* (hereafter 'naturally disturbed') (Fig. 1). The selection was made to ensure ecological homogeneity between sites. Therefore, we restricted selection to sites with mesic soils that contained no residual patches of mature trees. According to governmental forest maps dating from 1982 to 1983, more than 75% of the selected sites supported pure balsam fir stands before harvest. Other sites were composed of white birch mixed with balsam fir and black spruce, or only black spruce (about 5%). More than 65% of sites presented a relative density between 60 and 80% and stands aged between 41 and 60 year-old in 1981. Stands originating from the budworm outbreak showed lower densities (between 40 and 60%) and were older (more than 60 years).

We studied silviculture scenarios currently and frequently applied in these humid boreal forests. Therefore, four silviculture scenarios of increasing intensity were applied on the 20 managed sites originating from harvesting with careful logging around advance growth (CLAAG) between 1987 and 1989 (Figs. 1 and 2):

(i) On five sites, no additional silviculture treatment was applied (CLAAG only).
(ii) On five sites, we thereafter applied pre-commercial thinning in 2000 to reduce conifer density to 1500–3125 stem ha^{-1} (CLAAG + PCT).
(iii) On five sites, we thereafter applied soil scarification in autumn 1989, planted black spruce seedlings in spring 1990 at a density of 2000 stems ha^{-1} and released planted seedlings from competing vegetation in 1992 with a mechanical release using motor-manual brush saws (five plantations; all woody vegetation within a 1 m radius of each planted black spruce seedling was removed; PLM).

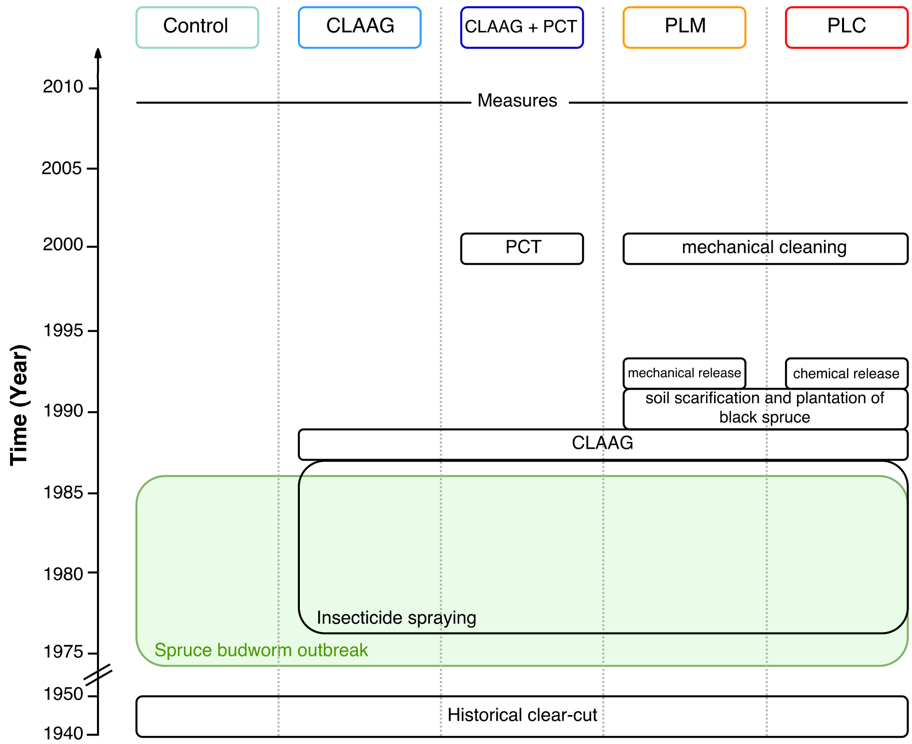

Fig. 2. Timeline of the history of disturbances and treatment application in our study area. See Fig. 1 for scenario description.

(iv) On five sites, we thereafter applied the same treatments as (iii) except that we performed release with chemical herbicides, using Vision® Silviculture herbicide (glyphosate) applied by plane at a rate of 5 L ha^{-1} (five plantations; PLC).

PLM and PLC sites were submitted to a mechanical juvenile cleaning (sensu Cyr and Thiffault, 2009) in 2000.

Combining the naturally disturbed stands with scenarios i to iv provided a gradient of increasing silviculture intensity (Fig. 2), defined here as "the degree to which the factors influencing growth and yield are manipulated" (Bell et al., 2008). Thus, we considered the silviculture intensity as the degree of stand manipulation affected by the number of treatments and their management objectives: the Control, CLAAG, CLAAG + PCT, PLM and PLC scenarios respectively experienced 0, 1, 2, 5 and 5 silviculture treatments. Moreover, for scenarios based on plantation (PLM and PLC), the yield was optimized at the stem level, whereas it was optimized at the stand scale for the scenarios based on natural regeneration (CLAAG and CLAAG + PCT) (Gravel and Meunier, 2013).

Vegetation surveys were conducted in four circular 100 m^2 plots on each naturally disturbed and managed sites in July 2009. One 100 m^2 plot was located at the center of the site, and the three other plots were separated by 150 m from each other. The density (number of stems per plot) of trees (defined as having a diameter at breast height (1.3 m), DBH $\geqslant$ 1.1 cm) and high regeneration (defined as having a height $\geqslant$ 60 cm and a DBH < 1 cm) was measured in the 100 m^2 plots and in concentric 25 m^2 subplots, respectively. For each tree, DBH was recorded. The percent cover of shrubs (height < 60 cm), herbaceous species and various taxonomic groups (ferns, mosses, sphagnum, lichens, grasses and *Lycopodium* L.) was visually assessed in each 100 m^2 plot using 10% cover classes. Height was measured on two conifers and two deciduous trees (when possible) representative of the dominant or co-dominant crown classes within the upper canopy (sensu Oliver and Larson, 1996) in each plot. Snags and their DBH were also surveyed in the 100 m^2 plots. Photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) at 1 m height was measured at the cardinal points of each 100 m^2 plot using a Sunfleck ceptometer (Decagon Devices, Pullman, WA). PPFD readings were averaged by plot and expressed as a ratio to full sunlight conditions based on concomitant light levels from open areas located near the plots.

2.3. Statistical analyses

For each managed and naturally disturbed sites, density of living trees and snags, mean DBH (cm) and cumulated basal area (BA, m^2 ha^{-1}) of conifer and deciduous species were calculated at the plot level; skewness and kurtosis of the DBH distribution of all living trees, conifer and deciduous species were determined at the site level using the R package "*moments*" (Komsta and Novomestky, 2015). We also calculated the mean DBH and the cumulated basal area of the merchantable trees (DBH $\geqslant$ 9.1 cm) at the plot level.

Species richness (*S*) was determined at the site level (i.e. on a 400 m^2 basis) for the four vegetation layers (trees, high regeneration, shrubs and herbaceous species), and the Simpson's index of diversity (*SID*, also referred to as the Gini-Simpson index) was determined for each plot and the four vegetation layers using the R package "*vegan*" (Oksanen, 2013). *SID* was calculated as:

$$SID = 1 - \sum_{1}^{n} p_i^2$$

with p_i being the proportion of individuals of the i^{th} species and n the number of the species. If species are equally present, *SID* = 0.8 whereas it tends to 0 if one species dominates the community.

We used analyses of variance (ANOVAs) to test for significant effects of silviculture scenarios on the variables. Analyses were conducted (i) with linear models for species richness, skewness and kurtosis of the DBH distribution – as these variables were determined at the site level – (ii) with mixed models including 'site' as a random factor for Simpson's index of diversity, height, DBH and cumulated basal area – as these variables were determined at the plot level – and (iii) with generalized linear mixed-effect models (GLMMs) including 'site' as a random factor and a negative binomial distribution of residuals for tree density. Indeed, GLMMs with a Poisson distribution of residuals were over dispersed, i.e. the ratio of residual deviance to residual degrees of freedom was greater than 1 (Zuur et al., 2009). Planned comparisons were carried out in case of significant ($P < 0.05$) values from the ANOVA (protected Fisher LSD) to answer the following questions regarding structure (skewness and kurtosis), composition (tree density, species richness and Simpson's index of diversity), snags (snag density and DBH) and stand productivity (DBH and BA):

(i) How naturally disturbed and managed stands compared to each other? (Control *vs.* CLAAG and CLAAG + PCT and PLM and PLC).
(ii) How naturally disturbed stands compared to scenarios based on natural regeneration? (Control *vs.* CLAAG and CLAAG + PCT).
(iii) How naturally disturbed stands compared to scenarios based on plantations? (Control *vs.* PLM and PLC).
(iv) How scenarios based on natural regeneration compared to scenarios based on plantations? (CLAAG and CLAAG + PCT *vs.* PLM and PLC).
(v) In case of natural regeneration, how harvesting alone compares to harvesting followed by pre-commercial thinning? (CLAAG *vs.* CLAAG + PCT).
(vi) In plantation scenarios, how mechanical release compares to chemical release? (PLM *vs.* PLC).
(vii) How the lowest and highest silviculture intensity scenarios compare with each other? (CLAAG *vs.* PLC).

Standard procedures for model diagnostics were conducted for all analyses. All analyses were performed using R version 3.0.1 (R Development Core Team, 2012) and the package "*nlme*" for linear mixed models, "*lme4*" for GLMMs (Bates et al., 2015) and "*multcomp*" for planned comparisons (Hothorn et al., 2015).

We performed a redundancy analysis (RDA) to assess the effect of different explanatory variables on community composition. The silviculture scenarios (Control, CLAAG, CLAAG + PCT, PLM and PLC) were considered as a qualitative variable. The quantitative explanatory variables were conifer and deciduous tree densities (Dens_C and Dens_D), DBH of conifer and deciduous trees (DBH_C and DBH_D), cumulated basal area of conifer and deciduous trees (BA_C and BA_D), density of conifer and deciduous snags (Snag_C and Snag_D), and PPFD. Prior to the RDA, we standardized quantitative explanatory variables as they were not all dimensionally homogeneous; we removed all species that appeared only once and averaged species abundance by site; the species × site matrix was therefore based at the site level. We then applied the Hellinger transformation to species data to allow the use of Euclidean distance (Legendre and Gallagher, 2001). Finally, we standardized species abundance variables as they consisted in density for trees and saplings and percent cover for shrubs, herbs and other taxonomic groups.

We detected as strong linear dependencies among the explanatory variables based on the variance inflation factors (VIF) (see Table S1 for details): DBH of conifer species and PPFD were strongly negatively correlated with density of deciduous trees and basal area of conifer species, respectively. We thus selected explanatory variables using a forward approach following the methods of Borcard et al. (2011) and computed a new RDA with the selected variables only (silviculture scenarios, BA_C, DBH_D, Dens_D, Snag_D). Problems of non-normal distributions are frequent for ecological data; we thus used a permutation test (1000 permutations) to test the significance of the global model results and the canonical axes (Borcard et al., 2011). RDAs were conducted using the package "*vegan*" (Oksanen, 2013).

3. Results

3.1. Stand structure

Increasing the intensity of silviculture induced a displacement of the distribution of DBH from an irregular to a more regular structure (Fig. 3) that is mainly shown by the decrease of the skewness and the kurtosis of the distribution of DBH of all trees. Differences in skewness and kurtosis were significant between naturally disturbed and managed stands (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. 3, Table 1). Planting had a strong effect on the distribution of DBH of all trees, with a lower skewness in plantations than in naturally regenerated stands (contrast CLAAG and CLAAG + PCT *vs* PLM and PLC, Fig. 3, Table 1). This response in the DBH distribution of all trees was mainly explained by the displacement of the DBH distributions of conifer species from smaller to larger trees, especially within plantations (contrasts on skewness, Control *vs* CLAAG and CLAAG + PCT and PLM and PLC; Control *vs* CLAAG and CLAAG + PCT; Control *vs* PLM and PLC; CLAAG and CLAAG + PCT *vs* PLM and PLC, Fig. 3, Tables S2a and S3a).

Tree height of dominant conifer and deciduous tree species tended to decrease with the increasing intensity of silviculture scenarios (Control > CLAAG > CLAAG + PCT > PLM > PLC), with a mean height of 9.5 ± 1.7 m and 8.0 ± 2.5 m for conifer and deciduous species, respectively, in naturally disturbed stands, 7.3 ± 1.3 m and 6.3 ± 1.1 m in CLAAG stands, 6.8 ± 0.5 m and 4.2 ± 1.0 m in CLAAG + PCT stands, 6.4 ± 0.5 m and 5.7 ± 1.9 m in PLM stands, and 6.2 ± 0.5 m and 2.9 m in PLC stands (only one dominant deciduous trees for this scenario). Moreover, dominant conifer trees in naturally disturbed stands had significantly higher height than trees in managed stands (contrasts Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, *z-value* = 5.00, $P < 0.001$).

3.2. Snags

Conifer snags were rare in managed stands compared to naturally disturbed ones (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. 4a, Table 2a). Moreover, we observed larger conifer snags within naturally disturbed stands (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, *z-value* = 3.44, $P = 0.004$, Fig. S1). The increasing silviculture intensity also impacted the density of deciduous snags, in particular within PLC stands where deciduous snags were rare (contrast CLAAG *vs* PLC, Fig. 4b).

3.3. Stand composition

Overall, densities of conifer and deciduous species of managed stands greatly differed from those of naturally disturbed stands (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Figs. 3, 4c and d Table 2b). CLAAG stands presented the highest stem density of both conifer and deciduous species among the tested scenarios (Figs. 3, 4a and b, Table 2b). For conifer species, densities of CLAAG and naturally disturbed stands were similar (Figs. 3 and 4a), whereas CLAAG greatly increased deciduous species density compared to naturally disturbed stands (Figs. 3 and 4b). As a general trend, densities of conifer and deciduous species of managed stands decreased with increasing intensity of silviculture scenarios (excluding the Control scenario) (Figs. 3, 4a and b). Plantations presented a lower density of conifer and deciduous stems than unplanted stands (contrast CLAAG and CLAAG + PCT *vs* PLM and PLC, Figs. 3, 4a and b, Table 2b). CLAAG

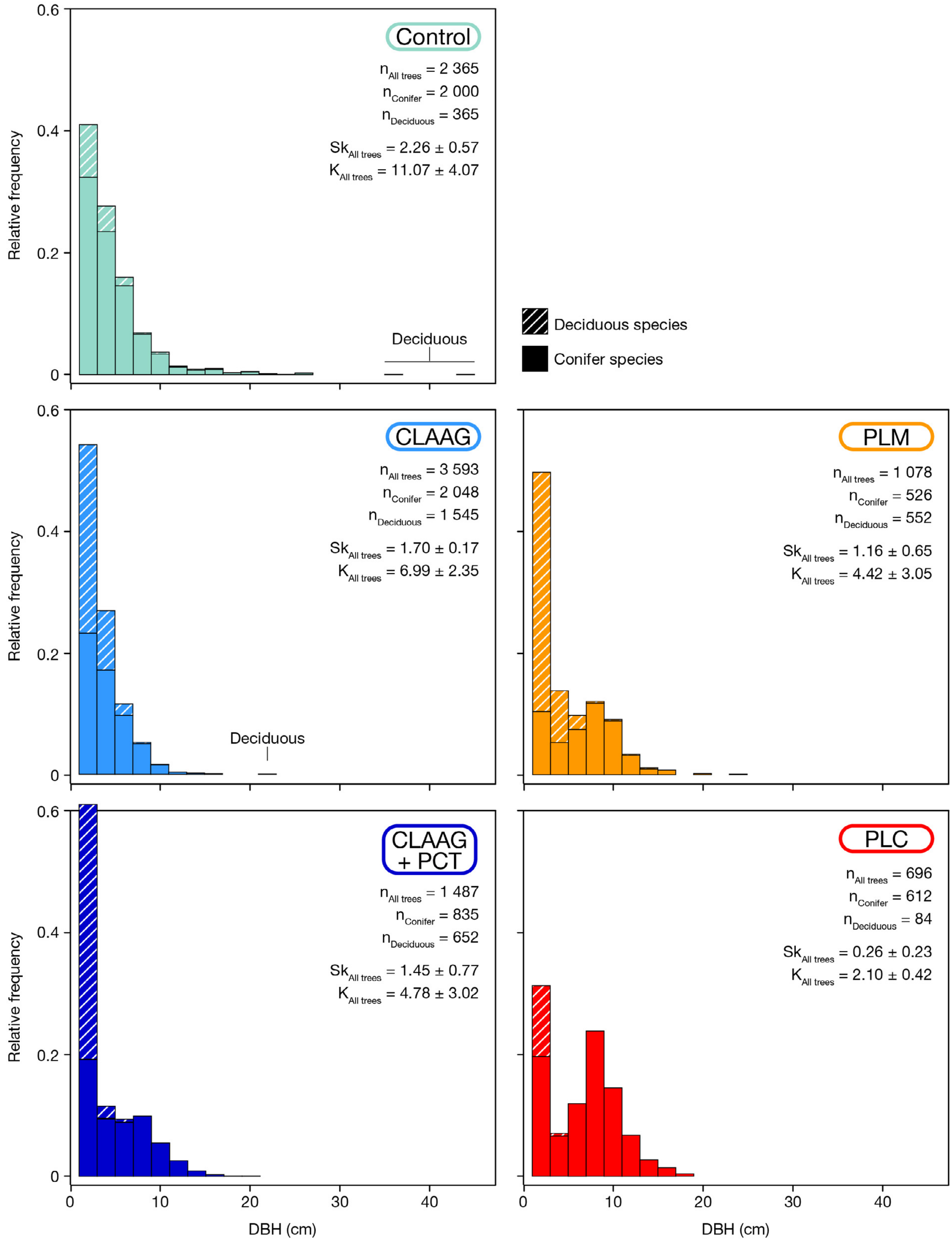

Fig. 3. Frequency distribution of tree diameter at breast height (DBH; cm) for naturally disturbed stands (Control) and managed stands representing an increasing gradient of silviculture intensity. Skewness and kurtosis of frequency distribution are presented as mean ± standard deviation (n = 5). See Fig. 1 for scenario description.

stands presented a higher density of conifer and deciduous species than CLAAG + PCT stands and PLC stands (contrasts CLAAG *vs* CLAAG + PCT, and CLAAG *vs* PLC, Figs. 3, 4a and b, Table 2b). In plantations, chemical release further reduced the density of deciduous species compared to mechanical release (contrast PLM *vs* PLC, Figs. 3 and 4b, Table 2b).

Globally, and regardless of the silviculture scenarios, a total of 8, 8, 7 and 17 species were surveyed in the tree, high

Table 1
ANOVA and planned contrast results for skewness and kurtosis of the distribution of diameter at breast height of all trees for naturally disturbed stands (Control) and managed stands representing an increasing gradient of silviculture intensity. See Fig. 1 for scenario description.

	Skewness		Kurtosis	
ANOVA	$F_{4,20}$	*P*	$F_{4,20}$	*P*
Silviculture intensity	*9.47*	**<0.001**	7.04	**0.001**
Contrast	*t*	*P*	*t*	*P*
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	4.17	**0.003**	4.56	**0.001**
Control *vs* CLAAG + (CLAAG + PCT)	2.34	0.135	3.32	**0.018**
Control *vs* PLM + PLC	5.27	**<0.001**	5.00	**<0.001**
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	3.59	**0.010**	2.06	0.223
CLAAG *vs* (CLAAG + PCT)	0.73	0.929	1.22	0.681
PLM *vs* PLC	2.66	0.073	1.29	0.642
CLAAG *vs* PLC	4.23	**0.002**	2.71	0.065

Values in bold are significant ($P < 0.05$).

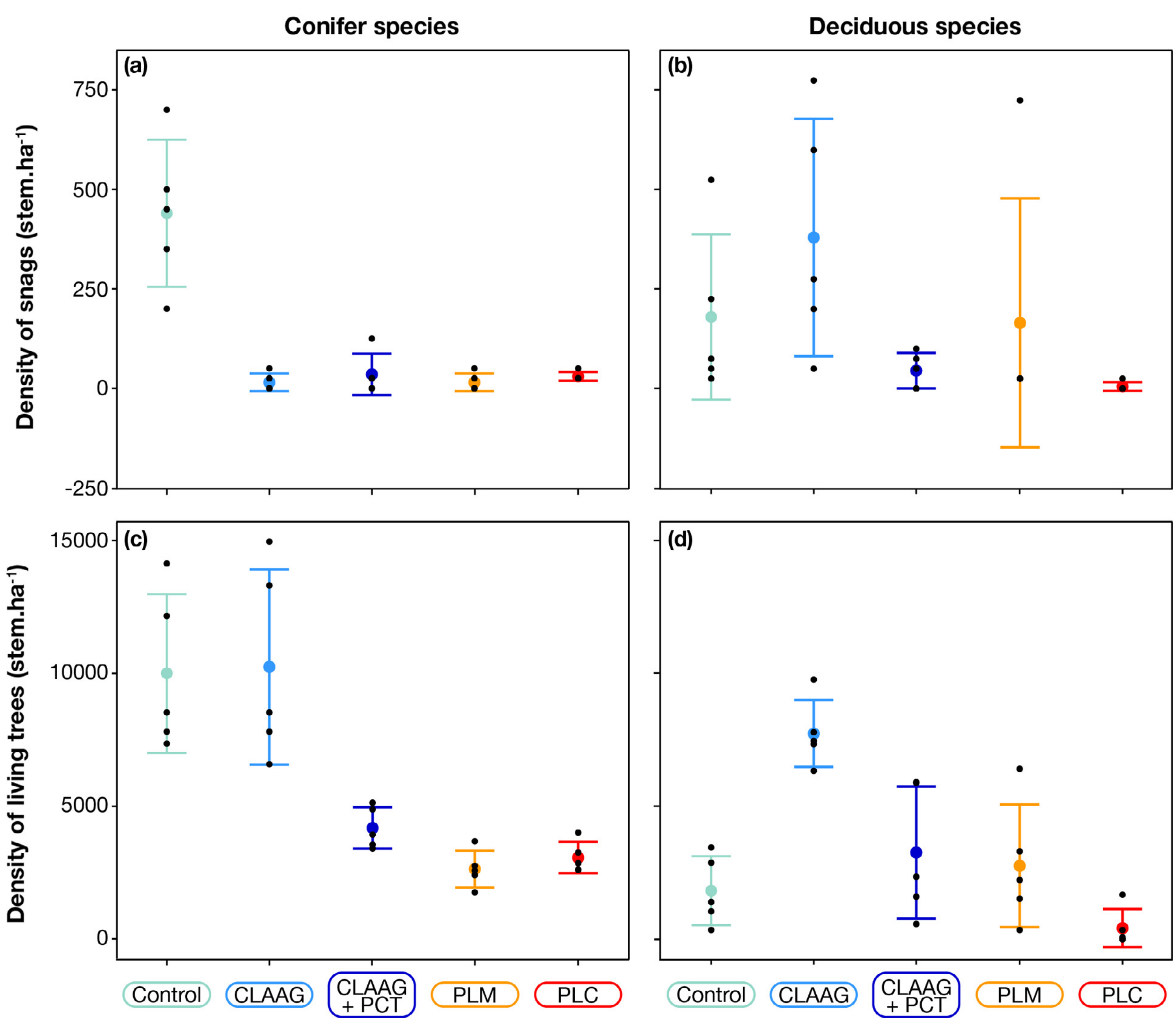

Fig. 4. Values of density (stem ha^{-1}) of (a) conifer and (b) deciduous snags, (c) conifer and (d) deciduous trees for naturally disturbed stands (Control) and managed stands representing an increasing gradient of silviculture intensity. Data are presented as mean ± standard deviation (n ⩽ 5 sites). See Fig. 1 for scenario description.

regeneration, shrub and herbaceous species layers, respectively (Fig. 5). Both components of diversity (species richness and relative abundance) were lower in naturally disturbed stands than in the managed stands for all vegetation layers (except for the relative abundance of the high regeneration and the herbaceous layers) (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. S2, Table S4). Our results evidenced the dominance of balsam fir and white birch in the tree and high regeneration layers of natural stands (Fig. 5a). The herbaceous layer was dominated by Canadian bunchberry (*Cornus canadensis* L., Fig. 5b) and species richness of shrub and herbaceous species were low (Figs. 5b, S2c and S2d). The percent cover of bryophytes species was higher than those of all herbaceous species in natural stands (Fig. 5b).

Table 2
ANOVA and planned contrast results for density of (a) snags and (b) living trees of conifer and deciduous species for naturally disturbed stands (Control) and managed stands representing an increasing gradient of silviculture intensity. See Fig. 1 for scenario description.

	Conifer species		Deciduous species	
(a) Snags				
ANOVA	$F_{4,20}$	*P*	$F_{4,20}$	*P*
Silviculture intensity	15.40	**<0.001**	4.54	**0.009**
Contrast	*z*	*P*	*z*	*P*
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	8.93	**<0.001**	1.50	0.476
Control *vs* CLAAG + (CLAAG + PCT)	6.99	**<0.001**	0.23	0.999
Control *vs* PLM + PLC	7.06	**<0.001**	2.26	0.113
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	0.15	1	2.34	0.093
CLAAG *vs* (CLAAG + PCT)	−1.15	0.717	2.38	0.084
PLM *vs* PLC	−0.92	0.849	2.21	0.128
CLAAG *vs* PLC	−0.92	0.849	3.47	**0.003**
(b) Living trees				
ANOVA	$F_{4,20}$	*P*	$F_{4,20}$	*P*
Silviculture intensity	38.53	**<0.001**	9.81	**<0.001**
Contrast	*z*	*P*	*z*	*P*
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	7.03	**<0.001**	−28.61	**<0.001**
Control *vs* CLAAG + (CLAAG + PCT)	3.25	**0.007**	−331.58	**<0.001**
Control *vs* PLM + PLC	9.48	**<0.001**	242.92	**<0.001**
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	7.55	**<0.001**	395.48	**<0.001**
CLAAG *vs* (CLAAG + PCT)	5.75	**<0.001**	164.65	**<0.001**
PLM *vs* PLC	−1.00	0.814	329.48	**<0.001**
CLAAG *vs* PLC	7.72	**<0.001**	575.25	**<0.001**

Values in bold are significant ($P < 0.05$).

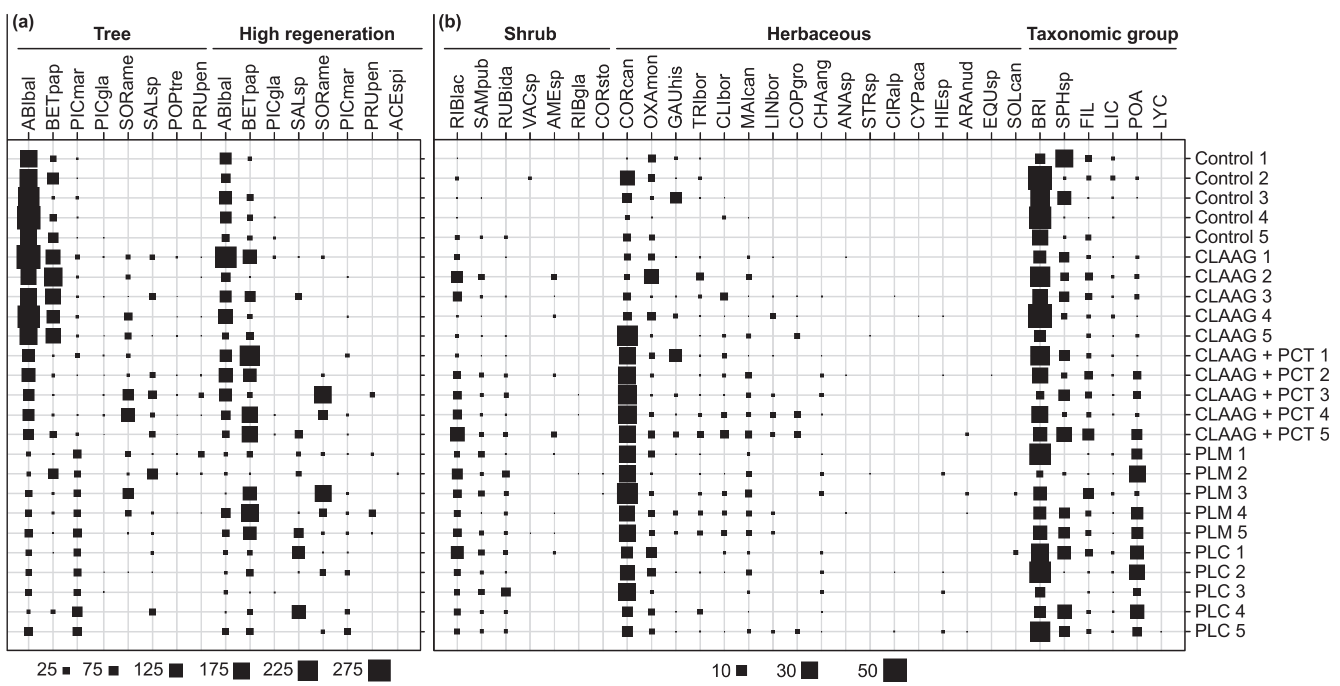

Fig. 5. Mean density or cover of sampled species on each site. (a) Mean density (stems 100 m^{-2}) of trees and high regeneration and (b) mean cover (%) of shrubs, herbaceous species and various taxonomic groups per site (naturally disturbed sites and managed sites). See Fig. 1 for scenario description. ABIbal: *Abies balsamea* (L.) Mill., ACEspi: *Acer spicatum* Lam., AMEsp: *Amelanchier* sp., ANAsp: *Anaphalis* sp., ARAnud: *Aralia nudicaulis* L., BETpap: *Betula papyrifera* Marsh., BRI: *Bryophyta*, CHAang: *Chamaenerion angustifolium* (L.) Scopoli subsp. *angustifolium*, CIRalp: *Circaea alpina* L., CLIbor: *Clintonia borealis* (Aiton) Raf., COPtri: *Coptis trifolia* (Linnaeus) Salisbury, CORcan: *Cornus canadensis* L., CORsto: *Cornus stolonifera* Michx., CYPaca: *Cypripedium acaule* Aiton, EQUsp: *Equisetum* sp., FIL: *Filicophyta*, GAUhis: *Gaultheria hispidula* (L.) Muhl. ex Bigelow, HIEsp: *Hieracium* sp., LIC: *Lichens*, LINbor: *Linnaea borealis* L., LYC: *Lycopodiales*, LYSbor: Lysimachia borealis (Rafinesque) U. Manns & Anderberg MAIcan: *Maianthemum canadense* Desf., OXAmon: *Oxalis montana* Raf., PICgla: *Picea glauca* (Moench) Voss, PICmar: *Picea mariana* (Mill.) BSP, POA: *Poaceae*, POPtre: *Populus tremuloides* Michx., PRUpen: *Prunus pensylvanica* L.f., RIBgla: *Ribes glandulosum* Grauer, RIBlac: *Ribes lacustre* (Pers.) Poir., RUBida: *Rubus idaeus* L., SALsp: *Salix* sp., SAMrac: *Sambucus racemosa* subsp. *pubens* var. *pubens* (Michaux) S. Watson., SOLcan: *Solidago canadensis* L., SORame: *Sorbus americana* Marsh., SPH: *Sphagnum* sp., STRsp: *Streptopus* sp., VACsp: *Vaccinium* sp.

Plantation scenarios had a significant effect on tree composition, with lower tree species richness in planted stands compared to unplanted stands (contrast CLAAG and CLAAG + PCT *vs* PLM and PLC, Figs. 5a and S2a, Table S4a). Spruce and balsam fir were dominant in plantation scenarios, whereas balsam fir was the only dominant species on CLAAG and CLAAG + PCT treated sites (Fig. 5a). Few deciduous trees and high regeneration were surveyed within naturally disturbed stands and all of them were white birch (Fig. 5a), whereas they were found in the managed stands (especially white birch, willow (*Salix* sp.) and American mountain ash

(*Sorbus americana* Marsh.), Fig. 5a). The higher density of deciduous trees within CLAAG stands compared to naturally disturbed stands (Figs. 3 and 4a) mainly resulted from the high density of white birch (Fig. 5a). In planted stands, chemical release reduced woody species richness compared to mechanical release (contrast PLM *vs* PLC), with lower tree and shrub species richness (Fig. 5a and b, S2a and S2c, Tables S4a and S4c) and a less balanced tree species relative abundance (Figs. 5a and S2e, Table S4a).

Variation in the intensity of silviculture scenarios had no effect on the Simpson index of diversity of the high regeneration (Fig. S2e, Table S4b) and herbaceous layers (Fig. 5d, Table S4d). Indeed, Canadian bunchberry and common wood-sorrel (*Oxalis montana* Raf.) dominated the herbaceous layer in all scenarios (Fig. 5b). For the high regeneration layer, *SID* was not significantly different with increasing silviculture intensity, as only two species were dominant in all scenarios. However, dominance differed with increasing silviculture intensity with a decrease in the abundance of balsam fir and white birch and an increase in the abundance of willow and American mountain ash (Fig. 5b).

The RDA explained 54% of the total variance in the vegetation dataset; the first and second axes respectively explained 27% and 10% of the variance. Results of permutation tests showed that the global model and canonical axes were highly significant ($P = 0.001$). Graphically, the DBH of deciduous species and the basal area of the conifer species were related to the first axis, whereas the density of the deciduous species and snags were related to the second axis (Fig. 6). The naturally disturbed sites and CLAAG scenarios were highly similar in terms of species composition and were associated with higher basal area of the conifer species, higher DBH of deciduous species, and higher density of deciduous snags than plantations sites (Fig. 6). Light-demanding and shade intolerant species such as willow, American mountain ash and grasses were dominant in the plantations. We measured a slight increase in available light along the gradient of intensity of the silviculture scenarios ($F_{4,20} = 18.52$, $P < 0.001$): PPFD was lower in naturally disturbed stands (12 ± 4%) than in the managed ones (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, *z-value* = −6.85, $P < 0.001$) and higher in CLAAG + PCT (37 ± 5%) and PLC (33 ± 8%) than in CLAAG (22 ± 4%) (contrasts CLAAG *vs* CLAAG + PCT, *z-value* = −4.68, $P < 0.001$ and CLAAG *vs* PLC, *z-value* = −3.63, $P = 0.002$). The CLAAG + PCT scenario was characterized by environmental variables and vegetation comprised between the naturally disturbed and planted sites (Fig. 6).

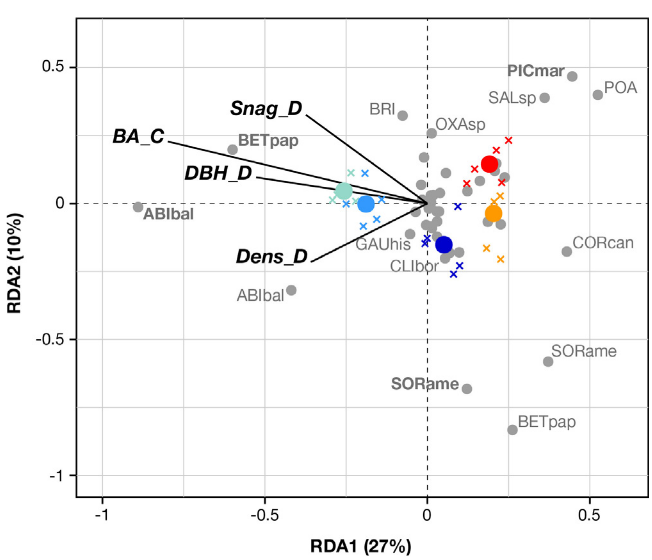

Fig. 6. Distance triplet of redundancy analysis (RDA) of plant composition. Lines represent continuous variables (SNAG_D: snags of deciduous species; BA_C: basal area of conifer species; DBH_D: diameter at breast height of deciduous species; Dens_D: density of deciduous species). Colored dots represent silviculture scenarios (green: Control; light blue: CLAAG; dark blue: CLAAG + PCT; orange: PLM; red: PLC). Colored cross represent sites (5 sites per silviculture scenarios). Gray dots represent species. Species names are only detailed for species with the highest contribution to axes RDA1 or RDA2, i.e. coordinate on one axis was < 10th quantile or > 90th quantile of the distribution of species coordinates on this axis. Trees are indicated in bold fonts. See Fig. 1 for scenario description and Fig. 5 for species names. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.4. Stand productivity

The DBH of conifer species increased with the increasing intensity of silviculture scenarios (excluding the Control scenario), with higher DBH achieved in plantations compared to naturally disturbed stands and to unplanted stands (contrasts Control *vs* PLM + PLC; CLAAG and CLAAG + PCT *vs* PLM and PLC, Fig. 7a, Table 3a). Trees achieved higher DBH in CLAAG + PCT stands than CLAAG only stands (contrast CLAAG *vs* CLAAG + PCT, Fig. 7a, Table 3a). Deciduous trees presented higher DBH in naturally disturbed stands than in managed stands (contrast Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. 7b, Table 3b).

We did not observe any trend for the basal area of conifer species in managed stands along the gradient of increasing intensity of silviculture scenarios (excluding the Control scenario) (Fig. 7d, Table 3a). Basal area of conifer species was higher in naturally disturbed stands than in managed stands (contrasts Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. 7d, Table 3a). Basal area of deciduous species was marginally significantly lower in CLAAG stands than in CLAAG + PCT stands (contrast CLAAG *vs* CLAAG + PCT, Fig. 7e, Table 3b).

DBH and basal area of merchantable conifer trees was higher in naturally disturbed stands than in managed stands (contrasts Control *vs* CLAAG and CLAAG + PCT and PLM and PLC, Fig. 7c and f, Table 3c). Although we did not detect any significant effect of increasing the intensity of silviculture scenarios (excluding the Control scenario) on the DBH of merchantable conifer trees in managed stands (Fig. 7c, Table 3c), the basal area of merchantable conifer trees increased along the gradient (contrasts CLAAG and CLAAG + PCT *vs.* PLM and PLC, CLAAG *vs.* PLC, Fig. 7f, Table 3c). This is explained by the net increase in the number of merchantable conifer trees along the gradient, ranging from 375 ± 279 stems ha^{-1} in CLAAG stands to 900 ± 252 stems ha^{-1} in PLC stands.

4. Discussion

4.1. Ecological distance between natural and managed stands

The ecological distance between naturally disturbed and managed stands increased with the increasing intensity of silviculture scenarios. As predicted, we observed a homogenization of the diameter stand structure in the most intensive scenarios, compared to the less intensive ones. This was expected, as uniformity in plantation structure is considered a beneficial characteristic; costs are reduced when stands are composed of relatively few big trees that are similar in size (Liechty et al., 1988). Variations in tree dimensions are low if release treatments are properly scheduled and done (Jobidon and Charette, 1997; Jobidon, 2000), as was the case in the more intensive scenarios studied here. Silviculture further impacted the quantity and the quality of deadwood; we measured lower snag density and smaller snags in managed stands than in the naturally disturbed ones. Our results support that natural disturbances are an important cause of deadwood production (Sturtevant et al., 1997) but that harvesting usually do not leave numerous and large snags.

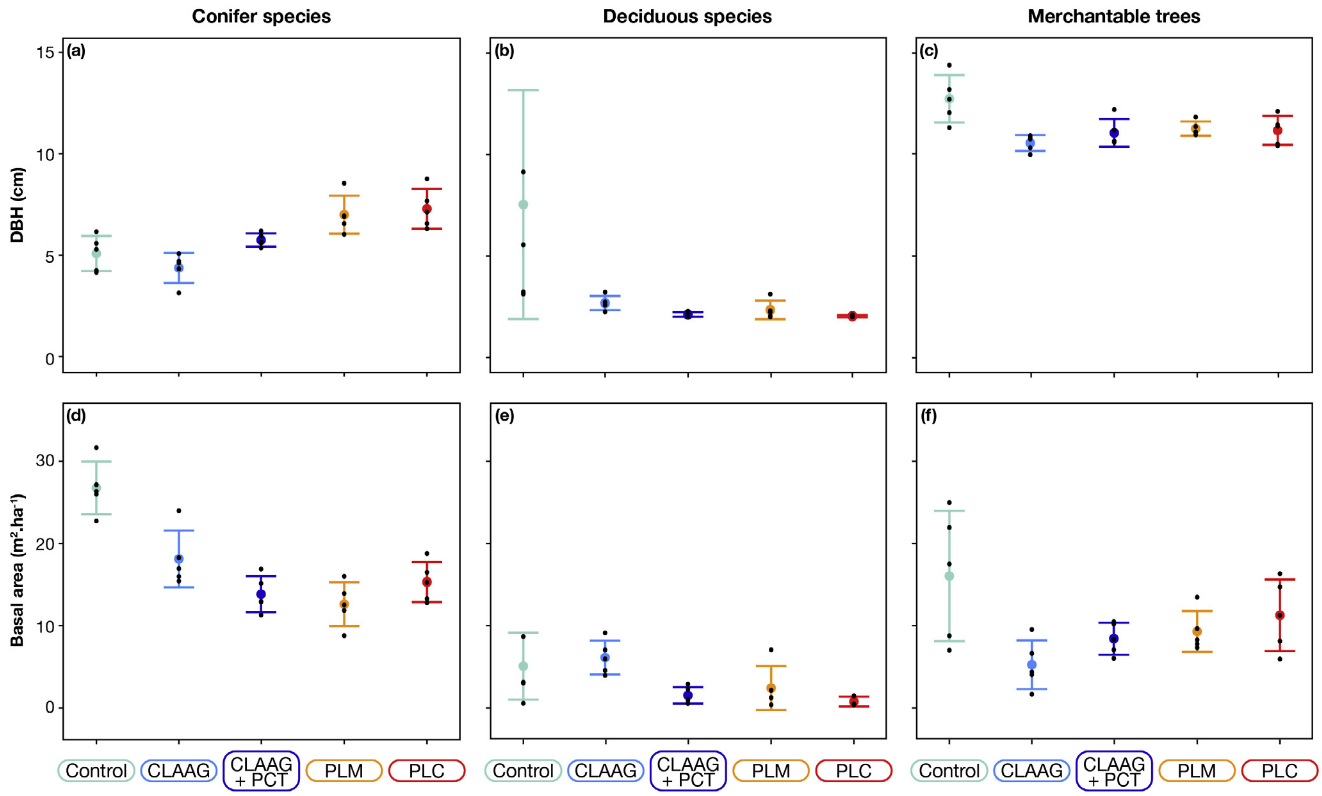

Fig. 7. Values of (a, b, c) diameter at breast height (DBH; cm) and (d, e, f) basal area ($m^2\ ha^{-1}$) of (a, d) conifer, (b, e) deciduous and (c, f) merchantable trees along an increasing gradient of silviculture intensity. Data are presented as mean ± standard deviation (n = 5 sites represented as black dots). See Fig. 1 for scenario description.

We hypothesized that the plant community composition would be modified along the gradient of silviculture intensity, with an increase in heliophilous species cover at the expense of sciaphilous species. We indeed observed the emergence of light demanding and shade intolerant species with increasing silviculture intensity, and this, despite small differences of available light in the understory. We believe the presence of these species is a legacy of the more drastic differences in light conditions among treatments that existed shortly after their application (Lindgren et al., 2006; Widenfalk and Weslien, 2009). Contrary to our prediction though, sciaphilous and generalist species typical of naturally disturbed stands (such as bryophytes, *Oxalis montana*, *Gaultheria hispidula* (L.) Muhl. ex Bigelow and *Cornus canadensis*) remained present in the most intensive scenarios. This overlap between the presence of shade tolerant, late successional species and light demanding, early successional species, resulted in a higher diversity in managed stands than in naturally disturbed stands. But while biodiversity indices such as richness and *SID* are useful to compare communities, they do not take into account changes in species composition (Lindgren et al., 2006), an essential aspect while assessing the ecological distance between naturally disturbed and managed stands. Moreover, in the context of ecosystem management, higher diversity in managed stands does not necessarily result in a lower ecological distance from natural forest. In particular, the humid boreal forest is naturally characterized by a low species diversity compared to other forest biomes, as biodiversity tends to increase from the poles to the Equator (Lomolino et al., 2010).

4.2. Productivity along a gradient of increasing silviculture intensity

We measured higher basal area of merchantable trees (and hence, a higher productivity from a forest management perspective) in plantations than in stands originating from natural regeneration scenarios. This suggests that these scenarios better controlled the availability of environmental resources (Bell et al., 2008) and concentrated them to desired crop trees. Moreover, mechanical and chemical release of the planted stands resulted in similar crop tree productivity, an observation in line with the conclusions of Jobidon et al. (1999) made five years after the application of these treatments in stands similar to those studied here. Our mid-term results thus support that is some ecosystems, mechanical release is an adequate alternative to herbicides for legislative contexts in which the use of chemicals is restricted or banned for forestry uses, such as in Québec (Thiffault and Roy, 2011). However, several mechanical treatments might be necessary (as was the case here), with important impacts on the economic viability of this approach (Dampier et al., 2006). Easier access to certification labels that discourage the use of herbicides could, on the other hand, compensate part of the increased costs (Hartley, 2002). The higher DBH and basal area of merchantable trees that we measured in naturally disturbed stands compared to the managed ecosystems could be explain by the presence of biological legacies, such as remnant trees from the upper canopy stratum of the original stands that had survived the spruce budworm outbreak.

4.3. Scenarios based on natural regeneration better emulate natural perturbations

Overall, our 20-y results show that the ecological distance from naturally disturbed stands was lower after CLAAG than after the other silviculture scenarios tested here. On these mesic sites, CLAAG better emulated the effects of the dominant natural disturbance compared to the other silviculture scenarios. This confirms that careful logging around advance growth is, until now, the form of harvesting the best adapted to stands with a cyclic dynamics driven by insect outbreaks (Bergeron et al., 1999). However, CLAAG

Table 3
ANOVA and planned contrast results for diameter at breast height (DBH) and basal area of (a) conifer, (b) deciduous and (c) merchantable trees for naturally disturbed stands (Control) and managed stands representing an increasing gradient of silviculture intensity. See Fig. 1 for scenario description.

	DBH		Basal area	
(a) Conifer trees				
ANOVA	$F_{4,20}$	*P*	$F_{4,20}$	*P*
Silviculture intensity	11.77	**<0.001**	10.81	**<0.001**
Contrast	*z*	*P*		
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	−2.51	**0.063**	5.90	**<0.001**
Control *vs* CLAAG + (CLAAG + PCT)	0.06	1.000	4.87	**<0.001**
Control *vs* PLM + PLC	−4.65	**<0.001**	5.90	**<0.001**
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	−5.76	**<0.001**	1.26	0.652
CLAAG *vs* (CLAAG + PCT)	−2.69	**0.038**	2.01	0.203
PLM *vs* PLC	−0.57	0.973	−1.68	0.373
CLAAG *vs* PLC	−5.70	**<0.001**	1.06	0.781
(b) Deciduous trees				
ANOVA	$F_{4,18}$	*P*	$F_{4,18}$	*P*
Silviculture intensity	7.38	**0.001**	3.28	**0.035**
Contrast	*z*	*P*	*z*	*P*
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	5.26	**<0.001**	1.11	0.738
Control *vs* CLAAG + (CLAAG + PCT)	4.74	**<0.001**	−0.07	1.000
Control *vs* PLM + PLC	4.61	**<0.001**	1.97	0.214
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	0.54	0.974	2.38	0.085
CLAAG *vs* (CLAAG + PCT)	1.25	0.639	2.58	0.051
PLM *vs* PLC	0.50	0.980	1.08	0.759
CLAAG *vs* PLC	1.04	**0.778**	3.07	**0.012**
(c) Merchantable trees				
ANOVA	$F_{4,20}$	*P*	$F_{4,20}$	*P*
Silviculture intensity	5.93	0.003	4.66	**0.008**
Contrast	*z*	*P*	*z*	*P*
Control *vs* CLAAG + (CLAAG + PCT) + PLM + PLC	4.64	**<0.001**	2.90	**0.020**
Control *vs* CLAAG + (CLAAG + PCT)	4.74	**<0.001**	3.75	**0.001**
Control *vs* PLM + PLC	3.72	**0.001**	1.53	0.469
CLAAG + (CLAAG + PCT) *vs* PLM + PLC	−1.33	0.607	−2.76	**0.034**
CLAAG *vs* (CLAAG + PCT)	−1.05	**0.788**	−1.97	0.220
PLM *vs* PLC	0.21	0.999	−0.49	0.984
CLAAG *vs* PLC	−1.34	**0.597**	−3.11	**0.010**

Values in bold are significant ($P < 0.05$).

favored an increase in the density of deciduous trees that likely established from buried seed banks or sprouting (Laflèche et al., 2000). This high relative abundance of northern hardwoods, compared to the natural stand dynamics, has the potential to limit conifer regeneration during the next revolution (Déry et al., 2000).

Pre-commercial thinning is often recommended to decrease the abundance of hardwood species (Thompson and Pitt, 2003). Our study showed that PCT resulted in crop trees reaching larger DBH than in CLAAG only plots, a well-documented effect of reducing stand density (Pothier, 2002, Pitt and Lanteigne, 2008). PCT did not significantly affect the diameter structure of the stands compared to CLAAG, when estimated using skewness and kurtosis of DBH distributions. The maintenance of a strongly skewed distribution in PCT treated stands resulted from the recruitment of deciduous individuals in the small diameter classes, a probable legacy of the increased light levels following the treatment that favored stump sprouting and suckering of northern hardwoods. Therefore, despite a lower abundance of white birch trees, stands submitted to thinning were indeed characterized by a higher abundance in willow and American mountain ash compared to CLAAG.

4.4. Conclusions and management implications

Finding perfect control stands representing "natural forests" constitutes a challenge in the Anthropocene; we acknowledge that the origin of the control and managed stands we used in our study were not exactly synchronized. However, spruce budworm outbreaks are diffused disturbances (i.e. ~10-y duration). We thus selected the control stands in an area submitted to the last outbreak that was documented to have ended the same decennial period as the CLAAG treatment. Therefore, the origin of the control and managed stands were within the same 10-y period, minimizing as much as possible the effect of this confounding factor.

Our mid-term study reveals a general antagonism between the impacts of silviculture on key ecosystem attributes and forest productivity in humid boreal ecosystems, posing a challenge in the context of a management that aims at reconciling ecological issues with the production of socioeconomic services. Indeed, increasing the intensity of silviculture enhanced stand quality in terms of crop tree productivity, but affected key ecosystem attributes compared to naturally disturbed stands. At the scale of the management unit, diversification of silviculture scenarios could allow reaching production objectives while maintaining biodiversity and ecological processes (Bergeron et al., 1999). For example, a functional zoning approach such as the TRIAD (Seymour and Hunter, 1992), which consists in dividing the forest in zones dedicated to specific management objectives (from conservation to wood production), could be favored. However, functional zoning is a landscape level conservation approach. Because some ecosystem-based management issues must be considered at the stand level, adjustments to silviculture scenarios should be considered to reduce the ecological distance between natural and managed forests while reaching expected wood production (Barrette et al., 2014). For instance, retention forestry allowing the maintenance of biological legacies during harvest is known to emulate natural disturbance at the stand scale (Gustafsson et al., 2012; Fedrowitz et al., 2014). Innovative modalities of CLAAG and PCT could be applied to ensure snag recruitment over time, as deadwood plays important ecological roles (e.g. habitat for animals and plant species). Further research is needed to determine retention parameters to achieve expected wood production while maintaining variability of key ecosystem attributes in humid boreal forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.01.007.

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