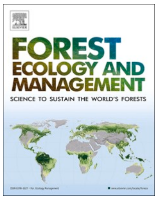
Forest Ecology and Management 593 (2025) 122815

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Understory community dynamics 12 years after commercial thinning and gap creation in naturally regenerated and planted stands

Raphaël Turquin [a,*], Isabelle Aubin [b], Françoise Cardou [c], Robert Schneider [a], Martin Barrette [d], Luc Sirois [a]

[a] Département de biologie, chimie et géographie, Université du Québec à Rimouski, Québec, Canada
[b] Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario, Canada
[c] Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada
[d] Direction de la recherche forestière, Ministère des ressources naturelles et des forêts, Québec, Canada

ARTICLE INFO

Keywords:
Thinning by crop-tree release
Gap creation
Understory
Taxonomic composition and diversity
Trait assemblage and diversity
Vertical structure

ABSTRACT

New commercial thinning methods, combined with small gap creation, were introduced to better achieve ecosystem-based management objectives and reduce structural differences between unmanaged and planted stands. However, some aspects of the understory response to these silvicultural treatments remains unknown. Here we evaluate the effect of commercial thinning (from below, crop-tree release) and gap creation on the understory communities in naturally regenerated balsam fir (*Abies balsamea*) stands and white spruce (*Picea glauca*) plantations in eastern Canada. Understory communities were surveyed before thinning and gap creation, and then again 1, 2, and 12 years after treatment. The split-split-plot experimental design included four levels of thinning (none, thinning from below, and thinning by the release of 50 or 100 crop trees per hectare) combined with three gap sizes (none, 100 m^2, and 500 m^2). Among the plots, we compared three understory characteristics: taxonomic composition and diversity, trait assemblage and diversity, and vertical structure. We found differences in trait assemblage and vertical structure between the naturally regenerated stands and plantations 12 years after treatment. Our results show that thinning has negligible effect on understory communities, whereas gaps influence understory structure and composition, and differences remained 12 years after treatment. Large gaps (500 m^2) produced the most conspicuous change in the understory communities. Relative to small gaps (100 m^2), large gaps favoured shade-intolerant, ruderal species (e.g., *Hieracium* spp., *Carex* spp., *Rubus idaeus*, *Chamaenerion angustifolium*), and the development of dense shrub and forb layers. The effect of large gaps was greater in planted stands than in naturally regenerated ones. Commercial thinning did not significantly affect understory communities. Gaps should be used sparingly, especially in plantations with site preparation, to avoid the development of a recalcitrant vegetation layer.

1. Introduction

There are important differences between the dynamics observed in natural forests and those imposed by silviculture in managed ones. These differences have led the province of Quebec (Canada) as well as other jurisdictions in Eastern North America to promote close-to-nature silviculture and forest management (Sustainable Forest Development Act, 2013). The former entails better mimicking natural disturbances in the application of silviculture, such as turning towards variable retention harvest systems instead of clearcuts or using some type of continuous cover systems instead of even-aged approaches in areas where natural disturbances are not stand-replacing. The latter refers to modulating the size and spatial distribution of the cut-blocks to close the gap between managed and unmanaged forest landscapes. The ultimate objective is increased forest resilience and resistance to disturbances by, among other strategies, preserving or restoring community composition and structural diversity (Barrette et al., 2014).

In Eastern North America, natural disturbances, such as windthrows and spruce budworm (*Chroristoneura fumiferana*) outbreaks, affect less than 5 % of the mixedwood forests each year, resulting in uneven-aged,

---

[*] Correspondence to: Département de biologie, chimie et géographie, Université du Québec à Rimouski, 300, allée des Ursulines, C.P. 3300, succ. A, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

E-mail address: Raphael.Turquin@uqar.ca (R. Turquin).

https://doi.org/10.1016/j.foreco.2025.122815
Received 23 September 2024; Received in revised form 14 May 2025; Accepted 17 May 2025

irregular structures in unmanaged stands (Boucher et al., 2011). In contrast, young managed stands have typically an even-aged structure and may undergo multiple silvicultural interventions, such as commercial thinning, to promote the growth of the remaining stems until the final cut (Pothier and Savard, 1998; Thiffault et al., 2003; Prégent et al., 2011). The most common form of commercial thinning used in even-aged management regime is thinning from below (Smith et al., 1997). This practice aims to preserve healthy dominant trees by consistently removing low-quality suppressed trees (too small, deformed or diseased) (Gagné et al., 2016). In the case of a plantation, site scarification is additionally required after clear cutting. In this process, the organic layer and the mineral soil are mechanically mixed to create favourable conditions for seedling growth (Thiffault et al., 2003; Chaves Cardoso et al., 2020). Obviously, plantations are composed of the planted species, mainly black spruce (*Picea mariana*) or white spruce (*Picea glauca*), whereas naturally regenerated stands after clearcutting are dominated by balsam fir (*Abies balsamea*). The consequences of these practises have prompted the development of new ecosystem-based silvicultural approaches to reduce the gap between the composition, structure and functioning of unmanaged mixedwood stands and managed forests. Additionally, young naturally regenerated stands and young plantations represent an opportunity to test these new ecosystem-based thinning methods and start structural conversion.

Alternative commercial thinning methods such as crop-tree release have been proposed to initiate structural conversion of even-aged stands (Schütz, 1997; Gagné et al., 2016). Crop tree release targets high-growth-potential stems by releasing them from their direct competitors (Grenon et al., 2007), leading to the felling of trees in every size classes. Other than ensuring that crop trees are spaced more than 5 m apart, there is no spatial constraint. This approach enhances the growth of the crop trees, resulting in high-quality stems at the time of harvest (Baar et al., 2004; Lundqvist et al., 2007). Crop trees play a structuring role in the stand, by forming the backbone of the developing irregular structure and providing dominant cover for the recruited trees (De Potter et al., 2012). Structural conversion can also be initiated by the creation of gaps, which can enhance the complexity of a stand's structure by promoting the regeneration of tolerant or intolerant tree species, depending on the size of the opening (Seymour et al., 2006; Schneider et al., 2021a). The combination of small gaps and crop-tree release appears as a promising approach, since stand yield is not diminished, and structural complexity is enhanced relative to managed even-aged stands (Weiskittel et al., 2011; Gagné et al., 2016; Schneider et al., 2021b). Although the short-term effects of commercial thinning on stand structure have been documented (Juodvalkis et al., 2005; Del Río et al., 2017; Dupont-Leduc et al., 2020), their effects on understory plant communities remain poorly understood. The understory is a vital component of forest biodiversity and supports many ecological functions, such as nutrient cycling, food supply, and habitat for wildlife (Willson and Comet, 1996; Zak et al., 2003; Nilsson and Wardle, 2005). Because this environment is characterized by limited light and nutrients, changes in the availability of these resources following silvicultural treatment can alter understory composition (Bartels and Chen, 2010; de Grandpré et al., 2011; Kumar et al., 2018). For example, increased canopy openness after disturbance leads to greater light availability, favouring resident species and increasing species richness by allowing early successional species to colonize (de Grandpré et al., 2011; Haughian and Frego, 2016). Other factors, such as the composition of the understory community prior to treatment and site fertility, can also modulate this response (Roberts, 2004; Carter et al., 2022). History of soil disturbance, such as site preparation prior to plantation, can also modulate the response of understory community after thinning treatments even after decades (Vanha-Majamaa et al., 2017; Wei et al., 2019). This alteration disrupts the pre-established plant communities and facilitates the invasion of ruderal species that can form a large persistent seed bank (Haeussler et al., 2002; Bork et al., 2021).

To evaluate the impact of disturbances on understory communities, three characteristics can be used (Carnus et al., 2006): 1) taxonomic composition and diversity, including the detection of endangered species or invasive exotics; 2) trait assemblage and diversity, which reflects the filtering processes affecting local species (Grime, 1977; Roscher et al., 2012) and provides a mechanistic understanding of the understory response to disturbance (Díaz and Cabido, 2001; Violle et al., 2007); and 3) structural diversity of the understory, which is linked to successional dynamics (Bartemucci et al., 2006). These three complementary aspects of diversity allow us to assess plant community response to disturbances as associated with thinning and gap creation. This, in turn, enables us to understand the processes driving the dynamics of the understory community. Ultimately, the results from this approach aim to provide foresters with a more comprehensive understanding of impacts of management practices.

Most studies (Smith et al., 2008; Hekkala et al., 2014; Eler et al., 2018; Haughian, 2018) have focused on the short-term (<5 years) response of the understory to disturbances or have considered only the taxonomic or trait assemblage and diversity of understory communities. The few studies that have monitored understory taxonomic composition and diversity over a longer time span (approximately 10 years) have shown that community resilience decreases with increasing disturbance severity (de Grandpré et al., 2011; Vanha-Majamaa et al., 2017). Differences in the response of understory communities may depend on the proportion of direct sunlight reaching the forest floor. In the boreal zone, most natural gaps are under 100 m^2 and do not allow direct sunlight to reach the ground due to the low sun angle (Kneeshaw and Bergeron, 1998). Thus, canopy openings created by low-intensity thinning and small gaps are too small to enhance the proportion of direct sunlight on the forest floor, resulting in an increased abundance of tolerant pre-established species (Kern et al., 2014; Vanha-Majamaa et al., 2017). Moreover, canopy rapidly closes after low-intensity thinning and small gaps, contributing to a rapid reduction in the proportion of light reaching the understory (Stiell, 1980; Martin-Ducup et al., 2017). On the other hand, if the canopy opening is sufficiently large to allow direct sunlight reaching the forest floor, taxonomic, functional and structural richness and diversity increase with the colonization and persistence of shade-intolerant herbs, shrubs, and trees for an extended period (Aubin et al., 2000; de Grandpré et al., 2011; Kern et al., 2014; Vanha-Majamaa et al., 2017).

In this study, we compared changes in taxonomic and functional trait composition and diversity and structural components of the understory immediately before and then 1, 2, and 12 years after commercial thinning (either none, thinning from below, thinning by release of 50 or 100 crop trees ha^{-1}) and gap creation (either none, 100 m^2 gap, of 500 m^2 gap) in naturally regenerated balsam fir stands and white spruce plantations. We hypothesized that the response of the understory is proportional to the intensity of silvicultural disturbance. We assumed that changes in the three characteristics of the understory (taxonomic, functional and structural) would be greater in response to gap creation than thinning and will persist even after 12 years. We also assumed that the three characteristics of the understory will show consistent responses to silvicultural treatments.

2. Material and methods

2.1. Study area

The study area is located in the Mid-Appalachian Hills eco-region of southeastern Canada (48°19'N, 67°58'W), which consists of low hills ranging from 200 to 400 m in elevation. The surficial deposits are primarily of glacial origin (i.e., till) or *in situ* weathering, with thicknesses ranging from 0 to 1 m or more (Blouin and Berger, 2012). The regional average annual temperature is 2.2 °C (Ministère de l'Environnement, de la Lutte contre les Changement Climatiques, de la Faune et des Parcs, 2024), and total precipitation is approximately 1000 mm, with 38 % falling as snow (Gagnon et al., 2018). Forests in the study area are dominated primarily by indigenous species such as balsam fir, white spruce, eastern white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), and paper birch (*Betula papyrifera*) (Blouin and Berger, 2012). Approximately 37,000 ha, or 28 %, of the study area comprises forests regenerated with white spruce plantations.

Our experimental design includes four stands that were regenerated following a total cut that occurred 38–48 years ago (Supplementary Table S1). Two of the stands were naturally regenerated, whereas the other two were reforested with white spruce (hereafter referred to as "plantations"). Prior to planting white spruce seedlings, the sites were prepared through scarification, followed by chemical clearing of competing vegetation, supplemented by mechanical removal if necessary, to ensure the survival and growth of the seedlings. The naturally regenerated stands consist of balsam fir ($>$87 %) with some rare white spruce, black spruce ($\approx$5 %), paper birch ($\approx$5 %) and other hardwoods ($\approx$3 %). In the plantations, balsam fir ($\approx$27 %) and some rare hardwoods (*Betula papyrifera*, *Populus tremuloides*) ($\approx$1 %) have sporadically regenerated alongside the planted white spruce ($>$72 %). Percentages represent the mean stem density proportion just after thinning and gap treatment in 2009 (Aubin et al., 2014).

The split-split-plot design, implemented 24–36 years after total cutting, consists of multiple experimental units of 7424 m^2 (99 m × 76 m) (Gagné et al., 2016) that were randomly assigned a thinning method: control; from below (FB); release of 50 or 100 crop trees per hectare (50CTs or 100CTs). In each plantation, there are 20 experimental units (5 controls, 5 FB, 5 50CTs, and 5 100CTs), and in each naturally regenerated stand, there are 16 experimental units (4 controls, 4 FB, 4 50CTs, and 4 100CTs). In the case of thinning from below, approximately 24 % of the basal area was removed. Thinning 50 crop trees per hectare resulted in a 6 % removal, while thinning 100 crop trees per hectare led to a 13 % removal of the basal area (Dupont-Leduc et al., 2020). All experimental units were further divided into three sub-units of 2258 m^2: control without a gap, with a 100 m^2 gap, or with a 500 m^2 gap (Supplementary Fig. S1). The location and orientation of the experimental units was random within each site. The survey lines were however always oriented in the same way within each sub-unit (i.e. perpendicular to the longest experimental unit side, as illustrated in (Fig. S1), as to avoid bias to distance from the gaps.

2.2. *Vegetation surveys*

The vascular flora was surveyed four times following the same protocol. For each survey, a team of two observers surveyed all of the four stands in August 2008, before the silvicultural treatment, and from mid-July to mid-August in 2009, 2010, and 2020 after the treatment. The understory taxonomic composition of each sub-unit was surveyed along two 40 m transects that were parallel to each other and to the skid trails. Each transect was at least 10 m away from the skid trails to minimize any edge effects. The two transects were spaced 10 m apart, except in sub-units with a 100 m^2 gap, where they were spaced 5 m apart to ensure comprehensive coverage of the sampling area. Circular points of 15 cm radius were systematically placed every 2 m along each transect, resulting in a total of 40 sampling points per sub-unit. The presence of species in each sampling point was recorded across four vertical strata to assess structural diversity: 0–50, 50–100, 100–200, and 200–500 cm. Within each stratum, every species present (foliage) was assigned an occurrence value of one. Species present in a 2 m corridor on each side of the transect, but absent from the sampling point, were assigned an occurrence value of 0.5. All plants were identified to the species level, except for *Salix*, *Carex*, *Nabalus*, and *Viola* at the vegetative stage, which were identified to the genus level, and species of the Poaceae family, identified to the family level. The nomenclature used for identification was that of VASCAN (Brouillet et al., 2010). Woody species with stem having a diameter at breast height greater than 9 cm or taller than 500 cm in height were not surveyed. Among the 216 sub-units, two sub-units in a naturally regenerated stand and five sub-units in a plantation could not be surveyed due to high proportion of windthrow in the sub-units.

2.3. *Traits and associated metrics*

Here we use the term trait in its broader definition and include morphological, physiological or phenological feature measurable at the individual level, as well as performance traits related to individual fitness (Violle et al., 2007). Traits for each taxon were documented from the TOPIC database (Aubin et al., 2020), supplemented with information from the literature and field sampling (Supplementary Table S2). Additionally, data on species' shade tolerance and soil humidity preference, Raunkiaer's biological type, and native or exotic status were documented. For easier reading, all species characteristics were considered as traits and each species had a trait value for every selected traits. Traits were chosen based on the mechanisms most relevant to our study's objective: understanding the effects of silvicultural treatments on understory communities, particularly in relation to light and soil humidity requirement. Our trait list includes key resource capture traits such as specific leaf area and root depth, which are directly influenced by gap creation and thinning. We also focused on traits related to dispersal and propagation capability to shed light on the dominant colonization and growth strategy in communities after treatment.

2.4. *Diversity metrics*

Our analysis focused on the taxonomic composition and diversity, trait assemblage and diversity, and structural response of the understory plant community. We choose to use relative occurrence as it allows us to study community structure, analyse diversity patterns and to ensure temporal comparability with earlier surveys in the same sites (Aubin et al., 2014). We acknowledge that absolute occurrence could have provided valuable insights into species dominance and population size, but it may have been less suitable for detecting patterns in community composition and evenness across sites and over time. Relative occurrence was calculated by dividing each absolute occurrence by 40, the number of sampling points per sub-unit (species matrix: species × sub-unit). A trait matrix was created, containing the value of each trait for each surveyed taxon (trait matrix: trait × species). Each trait value was weighted by the relative contribution of species with that trait to the total of relative occurrences in the community (community-weighted-means, CWM matrix) (Garnier et al., 2004):

$$\mathrm{CWM} = \sum_{i=1}^{S} p_i x_i, \tag{1}$$

where p_i is the contribution of species i ($i = 1, 2, \ldots, S$) to the total of all relative occurrences in the community of species richness S, and x_i is the trait value for i-th species. We used the 'functcomp' function from the package 'FD' to calculate the CWM matrix based on our matrix of relative occurrences (Laliberté and Legendre, 2010).

2.4.1. *Taxonomic diversity*

To measure taxonomic diversity, we calculated the first-order Hill number (Hill, 1973) using the Shannon diversity index (Shannon, 1948). We used the 'diversity' function from the package 'vegan' (Oksanen et al., 2025) to calculate the Shannon index, then applied the exponential transformation. For a given sub-unit, the first-order Hill number (N1) was calculated as:

$$N_1 = e^{\left(-\sum_{i=1}^{S} p_i \ln(p_i)\right)}, \tag{2}$$

2.4.2. *Trait diversity*

To assess the trait diversity of understory communities, we calculated a trait richness index (FRic) and a trait dispersion index (FDis) for each sub-unit using the 'dbFD' function from the package 'FD' (Laliberté and Legendre, 2010). The FRic index represents the functional space corresponding to the minimum convex envelope that comprises the entire trait space filled by a species assemblage (Villéger et al., 2008). It should be noted that this index does not consider species abundance and only represents the diversity of trait combinations within the species assemblage (Villéger et al., 2008; Laliberté and Legendre, 2010). The FDis index allows taking into account relative occurrence of each species and estimating their dispersion in a multidimensional trait space (Laliberté and Legendre, 2010). This index can thus be interpreted as a measure of functional diversity.

2.4.3. *Structural diversity*

There is currently no standardized way to measure understory vertical structural diversity. Emerging methods based on Lidar provide a transparent way to assess the vertical distribution of biomass, but these are blind to the distribution of species and traits in the vertical dimension. Here, we showcase a novel use of community trajectory analysis (CTA, De Cáceres et al., 2019) to quantify forest vertical structure. This method extends a geometric approach for studying spatial trajectories in two-dimensional space to analyse community change over time in a multidimensional ecological space, whether trait space or species space. A segment is drawn between two or more sequential points (surveys, or rows in the community matrix), yielding an overall trajectory that starts with the first survey, and ends with the final one. Metrics such as total length and overall direction can be calculated to characterize species turnover over time.

Forest ecologists have long been puzzled by the quantification of understory vertical compositional organization (e.g. Aubin et al., 2007, 2008). Multivariate taxonomic or functional descriptions of community composition can be separated in vertical strata. Because plants that are rooted to the ground must pass through lower stratum to reach upper ones; there is a strong statistical dependence between the composition of upper strata and lower ones, much like the dependence that exists in a time series. Because it captures this non-independence, CTA is a promising tool for evaluating vertical structure of forest composition. To do this, we replace time of survey with height stratum. To describe community change across the vertical distribution of vegetation, we computed pairwise distances among four successive vertical strata (0–50, 50–100, 100–200, and 200–500 cm) for each sub-unit at all treatment combinations (thinning x gap). The starting point was the 0–50 stratum, and the ending point the 200–500 stratum. By treating them as lines connecting four points in this multidimensional space, we quantified the geometric properties of the resulting trajectories such as total length and overall direction (Supplementary Fig. S2). The net total trajectory length reflects the magnitude of compositional changes, both in species and traits, between the forest floor and upper strata, with longer trajectories indicating greater cumulative shifts in composition (Supplementary Fig. S2). The trajectory's overall direction provides a measure of the extent to which compositional change across vertical strata is directional or not, in other words, whether it demonstrates a trend that is consistent in vertical space (e.g. Supplementary Fig. S2a and c). A non-directional trajectory can indicate either small and/or stochastic shifts in composition between strata (e.g. Supplementary Fig. S2d), or compositional similarities between regeneration stratum and canopy despite contrasting mid-story stratum (e.g. Supplementary Fig. S2b) (Matthews et al., 2013; De Cáceres et al., 2019). Together, these values provide a quantitative estimate of forest vertical compositional heterogeneity, whether taxonomic or functional.

One drawback of CTA for both time and vertical structure analysis is the way it handles “empty” communities. While a complete lack of occurrences may be rare over time (depending on the organism), it is something that occurs regularly in the context of forest vertical structure. In this case, lack of occurrences creates a community that is maximally different from all other communities and increasing the overall diversity community trajectory. In the context of this study, we assigned a trajectory length of 0 to all sub-units where only the 0–50 cm stratum was non-empty (n = 20). We included sub-units with at least 2 consecutive non-empty strata for the calculation of trajectory length and 3 consecutive non-empty strata for the calculation of overall direction to mitigate the problem. This left us with 209 and 113 sub-units, respectively.

The Bray–Curtis index was used as a measure of dissimilarity in the trajectory analysis (Bray and Curtis, 1957) for the species matrix. Gower's distance (Gower, 1971) served as a measure of dissimilarity for the trait matrix. Trajectories were calculated for the species matrices and trait matrices separately, and two metrics were calculated: total trajectory length and overall trajectory direction (De Cáceres et al., 2019). Both metrics were calculated based on the taxonomic composition in the last survey, 12 years after treatment. As vertical structure was surveyed differently between the 4 surveys, only the last survey was considered for the analysis of the vertical structure.

2.5. *Statistical analysis*

2.5.1. *Temporal change in taxonomic composition and diversity*

All analysis were done using R 4.3.1 (R Development Core Team, 2023). The effects of different silvicultural treatments on taxonomic composition and diversity across all floristic surveys (2008, 2009, 2010, and 2020) were estimated by performing a principal response curve analysis (van den Brink and Ter Braak, 1999) on the species matrix. The control sub-units without a gap nor thinning were used as a basis for a priori comparison. This analysis estimates the effects of treatments on community dynamics by comparing them with the dynamics observed in the control sub-units. Differences between treatments after 12 years were determined by performing a Tukey HSD post hoc test using the R package "emmeans" (Russell, 2021) on the basis of the site scores calculated by the main response curve analysis. Pairwise comparisons were conducted using the R package "multcomp" (Hothorn et al., 2008).

In addition, a linear mixed-effect model was used to estimate the effect of silvicultural treatments, regeneration type and time on taxonomic diversity (N1) using the "lme4" package (Bates et al., 2015). Stand, experimental units and sub-units were included as random effects (Eq. (3)):

$$
\begin{aligned}
N1_{ijkl} = {} & \mu + \beta_1 \bullet G_{ijk} + T_{ij} + R_i + Y_{ijkl} + G_{ijk} \bullet T_{ij} + G_{ijk} \bullet R_i + G_{ijk} \bullet Y_{ijkl} + T_{ij} \\
& \bullet R_i + T_{ij} \bullet Y_{ijkl} + R_i \bullet Y_{ijkl} + G_{ijk} \bullet T_{ij} \bullet R_i + G_{ijk} \bullet T_{ij} \bullet Y_{ijkl} + G_{ijk} \\
& \bullet R_i \bullet Y_{ijkl} + T_{ij} \bullet R_i \bullet Y_{ijkl} + G_{ijk} \bullet T_{ij} \bullet R_i \\
& \bullet Y_{ijkl} + \nu_i + \nu_{ij} + \nu_{ijk} + \varepsilon_{ijkl},
\end{aligned}
\tag{3}
$$

with $N1_{ijkl}$ corresponding to the first-order Hill number considered for sub-unit k in experimental unit j of stand i of survey l. G_{ijk} is the gap size (none, 100 m^2 or 500 m^2); T_{ij} is the intensity of thinning (control, FB, 50CTs, and 100CTs) applied to the experimental unit; R_i refers to the type of regeneration of the stand (natural or planted), and Y_{ijkl} corresponds to the year of survey (before treatment, 1, 2, and 12 years after treatment). All fixed effects (i.e. G_{ijk}, T_{ij}, R_i, Y_{ijkl}) were categorical. Finally, ν_i is the random effect of the stand that is randomly distributed with a mean of 0 and variance of σ_i^2 (i.e. $\nu_i \sim N(0, \sigma_i^2)$), ν_{ij} is the random effect of the experimental unit where $\nu_{ij} \sim N(0, \sigma_{ij}^2)$, ν_{ijk} is the random effect of the experimental sub-unit where $\nu_{ijk} \sim N(0, \sigma_{ijk}^2)$ and ε_{ijkl} is the unexplained random error with $\varepsilon_{ijkl} \sim N(0, \sigma^2)$.

2.5.2. Temporal change in trait assemblage and diversity. To illustrate trait assemblage by stand and gap size in year 12, principal component analysis (PCA) was performed using the centered and scaled CWM matrix for the last survey in 2020. To assess potential differences in trait richness and diversity, we used the same linear mixed-effect models as Eq. (3) with the effect of silvicultural treatments, regeneration type and time, with $N1_{ijkl}$ becoming F_{ijkl} corresponding to the functional indexes.

2.5.3. Structural diversity 12 years after treatment. For the structural diversity quantified using only the last survey, we also used linear mixed-effects models with the thinning treatments, gap size and regeneration type considered as fixed effects (Eq. (4)):

$$V_{ijk} = \mu + \beta_1 \bullet G_{ijk} + R_i + T_{ij} + G_{ijk} \bullet R_i + G_{ijk} \bullet T_{ij} + R_i \bullet T_{ij} + G_{ijk} \bullet R_i \bullet T_{ij} + \nu_i + \nu_{ij} + \varepsilon_{ijk}, \tag{4}$$

with V_{ijk} corresponding to the trajectory metrics (i.e. total length or direction). For the direction of the trajectory, only double interactions were considered in the model due to insufficient replicas for the triple interaction. For each model, a Tukey HSD post hoc test was performed when one of the factors was significant ($p < 0.05$) in ANOVA; the latter was run using the R package “car” (Fox and Weisberg, 2019). Residuals were visually checked for normality and homoscedasticity. For the first Hill’s number (N1) and the index of trait richness (FRic), a logarithm in base 10 transformation was applied to help reduce heteroscedasticity of the residuals. We used simple main effects to verify the significant interaction terms. In the case of FDis, where the year of survey X regeneration X gap size interaction term was significant, the simple main effects were used to compare regeneration type for each year between each gap size. We proceed the same way for the triple interaction term year of survey X gap size X thinning treatment where we compare gap size for each year between each thinning treatment.

3. Results

3.1. Temporal dynamic of taxonomic composition and diversity

The first-order Hill number (N1) significantly varied among survey years ($F_{3,\ 575} = 3.06$; $p < 0.05$) and with the interaction between gap size and survey year ($F_{6,\ 571} = 3.01$; $p < 0.01$) (Supplementary Table S3). In sub-units with a 500 m^2 gap, the maximum value of N1 was reached 2 years after treatment and then decreased by 12 years after treatment. Values observed 12 years after treatment in sub-units without a gap and with a 100 m^2 gap were similar to the values in sub-units prior to silvicultural treatments (Fig. 1).

The principal response curves showed that treatments in the naturally regenerated stands produced a persistent compositional change after 12 years relative to the control (RDA axis 1 = 42.3 %; F = 24.50; $p = 0.001$) (Fig. 2). Elapsed post-treatment time explained 11.9 % of the variance, and the time × treatments interaction explained 21.0 % of the variance. The post hoc test showed that the 500 m^2 gap treatment differed significantly from the other treatments and the control. The 100 m^2 gap treatment and sub-units without gaps did not differ significantly from each other nor from the control. No significant differences were observed between the different thinning treatments for each gap level. In the plantations, the main response curves showed that the treatments generated a persistent compositional change 12 years after treatment relative to the control (RDA axis 1 = 40.5 %; F = 23.44; $p = 0.001$) (Fig. 2). The elapsed post-treatment time explained 10.7 % of the variance and the time × treatments interaction explained 13.4 % of the variance. The post hoc test showed that all gap sizes differed significantly from each other. Only the sub-units without a gap did not differ significantly from the control. As for the naturally regenerated stands, no significant differences were observed between the different thinning treatments for each gap level. The species scores indicated that *Rubus idaeus* benefited most from the conditions created by the gaps, especially in the 500 m^2 gaps, in both naturally regenerated stands and plantations. Three species were favoured in the gaps of both types of regeneration including *Prunus pensylvanica*, *Carex* spp. and *Lactuca biennis*. Additionally, species such as *Chamaenerion angustifolium*, *Galeopsis tetrahit*, and *Hieracium* spp. benefited exclusively from gap creation in plantations, whereas *Sambucus racemosa* and *Ribes glandulosum* benefited from gap creation in naturally regenerated stands only. Conversely, in sub-units without a gap, *Abies balsamea*, *Oxalis montana*, and *Monotropa uniflora* were favoured in both naturally regenerated stands and plantations. In the latter, other species such as *Clintonia borealis*, *Coptis trifoliata*, and *Maianthemum canadense* were favoured in sub-units without gaps.

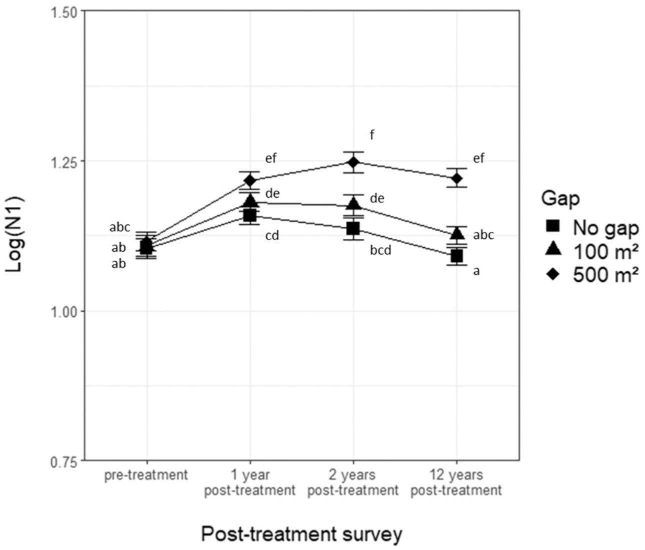


Fig. 1. Log transformed Hill’s first-order index (N1) during the four survey years (before treatment, 1-, 2-, and 12-years post-treatment) as a function of gap size, all sites combined, regardless of thinning treatment. Error bars show the standard error associated with the means. A Tukey HSD post hoc test was performed when one of the factors was significant in ANOVA (Supplementary Table S3). Letters indicate significant differences between the means of diversity indices calculated before (0) and then 1, 2, and 12 years after the commercial thinning and gap creation treatments.

3.2. Trait response 12 years after treatment

The first two axes of the PCA performed on the CWM matrix 12 years after treatment explained approximately 60 % of the total variation in the relative importance of traits in understory communities (Supplementary Fig. S3). The first (Dim1) and second axis (Dim2) slightly separated sub-units in plantation sites (on the upper left side of the PCA) from those in naturally regenerated sites (on the lower right side of the PCA). One plantation site showed a high proportion of multi-stem microphanerophytes (SF_multi and R_mc), annual herbs (R_t), exotic species (Status), anthropochorous species (D_hd), and species with graminoid-type leaves, decumbent or semi-rosette foliage structures (SF_g, SF_de, and SF_sr). In addition, traits such as shade intolerance (LI), high lateral extension (LE), persistent seed banks (SDPER) were also associated with this site. On the other hand, mono-stem megaphanerophytes (SF_mono and R_mg), species with significant height (HT), long-distance dispersal ability through anemochory (DI and D_w), higher carbon-to-nitrogen ratios (C/N), and deep root depth (RSD) were associated with one naturally regenerated stand. Overall, sub-units in plantations showed higher dispersion compared to naturally regenerated stands, particularly sub-units with a 500 m^2 gap, suggesting higher functional heterogeneity.

3.3. Temporal dynamics of trait richness and dispersion

The trait richness index (FRic) varied significantly with year of survey ($F_{3,\ 555} = 235.90$; $p < 0.001$) and the interaction between gap size and year of survey ($F_{6,\ 555} = 3.41$; $p < 0.001$) (Supplementary Table S5). For the interaction between gap size and year of the survey, the post hoc

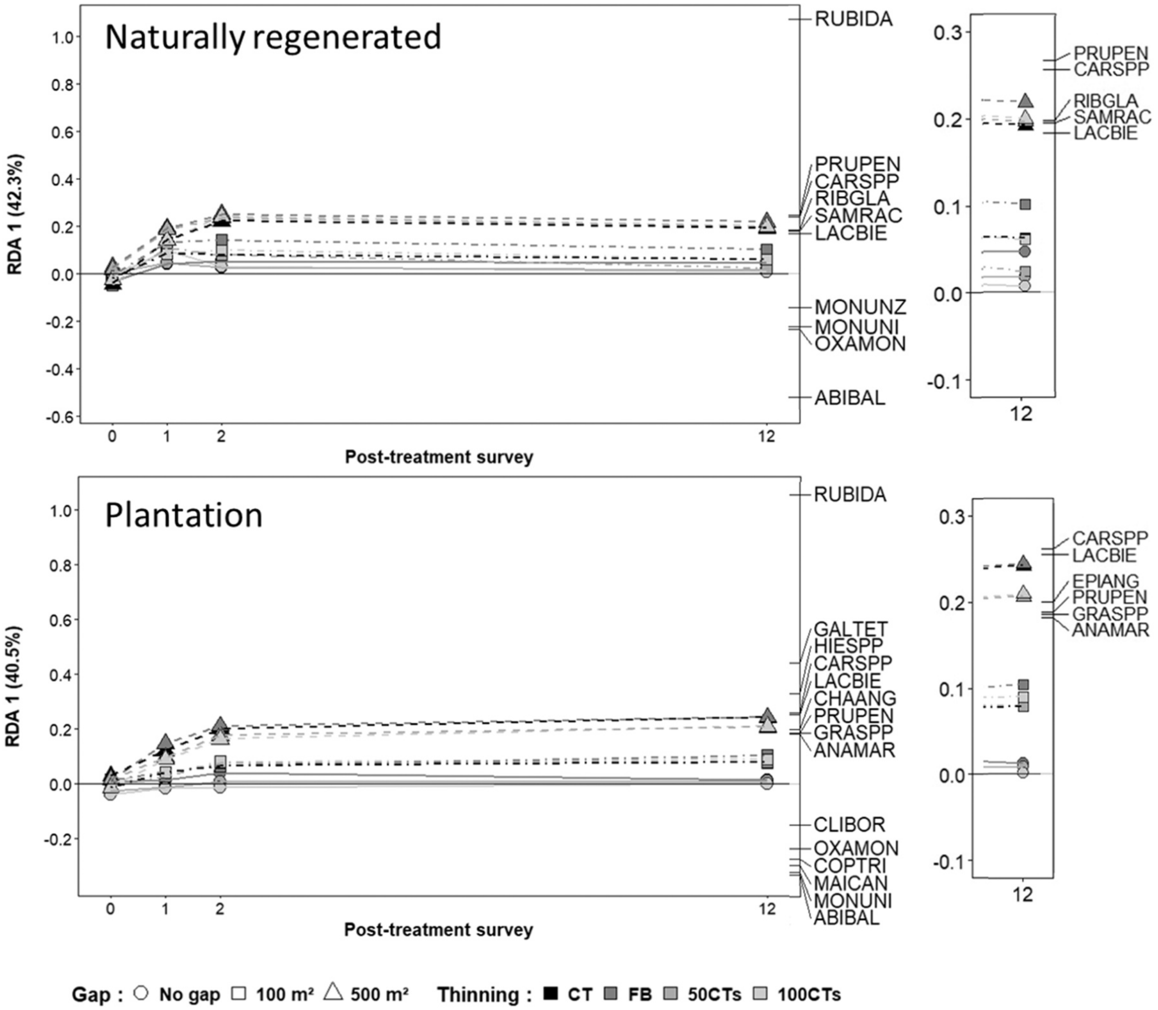


Fig. 2. Principal response curves for the first axis of the RDA testing the effect of silvicultural treatments and time on taxonomic composition. The curves represent the dominant time trajectory for the two sites in a naturally regenerated forest and plantation. Response curves are shown relative to the zero-line representing the control thinning treatment without gap treatment. The four thinning treatments are represented as CT: control, FB: from below, 50CTs/100CTs: release of 50/100 crop trees per ha, respectively. The scaling is symmetric has it allows a balanced representation of the variance of both sites and species. The boxes on the right zoom on the last year of survey to better show the position of each site score. The species presented on the right side of the chart have a score >0.15. See supplementary Table S4 for the definition of the species codes.

test showed that functional richness decreased for the two first post-harvest surveys (e.g. years 1 and 2) when compared to pre-harvest and 12 years after thinning, the latter having the highest value (Fig. 3). The values were the highest in the 500 m^2 gap, intermediate in the 100 m^2 gap, and lowest in the sub-unit without a gap (Fig. 3).

The trait dispersion index (FDis) varied significantly with year of survey ($F_{3,\,555} = 5.07$; $p < 0.01$), the interaction between gap size and regeneration ($F_{2,\,521} = 5.72$; $p < 0.01$), the interaction between gap size and year of survey ($F_{6,\,555} = 4.74$; $p < 0.001$), and the interaction between regeneration and year of survey ($F_{3,\,555} = 9.10$; $p < 0.001$). Significant effects were also found for the triple interaction between gap size, regeneration and year of survey ($F_{6,\,555} = 2.80$; $p < 0.05$) as well between thinning treatment, gap size and year of survey ($F_{9,\,555} = 0.42$; $p < 0.05$) (Supplementary Table S5). Functional dispersion decreased for years 1 and 2 and then increased 12 years after harvest (Fig. 4). It seems that community in naturally regenerated stands had higher functional dispersion than plantation across the 3 survey post-harvest in sub-units without a gap and with a 100 m^2 gap. In sub-units with a 500 m^2 gap, functional dispersion was similar between the two regeneration and show higher functional dispersion 12 years after harvest compared to sub-units without a gap and a 100 m^2 gap. When we look at the other triple interaction between thinning treatment, gap size and year of survey, the effect of the harvest was not clear and numerous intervals around means were overlapping (Fig. S4).

3.4. Structural diversity 12 years after treatment

The occurrence of plant groups (categorized by growth form and shade tolerance) across height strata varied depending on stand regeneration type and gap size (Fig. 5). In plantations, gap creation led to a diversification in strata from 0 to 200 cm in height, with an increase in shade-intolerant forbs, shrubs, and trees compared to sub-units without a gap (Fig. 5). In naturally regenerated stands, no detectable differences were found between sub-units without a gap and those with a 100 m^2 gap. However, differences were observed in the sub-units with a 500 m^2 gap, where the presence of shade-intolerant species contribute to the heterogeneity in the upper strata. Moreover, a greater proportion of tolerant tree species was observed in the 0–50 and 50–100 cm strata in naturally regenerated stands compared to the plantations. Conversely, a higher proportion of shade-intolerant forbs, shrubs, and trees was noted in plantations than in naturally regenerated stands. In general, vegetation was more developed in 500 m^2 gap compared to sub-units without a gap and 100 m^2 gap.

No significant differences were detected for taxonomic trajectory

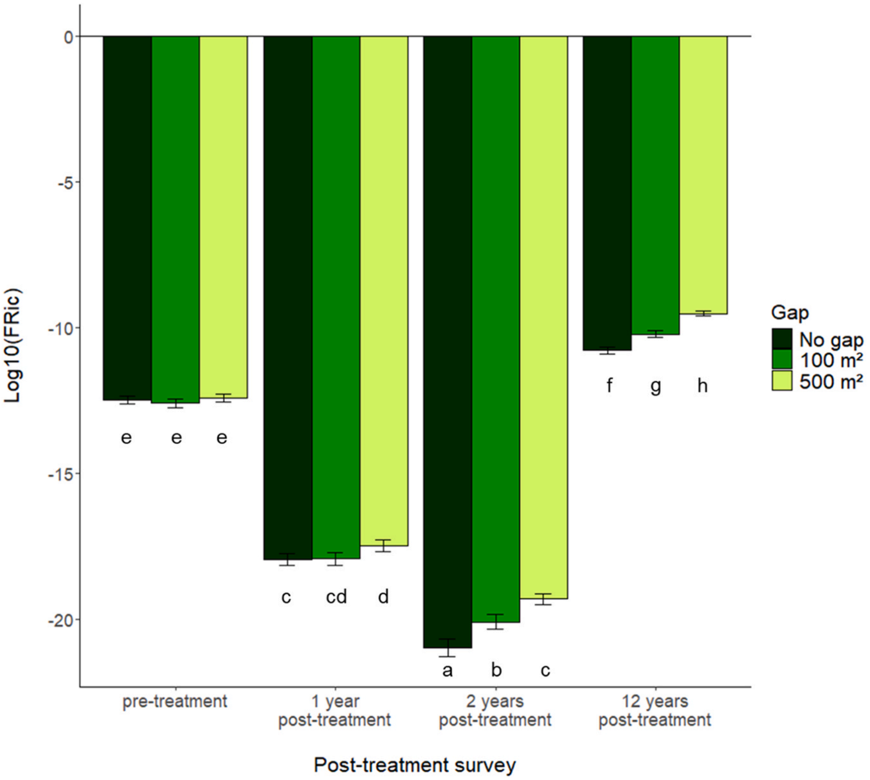


Fig. 3. Log transformed functional richness (FRic) during the four survey years (before treatment, 1-, 2-, and 12-years post-treatment) as a function of gap size. Error bars show the standard error associated with the means. A Tukey HSD post hoc test was performed when one of the factors was significant in ANOVA (Supplementary Table S5). Letters indicate significant differences between the means.

length between the treatments nor between regeneration type (Supplementary Table S6). For traits, trajectory length varied almost significantly with the interaction between stand regeneration and gap size ($F_{2,\,126} = 2.90$; $p = 0.059$) (Supplementary Table S6). Trait trajectory lengths were similar among gap sizes in naturally regenerated stands (Table 1). In plantations, trait trajectory lengths were longer in the sub-units with 100 m^2 and 500 m^2 gaps than in those without gaps (Table 1).

The taxonomic trajectory direction varied significantly between gap sizes ($F_{2,\,95} = 3.39$; $p < 0.05$), being straighter in the sub-units with a 500 m^2 gap than in sub-units lacking gaps and those with a 100 m^2 gap (Table 1). No significant differences were detected for trait trajectory direction between the treatments and stands (Supplementary Table S6).

4. Discussion

Our study comprehensively assessed the medium term (12 years) effect of gap size and thinning type on the forest understory vegetation. We found that low-intensity disturbances, such as commercial thinning, had no significant effect on taxonomic, trait, and structural diversity of understory plant communities in managed softwood stands. However, more severe disturbances, such as gaps, altered floristic assemblages with lasting impacts that remained even 12 years post-treatment. Furthermore, we observed marked differences in response to disturbance type and severity between communities in plantations when compared to those in naturally regenerated stands. In order to highlight the drivers of the understory community, we divided the discussion into three sections that differ from the results section: 1) we present the impact of thinning on understory communities; 2) we describe how gap creation and gap size can affect understory composition and finally, 3) we discuss the limitations on comparing regeneration type and the influence of soil disturbance on understory communities.

4.1. Understory response to commercial thinning

In the stands 12 years post-treatment, the thinning treatment have a significant effect on functional dispersion, but drawing conclusion about its impact on this diversity metric is challenging since no clear trend is observed. For understory species diversity and trajectory metrics, we found no difference between thinning treatments, similar to findings from mixed forests in Finland (Vanha-Majamaa et al., 2017). Thinning causes the crown of residual trees to expand or rearrange over a short period of time (<5 years), leading to canopy closure (Juodvalkis et al., 2005; Martin-Ducup et al., 2017) and reduction of light reaching the ground from 24 % (of above-canopy radiation) to 7 % ten years later (Stiell, 1980). In our plantations, 10 % of above canopy light reached the ground in sub-units without a gap 11–12 years after thinning (Begni, 2022). This decrease in light reaching the ground could lead to the competitive exclusion of shade-intolerant species (Reich et al., 2012). Therefore, it appeared that the thinning-related canopy opening might have been too small in size and short in duration to sufficiently increase ground-level light and allow shade-intolerant species to colonize and persist in the understory (Beggs, 2004).

4.2. Understory community response to gap size

The increase in taxonomic and trait diversity observed in the 500 m^2 gap sub-units 1, 2 after treatment and still significant 12 years after treatment appeared to be associated with sufficient light availability for shade-intolerant species (de Grandpré and Bergeron, 1997; Macdonald and Fenniak, 2007; Fahey and Puettmann, 2008). In our plantations, Begni (2022) found that 20 % and 60 % of the photosynthetically active radiation reached the ground in the 100 m^2 and 500 m^2 gaps, respectively. Our results aligned with studies in softwood-dominated forests, where shade-intolerant species persisted for 5–10 years after gap creation (Ares et al., 2009; Vanha-Majamaa et al., 2017). In our study, the

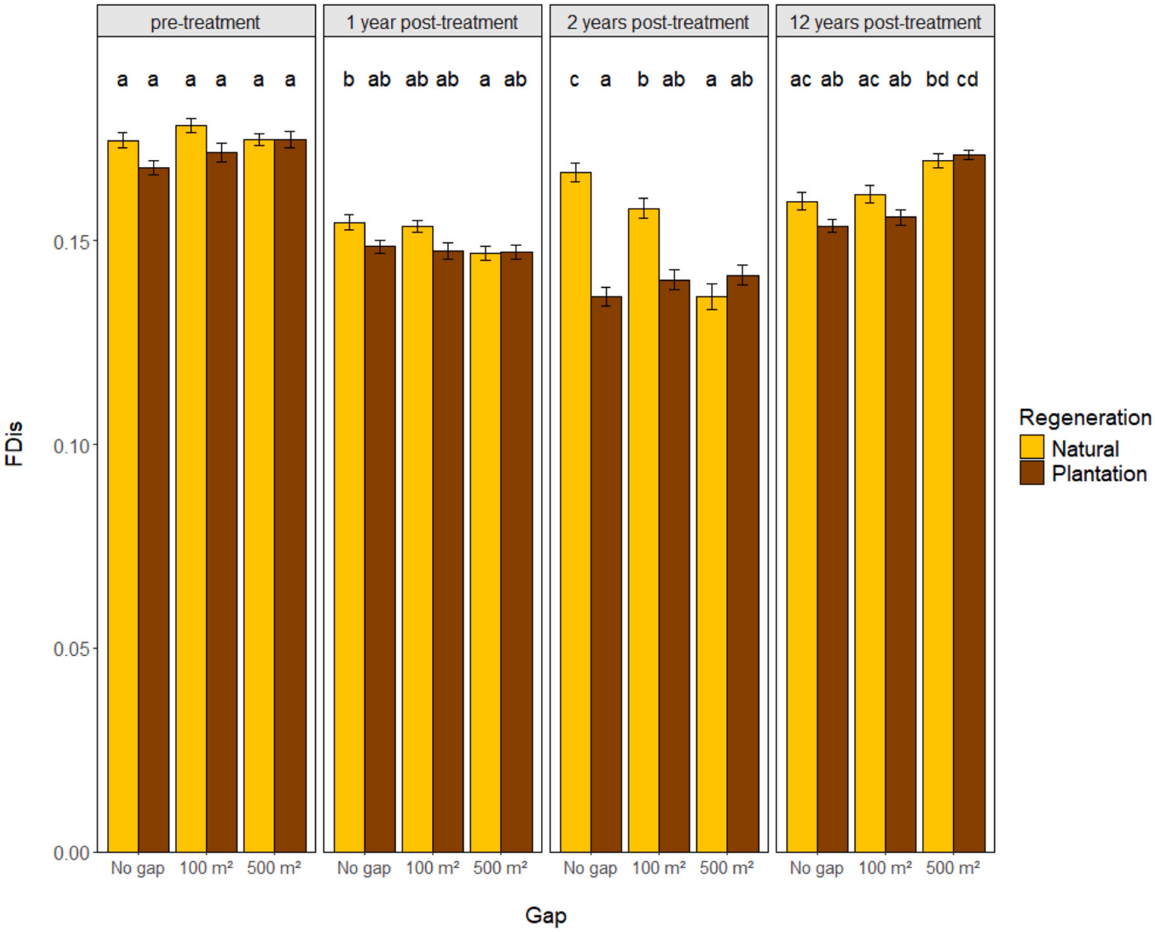


Fig. 4. Functional dispersion (FDis) for each gap size under study as a function of site regeneration during the four survey years (before treatment, 1-, 2-, and 12-years post-treatment). Error bars show the standard error associated with the means. A Tukey HSD post hoc test was performed when one of the factors was significant in ANOVA (Supplementary Table S5). Comparisons were performed on the interaction of gap size and regeneration within each year to ensure readability as triple interaction was significant. Letters indicate significant differences between the means.

500 m^2 gap sub-units favoured species such as *Rubus idaeus*, *Chamaenerion angustifolium*, *Hieracium* spp., *Lactuca biennis*, *Carex* spp., *Prunus pensylvanica*, and *Sambucus racemosa*. In addition, trait richness increased with gap size and reached a peak 12 years after harvest. Moreover, functional dispersion was greater in 500 m^2 gaps 12 years after harvest. Because changes in functional dispersion capture changes in species relative abundance, while functional richness captures only the total volume occupied by communities, irrespective of species' abundance, our results suggest that increases in total trait diversity (richness) after 12 years were primarily due to the appearance of species that were both functionally different from the rest of the community and numerically rare. In sub-units without gaps, low light levels may have induced competitive exclusion of shade-intolerant species that colonized the stands immediately after treatment. When a large gap (i.e. 500 m^2) was created, species with trait values favouring rapid colonization of open environments and those with high vegetative propagation and large persistent seed banks dominated, leading to a reduced functional diversity. Nonetheless, other intolerant species with different trait combinations succeeded in colonizing and persisting in openings, leading to an increased functional richness.

Differences in understory response were observed between sub-units with 100 m^2 and 500 m^2 gaps, particularly concerning vertical structure. The minimum size of the gap necessary for pioneer and shade-intolerant species to colonize and persist varies depending on the forest type and region (Fahey and Puettmann, 2008; Kneeshaw and Prévost, 2007). In mixed forests of northwestern Quebec, this threshold is 200 m^2 for tree species (Vepakomma et al., 2011), whereas in old-growth Appalachian forests of Tennessee, it is 400 m^2 (Busing, 1994). In boreal mixed forests, gaps under 100 m^2 produce slight changes in understory taxonomic composition and diversity, leading to an increase in the abundance of pre-established species (de Grandpré et al., 2011). In this study, the CTA shows that the trajectory direction was straighter in 500 m^2 gap sub-units indicating a compositional gradient between the vertical strata. In plantations, values of total trajectory length were higher in 100 m^2 and 500 m^2 compared to sub-units without gap. These results suggest that a more heterogeneous vertical structure develop in the understory of 500 m^2 gap relative to those without a gap or with a 100 m^2 gap. Larger gaps provided higher light conditions, which benefit shade-intolerant forbs and shrubs species such as *Galeopsis tetrahit*, *Chamaenerion angustifolium*, and *Rubus idaeus*. Moreover, tree regeneration in the large gaps was poor as only one tree species (*Prunus pensylvanica*) was generally found. These results raised some concerns, as the creation of gaps seemed to favour shrub species able to form a recalcitrant layer, potentially limiting the regeneration of commercial tree species (Royo and Carson, 2006). The gaps may have been created at a time when the trees in the stand were not yet sexually mature, and therefore did not produce enough viable seeds to establish regeneration in the understory. In the sub-units with a 100 m^2 gap, canopy closure and shading from adjacent trees may have led to the competitive exclusion of shade-intolerant species in a portion of the gap (Busing, 1994; Kneeshaw and Prévost, 2007; Vepakomma et al., 2011; Reich et al., 2012). Therefore, species trait and structural diversification were limited in the sub-units with a 100 m^2 gap relative to those with a 500 m^2 gap where the forest canopy remained open for a longer time.

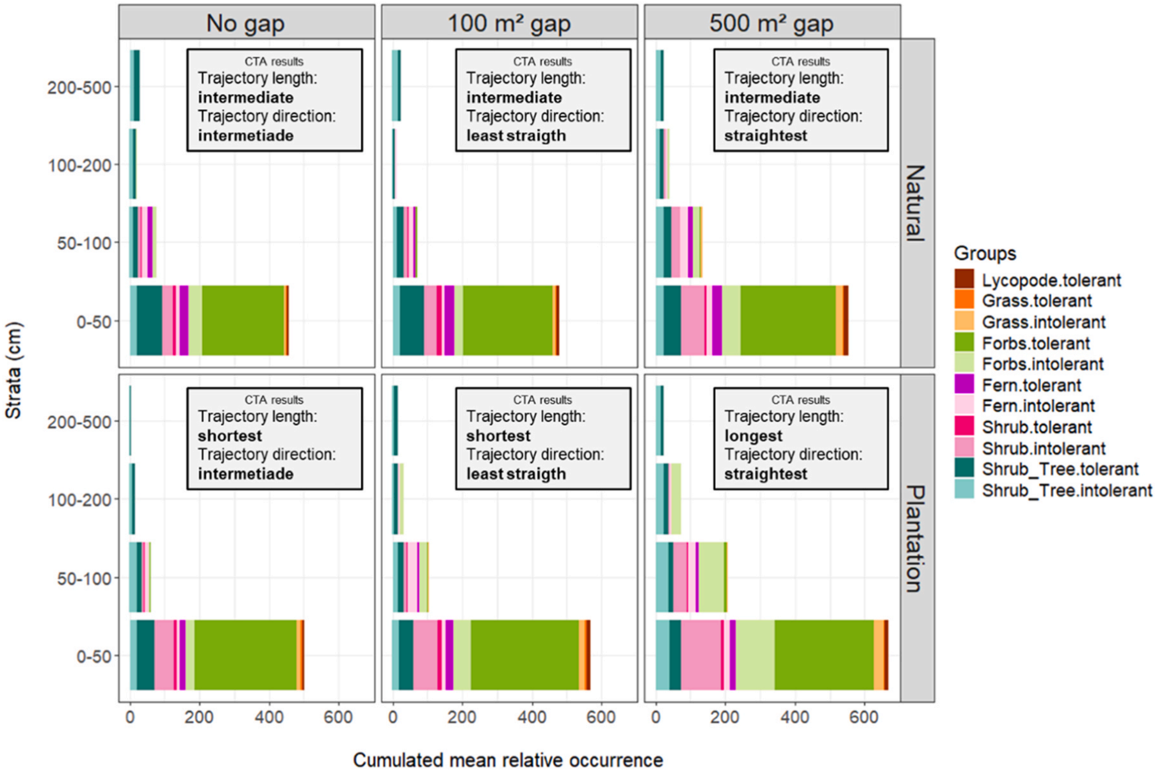


Fig. 5. Cumulated mean relative occurrence of species groups in the understory flora according to the four inventoried vertical strata, regeneration of the site (natural or plantation), and gap size at year 12. The species are grouped as a function of their growth form and shade tolerance. Light shades represent shade-intolerant species, and dark shades represent shade-tolerant species. Insert boxes show CTA results using Table 1 and show the significant differences in trajectory length and direction as a function of the combination of factors. For sites in natural regeneration, length of the pathways was similar between each gap treatments. For sites in plantations, length of the pathways was lower in sub-units without gap compared to 100 m^2 and 500 m gap. For both type of regeneration, the direction of the trajectories was lower in 100 m^2 gap, resulting in more curved pathways. The direction was higher in 500 m^2 gap resulting in more straight pathways. See supplementary Figs. S5 and S6 for a graphical representation of the trajectory analyses.

Table 1

Mean values (±standard error) of the different trajectory metrics from the CTA as a function of site regeneration and gap size 12 years after treatments. A pairwise Tukey HSD post hoc test was performed when ANOVA determined one of the factors to be significant (Supplementary Table S6). A post hoc test was also performed on the gap size X regeneration interaction for the trait trajectory length, as these factors were almost significant and relevant in the study. Letters next to the mean values indicate significant differences. See Supplementary Figs. S5 and S6 for a graphical representation of path analyses.

	Regeneration	**Gap size**		
		No gap	**100 m^2**	**500 m^2**
Taxonomic trajectory length	Natural	1.25 ± 0.13	1.28 ± 0.12	1.61 ± 0.07
	Plantation	0.89 ± 0.09	1.40 ± 0.12	1.69 ± 0.08
Trait trajectory length	Natural	0.33 ± 0.03**ab**	0.33 ± 0.03**ab**	0.41 ± 0.01**ab**
	Plantation	0.31 ± 0.03**a**	0.42 ± 0.03**b**	0.51 ± 0.02**b**
Taxonomic trajectory direction	Natural	0.38 ± 0.01**ab**	0.40 ± 0.01**a**	0.43 ± 0.01**b**
	Plantation	0.40 ± 0.02**ab**	0.38 ± 0.01**a**	0.41 ± 0.01**b**
Trait trajectory direction	Natural	0.41 ± 0.03	0.46 ± 0.05	0.52 ± 0.02
	Plantation	0.48 ± 0.04	0.53 ± 0.03	0.52 ± 0.02

4.3. *Limits to the evaluation of the effect of regeneration type on understory vegetation*

We found no significant differences in taxonomic diversity indices between naturally regenerated stands and plantations. However, our two plantations exhibited greater values of total length and direction of trajectories in the CTA, suggesting significant heterogeneity of the vertical structure, particularly in 500 m^2 gaps, which also had higher functional diversity. Additionally, functional dispersion in plantations was lower in sub-units without gap and in those with 100 m^2 gaps compared to naturally regenerated stands. Finally, the principal component analysis indicated greater functional heterogeneity in plantation sub-units. These differences could be attributed on how site preparation prior to plantation affects viable propagules and breaks up root systems of advanced regeneration established prior to clearcutting (Haeussler et al., 2002; Newmaster et al., 2007). Intolerant species that create seed banks and those that sprout from roots or rhizomes may rapidly colonize after site preparation (Haeussler et al., 2002; Härdtle et al., 2003). Consequently, soil disturbance favours ruderal species, such as *Rubus idaeus, Chamaenerion angustifolium* or grasses, which occurred more frequently in gaps created in stands that had undergone site preparation, such as in plantations (Vanha-Majamaa et al., 2017). The application of these results to forest management should be done with caution as they are based on a limited number of stands (two plantation and two naturally regenerated stands).

Furthermore, there might be a confounding effect between time since clearcut and regeneration type. The age of the trees in all four stands are very similar (unpublished results), the harvesting was carried out earlier in the naturally regenerated stands when compared to the planted ones.

However, a study carried out in the same sites by Aubin et al. (2014) demonstrated significant taxonomic and functional differences in understory communities of 20-year-old planted and naturally regenerated stands. Planted stands had a higher prevalence of trait values and species typically associated with younger stands, suggesting that the understory of planted sites may require more time to achieve compositional and functional attributes comparable to those of naturally regenerated stands.

5. Conclusions and implications for softwood stand management

In this study, we used taxonomic, functional, and structural metrics to understand how the understory responds to various silvicultural practices that aim to establish an uneven-aged structure in young regenerating stands. Our findings on understory response serve as an empirical foundation for refining these silviculture practices and minimizing their impact on the understory.

Our results revealed that low-intensity silvicultural practices, such as commercial thinning and gap creation that produces canopy openings of less than 100 m^2 have only a temporary effect on the understory. Silvicultural practices that result in larger canopy openings can promote heterogeneity in understory taxonomic composition and diversity, trait assemblage and diversity and vertical structure. However, caution is required when implementing these practices in intensively managed stands, such as those originating from plantations, as they may lead to the extensive recruitment of ruderal and recalcitrant species. Consequently, in plantations with site preparation, more time may be required after gap creation to allow for dispersal and growth of native species that will contribute to the recovery and convergence of understory flora toward that observed in naturally regenerated stands. Furthermore, as trees were not sexually mature to establish regeneration in the understory when gaps were created, large gaps mainly favour the formation of a recalcitrant layer of shrub and forb species to the detriment of commercial tree species. Then, in this particular case, the planting of trees coupled with mechanical clearance of competing vegetation could help restore complexity in the future stand’s composition and structure.

CRediT authorship contribution statement

Luc Sirois: Visualization, Validation, Supervision, Methodology. **Martin Barrette:** Validation, Supervision, Funding acquisition. **Robert Schneider:** Visualization, Validation, Supervision, Methodology, Funding acquisition, Formal analysis. **Isabelle Aubin:** Validation, Supervision, Methodology. **Françoise Cardou:** Visualization, Validation, Supervision, Methodology, Formal analysis. **Raphaël Turquin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

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

Acknowledgments

This work was funded jointly by the Conférence régionale des éluEs du Bas Saint-Laurent and by Quebec’s Ministère des Ressources Naturelles et des Forêts, Forest contract number 3329-2019-142332176 obtained by Luc Sirois and Robert Schneider in collaboration with Martin Barrette. The authors thank Laura Boisvert-Marsh and Kierann Santala from the Canadian Forest Service for their help with trait documentation and analysis, as well as the Plant and Soil Analysis Laboratory at the Canadian Forest Service for conducting the chemical analysis. We also thank Catherine Fortin-Tanguay, Daphnée Delisle, and Aurélien Martin for their assistance in the field.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122815.

Data availability

Data will be made available on request.

References

Ares, A., Berryman, S.D., Puettmann, K.J., 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Appl. Veg. Sci. 12 (4), 472–487. https://doi.org/10.1111/j.1654-109X.2009.01042.x.

Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. Can. J. For. Res. 30, 10.

Aubin, I., Cardou, F., Boisvert-Marsh, L., Garnier, E., Strukelj, M., Munson, A.D., 2020. Managing data locally to answer questions globally: the role of collaborative science in ecology. J. Veg. Sci. 31 (3), 509–517. https://doi.org/10.1111/jvs.12864.

Aubin, I., Deshaies, O., Cardou, F., Sirois, L., 2014. Management legacy in the understory of North American mixed boreal regenerating stands. For. Ecol. Manag. 320, 129–137. https://doi.org/10.1016/j.foreco.2014.02.001.

Aubin, I., Gachet, S., Messier, C., Bouchard, A., 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience 14 (2), 259–271. https://doi.org/10.2980/1195-6860(2007)14[259:HRANHF]2.0.CO;2.

Aubin, I., Messier, C., Bouchard, A., 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biol. Conserv. 141 (10), 2461–2476. https://doi.org/10.1016/j.biocon.2008.07.007.

Baar, F., Snoeck, B., Balleux, P., Claessens, H., 2004. La sylviculture d’arbres" objectif" ou d’arbres de place (cahier technique n° 27). For. Wallonne 68, 2–8.

Barrette, M., Leblanc, M., Thiffault, N., Paquette, A., Lavoie, L., Bélanger, L., Bujold, F., Côté, L., Lamoureux, J., Schneider, R., Tremblay, J.-P., Côté, S., Boucher, Y., Deshaies, M.-È., 2014. Issues and solutions for intensive plantation silviculture in a context of ecosystem management. For. Chron. 90 (06), 748–762. https://doi.org/10.5558/tfc2014-147.

Bartels, S.F., Chen, H.Y.H., 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91 (7), 1931–1938. https://doi.org/10.1890/09-1376.1.

Bartemucci, P., Messier, C., Canham, C.D., 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Can. J. For. Res. 36 (9), 2065–2079. https://doi.org/10.1139/x06-088.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Beggs, L.R., 2004. Vegetation Response Following Thinning in Young Douglas-fir Forests of Western Oregon: Can Thinning Accelerate Development of Late-successional Structure and Composition? (M.Sc. thesis). Oregon State University.

Begni, A., 2022. Évaluation de la régénération naturelle dans les plantations d’épinettes au Bas St-Laurent (M.Sc. thesis). Université du Québec à Rimouski.

Blouin, J., Berger, J.-P., 2012. Guide de reconnaissance des types écologiques de la région écologique 4f – Collines des moyennes Appalaches (2ème édition). Ministère des Ressources naturelles et de la Faune, Forêt Québec, Direction des inventaires forestiers, Division de la classification écologique et productivité des stations.

Bork, E.W., Osko, T.J., Frerichs, L., Naeth, M.A., 2021. Low soil disturbance during boreal forest well site development enhances vegetation recovery after 10 years. For. Ecol. Manag. 482, 118849. https://doi.org/10.1016/j.foreco.2020.118849.

Boucher, Y., Bouchard, M., Grondin, P., Tardif, P., 2011. Le registre des états de référence: Intégration des connaissances sur la structure, la composition et la dynamique des paysages forestieres naturels du Québec méridional. Ministére des Ressources naturelles et de la Faune, Direction de la recherche forestière.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27 (4), 325–349. https://doi.org/10.2307/1942268.

Brouillet, L., Desmet, P., Coursol, F., Meades, S., Favreau, M., Anions, M., Bélisle, P., Gendreau, C., Shorthouse, D., , 2010. Database of Vascular Plants of Canada (VASCAN) [Jeu de données]. 〈https://data.canadensys.net/vascan/search〉.

Busing, R.T., 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. Vegetatio 115 (1), 19–27. https://doi.org/10.1007/BF00119383.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O’Hara, K., Walters, B., 2006. Planted forests and biodiversity. J. For. 104 (2), 65–77.

Carter, T.A., Fornwalt, P.J., Dwire, K.A., Laughlin, D.C., 2022. Understory plant community responses to widespread spruce mortality in a subalpine forest. J. Veg. Sci. 33 (1). https://doi.org/10.1111/jvs.13109.

Chaves Cardoso, J., Burton, P.J., Elkin, C.M., 2020. A disturbance ecology perspective on silvicultural site preparation. Forests 11 (12), 1278. https://doi.org/10.3390/f11121278.

De Cáceres, M., Coll, L., Legendre, P., Allen, R.B., Wiser, S.K., Fortin, M., Condit, R., Hubbell, S., 2019. Trajectory analysis in community ecology. Ecol. Monogr. 89 (2), e01350. https://doi.org/10.1002/ecm.1350.

De Potter, B., Perin, J., Ponette, Q., Claessens, H., et al., 2012. Détourage d'arbres-objectif: Enseignements des dispositifs installés en Wallonie après six années. For. Wallonne 43–54.

Del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017. A review of thinning effects on Scots pine stands: from growth and yield to new challenges under global change. For. Syst. 26 (2), eR03S. https://doi.org/10.5424/fs/2017262-11325.

van den Brink, P.J., Ter Braak, C.J.F., 1999. Principal response curves: analysis of time-dependent multivariate responses of biological community to stress. Environ. Toxicol. Chem. 18 (2), 138–148. https://doi.org/10.1002/etc.5620180207.

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16 (11), 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Dupont-Leduc, L., Schneider, R., Sirois, L., 2020. Preliminary results from a structural conversion thinning trial in eastern Canada. J. For. 118 (5), 515–533. https://doi.org/10.1093/jofore/fvaa022.

Eler, K., Kermavnar, J., Marinšek, A., Kutnar, L., 2018. Short-term changes in plant functional traits and understory functional diversity after logging of different intensities: a temperate fir-beech forest experiment. Ann. For. Res. 61 (2), 223. https://doi.org/10.15287/afr.2018.1192.

Fahey, R.T., Puettmann, K.J., 2008. Patterns in spatial extent of gap influence on understory plant communities. For. Ecol. Manag. 255 (7), 2801–2810. https://doi.org/10.1016/j.foreco.2008.01.053.

Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression, third ed. Sage https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Gagné, L., Sirois, L., Lavoie, L., 2016. Comparaison du volume et de la valeur des bois résineux issus d'éclaircies par le bas et par dégagement d'arbres-élites dans l'Est du Canada. Can. J. For. Res. 46 (11), 1320–1329. https://doi.org/10.1139/cjfr-2015-0395.

Gagnon, L., Perreault, M., Ruel, M., St-Hilaire, G., Raby, D., Santerre, M.-H., Sénéchal, P., 2018. Sommaire du plan d'aménagement forestier intégré tactique 2018-2023. Ministère des ressources naturelles, Direction générale du Bas-Saint-Laurent. ⟨http://collections.banq.qc.ca/ark:/52327/3429802⟩.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functionnal markers capture ecosystem properties during secondary succession. Ecology 85 (9), 2630–2637. https://doi.org/10.1890/03-0799.

Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 27 (4), 857–871. https://doi.org/10.2307/2528823.

de Grandpré, L., Bergeron, Y., 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. J. Ecol. 85 (6), 777–784. https://doi.org/10.2307/2960601.

de Grandpré, L., Boucher, D., Bergeron, Y., Gagnon, D., 2011. Effects of small canopy gaps on boreal mixedwood understory vegetation dynamics. Community Ecol. 12 (1), 67–77. https://doi.org/10.1556/ComEc.12.2011.1.9.

Grenon, F., Lussier, J.M., Sirois, L., 2007. Conversion de jeunes forêts du Bas-St-Laurent en peuplements inéquiennes dans un contexte d'aménagement forestier écosystémique. Université du Québec à Rimouski, Service canadien des forêts et Centre canadien sur la fibre de bois.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111 (982), 1169–1194. https://doi.org/10.1086/283244.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., Kranabetter, J., 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fenn. 36 (1), 307–327. https://doi.org/10.14214/sf.565.

Härdtle, W., Von Oheimb, G., Westphal, C., 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). For. Ecol. Manag. 182 (1–3), 327–338. https://doi.org/10.1016/S0378-1127(03)00091-4.

Haughian, S.R., 2018. Short-term effects of alternative thinning treatments on the richness, abundance and composition of epixylic bryophytes, lichens, and vascular plants in conifer plantations at microhabitat and stand scales. For. Ecol. Manag. 415–416, 106–117. https://doi.org/10.1016/j.foreco.2018.02.019.

Haughian, S.R., Frego, K.A., 2016. Short-term effects of three commercial thinning treatments on diversity of understory vascular plants in white spruce plantations of northern New Brunswick. For. Ecol. Manag. 370, 45–55. https://doi.org/10.1016/j.foreco.2016.03.055.

Hekkala, A.-M., Tarvainen, O., Tolvanen, A., 2014. Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. For. Ecol. Manag. 330, 55–66. https://doi.org/10.1016/j.foreco.2014.07.001.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54 (2), 427–432. https://doi.org/10.2307/1934352.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Juodvalkis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. Eur. J. For. Res. 124 (3), 187–192. https://doi.org/10.1007/s10342-005-0070-x.

Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. For. Sci. 60 (2), 335–344. https://doi.org/10.5849/forsci.13-015.

Kneeshaw, D., Bergeron, Y., 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79 (3), 783–794.

Kneeshaw, D.D., Prévost, M., 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. Can. J. For. Res. 37 (9), 1534–1544. https://doi.org/10.1139/X07-112.

Kumar, P., Chen, H.Y.H., Thomas, S.C., Shahi, C., 2018. Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. J. Ecol. 106 (3), 1266–1276. https://doi.org/10.1111/1365-2745.12861.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. https://doi.org/10.1890/08-2244.1.

Lundqvist, L., Chrimes, D., Elfving, B., Mörling, T., Valinger, E., 2007. Stand development after different thinnings in two uneven-aged Picea abies forests in Sweden. For. Ecol. Manag. 238 (1), 141–146.

Macdonald, S.E., Fenniak, T.E., 2007. Understory plant communities of boreal mixedwood forests in western Canada: natural patterns and response to variable-retention harvesting. For. Ecol. Manag. 242 (1), 34–48. https://doi.org/10.1016/j.foreco.2007.01.029.

Martin-Ducup, O., Schneider, R., Fournier, R.A., 2017. A method to quantify canopy changes using multi-temporal terrestrial lidar data: tree response to surrounding gaps. Agric. For. Meteorol. 237–238, 184–195. https://doi.org/10.1016/j.agrformet.2017.02.016.

Matthews, W.J., Marsh-Matthews, E., Cashner, R.C., Gelwick, F., 2013. Disturbance and trajectory of change in a stream fish community over four decades. Oecologia 173 (3), 955–969. https://doi.org/10.1007/s00442-013-2646-3.

Ministère de l'Environnement, de la Lutte contre les Changement Climatiques, de la Faune et des Parcs, 2024. Normales climatiques du Québec. ⟨https://www.environnement.gouv.qc.ca/climat/normales/index.asp⟩.

Newmaster, S.G., Parker, W.C., Bell, F.W., Paterson, J.M., 2007. Effects of forest floor disturbances by mechanical site preparation on floristic diversity in a central Ontario clearcut. For. Ecol. Manag. 246 (2–3), 196–207. https://doi.org/10.1016/j.foreco.2007.03.058.

Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front. Ecol. Environ. 8 (3), 421–428. https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borman, T., Carvalho, G., Chirico, M., De Cáceres, M., Durand, S., Weedon, J., 2025. Vegan: Community Ecology Package. R package version 2.7-0. ⟨https://vegandevs.github.io/vegan/⟩.

Pothier, D., Savard, F., 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des ressources naturelles et de la Faune du Québec, Québec.

Prégent, G., Picher, G., Auger, I., 2011. Tarif de cubage, tables de rendement et modèles de croissance pour les plantations d'épinette blanche au Québec [Mémoire de recherche forestière n°160]. Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière du Québec.

R Development Core Team, 2023. R: A Language and Environment for Statistical Computing. [Logiciel]. R Foundation for Satistical Computing. ⟨https://www.R-project.org/⟩.

Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P., Adair, E.C., 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. J. Ecol. 100 (2), 539–545. https://doi.org/10.1111/j.1365-2745.2011.01922.x.

Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. 82 (9), 1273–1283. https://doi.org/10.1139/b04-091.

Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., Schmid, B., Schulze, E.-D., 2012. Using plant functional traits to explain diversity–productivity relationships. PLOS ONE 7 (5). https://doi.org/10.1371/journal.pone.0036760.

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36 (6), 1345–1362. https://doi.org/10.1139/x06-025.

Russell, V.L., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. ⟨https://CRAN.R-project.org/package=emmeans⟩.

Schneider, R., Dupont-Leduc, L., Gauthray-Guyénet, V., Cattaneo, N., LaraMelo, Simard, T., Begni, A., Turquin, R., Morache-Mercier, A., Pinna, S., Rémillard, U., Nock, C., 2021. Close-to-nature silviculture in eastern Quebec: advances over the last decade. For. Chron. 97 (3), 250–262. https://doi.org/10.5558/tfc2021-027.

Schneider, R., Franceschini, T., Duchateau, E., Bérubé-Deschênes, A., Dupont-Leduc, L., Proudfoot, S., Power, H., de Coligny, F., 2021. Influencing plantation stand structure through close-to-nature silviculture. Eur. J. For. Res. 140 (3), 567–587. https://doi.org/10.1007/s10342-020-01349-6.

Schütz, J.-P., 1997. La gestion des forêts irrégulières et mélangées. Presses polytechniques et universitaires romandes [diff. Tec & doc].

Seymour, R.S., Guldin, J., Marshall, D., Palik, B., 2006. Large-scale, long-term silvicultural experiments in the United States: historical overview and contemporary examples. Allg. Forst Jagdztg. 177, *104–112*.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27 (3), 379–423.

Smith, K.J., Keeton, W.S., Twery, M.J., Tobi, D.R., 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood–conifer forests. Can. J. For. Res. 38 (6), 1303–1318. https://doi.org/10.1139/X07-236.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M., 1997. The Practice of Silviculture: Applied Forest Ecology, ninth ed. Wiley.

Stiell, W.M., 1980. Response of white spruce plantation to three levels of thinning from below 1958-1978. For. Chron. 56 (1), 21–27. https://doi.org/10.5558/tfc56021-1.

Sustainable Forest Development Act, 2013. Pub. L. No. A-18.1, CQLR c A-18.1. ⟨http://legisquebec.gouv.qc.ca/en/ShowDoc/cs/A-18.1⟩.

Thiffault, N., Roy, V., Prégent, G., Cyr, G., Jobidon, R., Ménétrier, J., 2003. La sylviculture des plantations résineuses au Québec. Le. Nat. Can. 127, 63–80.

Vanha-Majamaa, I., Shorohova, E., Kushnevskaya, H., Jalonen, J., 2017. Resilience of understory vegetation after variable retention felling in boreal Norway spruce forests – a ten-year perspective. For. Ecol. Manag. 393, 12–28. https://doi.org/10.1016/j.foreco.2017.02.040.

Vepakomma, U., St-Onge, B., Kneeshaw, D., 2011. Response of a boreal forest to canopy opening: assessing vertical and lateral tree growth with multi-temporal lidar data. Ecol. Appl. 21 (1), 99–121. https://doi.org/10.1890/09-0896.1.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functionnal ecology. Ecology 89 (8), 2290–2301. https://doi.org/10.1890/07-1206.1.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116 (5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Wei, L., Fenton, N.J., Lafleur, B., Bergeron, Y., 2019. The combined role of retention pattern and post-harvest site preparation in regulating plant functional diversity: a case study in boreal forest ecosystems. Forests 10 (11), 1006. https://doi.org/10.3390/f10111006.

Weiskittel, A.R., Kenefic, L.S., Li, R., Brissette, J., 2011. Stand structure and composition 32 years after precommercial thinning treatments in a mixed northern conifer stand in central Maine. North. J. Appl. For. 28 (2), 92–96. https://doi.org/10.1093/njaf/28.2.92.

Willson, M.F., Comet, T.A., 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. Condor 98 (2), 350–362. https://doi.org/10.2307/1369153.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84 (8), 2042–2050. https://doi.org/10.1890/02-0433.