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The Combined Role of Retention Pattern and Post-Harvest Site Preparation in Regulating Plant Functional Diversity: A Case Study in Boreal Forest Ecosystems

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Abstract: Changes in the light availability in forests generated by diversified retention patterns (e.g., clear cut, partial harvest) have been shown to strongly filter the plant species present. Modified soil microsite conditions due to post-harvest site preparation (e.g., mechanical site preparation, prescribed fire) might also be an important determinant of plant diversity. The objective here was to detect how retention pattern and post-harvest site preparation act as filters that explain the understory functional diversity in boreal forests. We also assessed whether these effects were dependent on forest attributes (stand type, time since fire, and time since harvest). We retrieved data from seven different studies within 101 sites in boreal forests in Eastern Canada. Our data included forests harvested with two retention patterns: careful logging and clear cut, plus unharvested control forests. Three post-harvest site preparation techniques were applied: plow or disk trenching after careful logging, and prescribed fire after clear cut. We collected trait data (10 traits) representing plant morphology, regeneration strategy, or resource utilization for common species. Our results demonstrated significant variation in functional diversity after harvest. The combined effect of retention pattern and site preparation was the most important factor explaining understory diversity compared to retention pattern only and forest attributes. According to RLQ analysis, harvested forests with site preparation favored traits reflecting resistance or resilience ability after disturbance (clonal guerilla species, geophytes, and species with higher seed weight). Yet harvested forests without site preparation mainly affected understory plant species via their light requirements. Forest attributes did not play significant roles in affecting the relationship between site preparation and functional diversity or traits. Our results indicated the importance of the compounding effects of light variation and soil disturbance in filtering understory diversity and composition in boreal forests. Whether these results are also valid for other ecosystems still needs to be demonstrated.

Keywords: functional trait; RLQ analysis; site preparation; time since fire; stand type

1. Introduction

Forest management practices induce long-lasting changes in the distribution of stand types in forested landscapes and the distribution of biota within them [1]. Besides effects on α-diversity, management disturbances could alter community heterogeneity (β-diversity) by imposing more stringent environmental filters [2] or increasing selection for disturbance-tolerant species [3]. In Europe and in North America, clear cuts were the main harvesting practice until the 1980s [4]. Concerns about biodiversity conservation, soil protection, and tree regeneration led to the development of alternative retention patterns (e.g. partial harvesting, careful logging, continuous-cover forestry) that have less conspicuous effects on forest ecosystems than clear cuts [5–8]. Generally, retention forestry is defined as an approach to forest management based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest, at the time of harvest [8]. The variation in understory light availability, generated by different retention patterns in a region, has been shown to be a dominant filter affecting post-harvest understory plant composition and diversity [9–12].

Light availability may not completely explain post-harvest plant diversity. As following harvesting, different site preparation techniques may be applied in order to create favorable microsite conditions (e.g., soil temperature and moisture regulation, competition control) for reforestation. Two common examples in Europe and North America are mechanical site preparation [13,14] and prescribed burning after harvest [15,16]. Site preparation techniques have varying levels of soil disturbance (e.g., exposed mineral soil, a mixture of organic matter and mineral soil) and have been shown to impact tree survival and growth, as well as understory composition [13,14]. Previous studies have focused on retention patterns or site preparation disturbance effects on the composition or diversity of understory plant communities [17–20]. Few studies have investigated diversity changes due to both retention patterns and post-harvest site preparation, or identified whether the combined effects of retention pattern and site preparation better explained understory diversity than retention pattern.

Furthermore, inconsistent conclusions on the effect of a specific retention pattern or a site preparation technique on understory community are found in different studies. Many previous studies have suggested that forest management strategies should be based on knowledge of the basic characteristics of stand type and time since last fire or harvesting disturbance [21,22], because the density and composition of canopy trees can modify resource availability [23,24] and competition in the understory (e.g., shade-tolerant and intolerant species) [25]. Moreover, the responses of the understory plant community to disturbance can vary over time since harvest or fire disturbance. For example, while some species colonize habitat patches rapidly, other species might need a long and continuous period of time to exploit a suitable habitat patch.

The understory plant community represents a substantial proportion of overall plant diversity in most boreal or temperate forests [26], and plays essential roles in biodiversity and ecosystem structure and function [27]. Due to its sensitivity to a variety of factors such as overstory characteristics [23], soil properties [28–30], and forest disturbances or management practices [31,32], understory diversity might also be an important indicator of forest site quality and of the environmental impact of management [33]. Furthermore, simplifying species composition and diversity to functional trait diversity can provide a synthetic view of a plant community [34,35]. Plant functional traits are characteristics of plants which reflect their abilities to adapt to a habitat or influence their responses to environmental changes [36,37]. Hence, the co-occurrence of species with similar traits, such as shade-intolerant species co-occurring in open canopy habitats, is considered to be evidence that communities are limited by environmental filters [28,38].

The present study aimed to analyze how retention patterns and post-harvest site preparation act as filters that explain local understory plant communities using the boreal forest as a case study ecosystem. We also assessed whether these effects were dependent on forest attributes (stand type, time since fire, and time since harvest). Here, retention patterns were clear cut, careful logging, plus unharvested control. Careful logging is defined as the harvest of commercial trees (i.e., diameter at breast height >9.1 cm) with the retention of non-commercial trees and with the protection of tree regeneration and soils [39–41]. The three site preparation techniques included plow or disk trenching after careful logging, and prescribed fire after clear cut. A large database from seven separate studies conducted in the Canadian Clay Belt region was used in the present study. We collected 10 functional response traits of dominant species that reflect plant morphology, regeneration strategy, and resource utilization.

The research questions were: 1) How does the functional diversity of the understory community vary among retention patterns, as well as in relation to the combined effect of retention pattern and site preparation? 2) Does the combined effect of retention pattern and site preparation better explain functional diversity than retention pattern only? 3) How does the combined disturbance of retention pattern and site preparation correlate with functional trait groups? We hypothesized that the functional diversity increased after harvest, and the combined effect of retention pattern and site preparation better explained diversity than the effect of retention pattern only. We also hypothesized that traits favored by site preparation were those reflecting species' resistance or resilience to disturbance (e.g., clonal guerilla species, geophytes). Therefore, traits favored by careful logging or clear-cut forests without site preparation would be those related to their resource utilization, particularly light. Finally, we also assessed whether the relationships between retention pattern/site preparation techniques and traits are affected by forest attributes.

2. Methods

2.1. Study Area

The study area was located in the Clay Belt region of Quebec and Ontario (49°48′ N, 79°01′ W) (Figure 1). A total of 69 sites were located within the western black spruce (*Picea mariana* (Mill.) B.S.P.) feather moss bioclimatic domain, and 32 sites were located in black spruce (*P. mariana*) stands in the boreal mixedwood bioclimatic domain [4]. Both of these domains are characterized by lacustrine clay deposits that have been left by proglacial lakes [42].

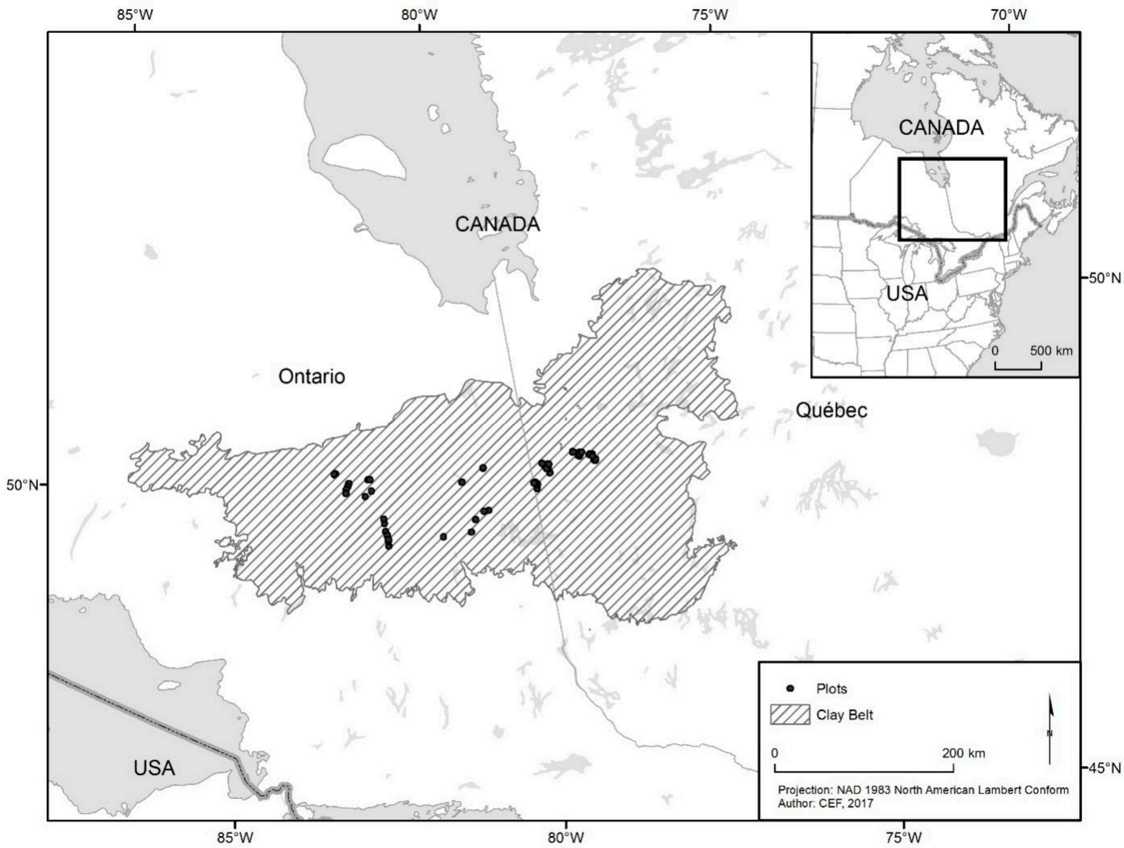

Figure 1. Map of the research area in Clay Belt region in Quebec and Ontario. Black dots represent study sites; many are overlapped on the map.

2.2. Data Collection

Our database was composed of the original data sets used for all the studies in Table 1. The objectives of the studies reanalyzed here were to identify the effects of specific retention patterns, and their combined effect with post-harvest site preparation techniques (Table 1) on understory diversity. Most (70%) of the pre-disturbance sites were black spruce (*P. mariana*)-dominated forests, and 30% of the sites were either jack pine (*Pinus banksiana* Lamb.)-dominated forests or mixed black spruce (*P. mariana*) and white birch (*Betula papyrifera* Marshall) forests (Table 1). The time since the last fire ranged from 45 to 350 years, and the time since harvest and silvicultural disturbance was 2 to 32 years (Table 1).

Our data included two canopy retention pattern—careful logging (CL) and clear cut (CC) (Tables 1 and 2)—and unharvested control forests, and thus different retention patterns are mainly distinguished by their difference in available light, although soil disturbance also varied among these three types of forests. Three post-harvest site preparation techniques were applied: plow (CLPL) or disk trenching (CLDT) after careful logging, and prescribed burning after clear cut (CCPB). Those combinations of a site preparation technique with a specific retention pattern type are very commonly used in North America. Obviously, our study should not be considered as a fully factorial experimental design that tests the interaction between retention pattern and post-harvest site preparation. The aim of plowing after careful logging is to incorporate the organic layer into the underlying mineral soil creating a homogeneous profile, and results in the full exposure of favorable top soil layers. For disk trenching after careful logging, the aim was to produce three microsites: trench, berm, and hinge. Further aims were to break up compacted soil, to reduce hardwood competition, and to disturb part of the soil surface leading to on average 48% exposure of the mesic and humic layers in our studied sites. The mesic layer is composed of materials at an intermediate stage of decomposition, while the humic layer is composed of well-decomposed materials. Meanwhile, prescribed burning was applied after clear cut (CCPB) emulating some of the effects of wildfire, such as an increase in soil pH, nutrient inputs due to ash deposition, higher soil decomposition rates, and enhanced microbial activity. Therefore, the soil disturbance degree increased from unharvested forests to forests under CLPL, CLDT, and CCPB. Due to the mimicry of wildfire natural disturbance by CCPB, we also assumed that the mechanism behind the effects of CCPB on understory diversity was different from that of CLPL and CLDT. Besides, we also had careful logging only (CLOL) and clear cut only (CCOL) forests, neither of which had site preparation.

Table 1. Sample size and site characteristics of the variables in different studies.

	Retention Pattern	Retention Pattern + Site Preparation	Code	Study	Stand Type	Site Number	Plot (400 m^2) Number	Mean Time Since Fire When Harvested or When Sampled, (Years)	Mean Time Since Harvest When Sampled, (Years)
Harvested	Careful logging (CL)	Careful logging only, no soil disturbance after CL	CLOL	Kpodo, 2014 [43]	bS	3	38	92	2
				Lafleur et al., 2010 [44], and Lafleur et al., unpublished	bS	10	30	>100	20
				Bescond et al., 2011 [11]	bS, bS, jP or bS-wB	11	150		5.5
				Renard et al., 2016 [45]	bS	5	12	>120	29
		Plow after careful logging	CLPL	Kpodo, 2014 [43]	bS	3	43	92	2
		Disk trenching after careful logging	CLDT			3	40		2
	Clear cut (CC)	Clear cut only, no soil disturbance after CC	CCOL	Lafleur et al., 2010 [44]	bS	20	56	>100	20
				Renard et al., 2016 [45]	bS	5	17	>120	24
		Prescribed burning after clear cut	CCPB	Renard et al., 2016 [45]	bS	3	17		21
Unharvested	—	—	unharv	Kpodo, 2014 [43]	bS	9	120	92	—
				Bescond et al., 2011 [11]	bS, jP or bS-wB	11	152	>100	
				Grandpré et al., 1993 [46]	bS-bF-wB	10	81	123, 45–250	
				Higelin, unpublished	bS	8	39	185, 50–350	

bS: black spruce, *Picea mariana*, bF: balsam fir, *Abies balsamea*, wB: white birch, *Betula papyrifera*, jP: jack pine, *Pinus banksiana*

Table 2. Ecological variables used in the models.

Variable	Levels	Description	Major Environmental Gradient
Retention pattern	Unharv	Pre-harvested or unharvested forests	Light availability from low to high
	CL	Harvest of commercial trees with retention of non-commercial trees, and with the protection of regeneration and soils	
	CC	Clear cut	
Combined disturbance of retention pattern and site preparation	CLOL	Careful logging only, no soil disturbance after CL	Soil disturbance degree from low to high
	CCOL	Clear cut only, no soil disturbance after CC	
	CLPL	Plowing after CL, to incorporate the organic layer into the underlying mineral soil	
	CLDT	Disk trenching after CL, to produce three microsites: trench, berm, and hinge	
	CCPB	Prescribed burning after CC, to emulate wildfire in an ecosystem and to prepare microsites for tree planting	
Stand type (STP)	bS	Black spruce-dominated forests	
	Mixed	Two mixed forests, 1 bS.bF.wB: black spruce, balsam fir, and white birch; 2 bS.wP.wB: black spruce, white pine, and white birch	
Time since fire (TSF)	≤100 yr >100 yr	Time since fire when harvested, or when sampled for unharvested	
Time since harvest (TSH)	≤15 yr >15 yr	Time since harvest when sampled	

In total, 795 circular plots of 400 m^2 were established for vegetation survey in 101 sites between 1993 and 2012, and within each circular plot, four 1-m^2 quadrats were set for estimating vascular plant cover (including woody and herbaceous species with height <2 m). We selected 10 traits (Table 3) representing plant regeneration, growth, and responses to disturbance and environmental conditions (e.g., [28,34,38,47]). We gathered trait data on the 59 most common species using the TOPIC database (Traits Of Plants In Canada, [48]).

Table 3. Summary of functional trait groups.

Category	Trait	Group Code	Description	Importance
Morphology	Raunkiaer life form	Rauk.cha Rauk.geo Rauk.hem Rauk.mcpha Rauk.mgpha	Chamaephyte, bud between 1 mm and 25 cm from the ground Geophyte, bud is located in the ground Hemicryptophyte, bud on the surface of the ground Micro and nano phanerophyte, bud between 25 cm and 8 m from the ground Mega and meso phanerophyte, bud ≥8 m from ground	Bud position in relation to forest soil surface affects plant species' ability to survive disturbance
	Lateral extension	Clone.compact Clone.phalanx Clone.guerilla	Clonal compact, <10 cm, includes caespitose, caespitose with minimal horizontal spread Clonal phalanx, 10 to 25 cm, spreads in multiple simultaneous directions Clonal guerilla, >25 cm, mostly rapid unilateral spread	Colonize available space in disturbed habitat
	Vegetative propagation	Rhizome Non-rhizome	Rhizome, suckering root or stolon, runner The Others, mainly collar sprout, and layering	Recolonization from surviving buried structures
	Maximum height	Height, numeric, cm	The shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level	Competitive ability
Regeneration	Mode of reproduction	Repro.veg Repro.mse	Mainly vegetative propagation Non-clonal, seeds only or mostly by seeds, vegetative propagation possible	Adaptability to transient, unpredictable, and disturbed habitat
	Flowering phenology	Flower.sp Flower.su	The presence of flower in spring The presence of flower in summer or in early fall	The periodicity of flowering is affected by management disturbance
	Seed bank persistence	Seed.short Seed.semi-permanent Seed.permanent	Short viability, ≤1 year Semipermanent seed bank, >1–5 years Bank of seeds, >5 years	Ensuring population persistence in disturbed habitats
	Seed weight	Seed.weight, numeric, mg	The oven-dry mass of an average seed of a species	Survive and establish in the face of environmental hazards
Resource utilization	Humidity preference	Humid Xeric Broad.humid	Plant species prefer humid or humid–mesic habitat Habitat xeric or xeric–mesic Habitat from humid to xeric	Competitive ability
	Light requirement	Shad.int Shad.mid Shad.tol	Shade intolerant, needs >6 hours of direct sunlight at mid-summer Mid tolerant, 2–5 hours of direct sunlight Shade tolerant, <2 hours of direct sunlight	Competitive ability

Data source: TOPIC database, Traits of Plants in Canada.

2.3. Data Analysis

2.3.1. Functional Diversity Calculations

Functional diversity indices and community-weighted mean (CWM) respectively summarized the dispersion and the mean of functional traits within a given community [49]. We calculated three functional diversity indices—functional richness, evenness, and divergence (FRic, FEve, and FDiv) [50]—using the dbFD function of the FD (functional diversity) R package [51] weighted by the species' relative abundances. Functional richness (FRic) quantifies the volume of functional space that a set of species occupies, functional evenness (FEve) describes how species' abundances are distributed throughout the occupied functional space, and functional divergence (FDiv) summarizes the variation in species abundances with respect to the center of functional space [50]. As discussed by Villéger [50], none of the three indices meets all the criteria required for a functional diversity index, but the set of three complementary indices does. Before running the dbFD function, we calculated multivariate distances between species (Gower's distance) for raw trait data, which were a mixture of variable types (quantitative, nominal, and ordinal) [52]. The CWM was calculated by weighting the species abundance for each quantitative trait and for each trait group (Table 3) of a categorical trait [53]. This metric defines dominant traits in a community and is directly related to the mass ratio hypothesis of Grime [54], which considers the traits of the most abundant species to largely determine ecosystem processes.

We analyzed the variation of each functional diversity indicator (FRic, FEve, FDiv, or CWM) with different retention patterns (clear cut, careful logging, unharvested forests). We used analysis of variance (ANOVA) and Tukey's HSD (Honestly Significant Difference) test to make pairwise comparison on the mean values of each functional diversity indicator among different retention patterns.

2.3.2. Model Comparison

We modeled the responses of the three functional diversity indices (FRic, FEve, and FDiv) and community-weighted mean to variables that related to the retention pattern and its combined effect with post-harvest site preparation, as well as to variables related to forest attributes: stand type, time since fire, or time since harvest. We then made model comparisons among the five models using generalized linear mixed models (GLMMs). We used the lmer function from the lme4 R package [55] with a default Laplace approximation to the log likelihood. Two random effects of "site" and "plot" were incorporated on the intercept into all models. We ranked models by their AICc (the second-order Akaike Information Criterion), and computed associated measures (delta AICc, Akaike weights) as well as model-averaged estimates for the variables in the models with a delta AICc less than four, using the AICcmodavg package [56]. All analyses were completed using R version 3.4.3.

2.3.3. RLQ Analysis

RLQ analysis is an extension of co-inertia analysis that performs a double inertia analysis of two arrays (R (environment) and Q (plant species) with a link expressed by a contingency table L (traits)) [57]. RLQ combines the three separate analyses of R, L, and Q and aims at identifying the main relationships between site preparation techniques and trait syndromes mediated by species abundances. The Monte Carlo permutation (n = 10000) test was also performed to test the significance of the link between R and Q [57,58]. To identify the potentially confounding effects of forest attributes on trait performance, we carried out a novel RLQ analysis: partial RLQ introduced by Wesuls [59]. The input variables of R, L, and Q were exactly the same as that of the basic RLQ; the main difference was that in this new analysis, the variation in R and L linked to the co-variable table (forest attributes) had been removed. The higher percentage of co-inertia explained by the most representative axis of partial RLQ compared to that of the basic RLQ could indicate that the influence of forest attributes is relevant.

3. Results

3.1. Variation of Functional Diversity Among Retention Patterns

We analyzed the variation of each functional diversity indicator (FRic, FEve, FDiv, or CWM) with different retention patterns (clear cut, careful logging, and unharvested forests). Compared to unharvested forests, FRic and FEve were significantly higher, while FDiv was lower in forests with careful logging (CL) and clear cut (CC) (Figure S1). Meanwhile, no difference in FRic was found between CL and CC forests. FEve was significantly greater and FDiv was significantly lower in CL forests than in CC forests. There were also significant variations in the community-weighted mean (CWM) of the trait groups in both careful logging and clear-cut forests compared to unharvested forests (Figure S2). Compared to unharvested forests, the CWM of 11 trait groups (25 groups in total) (Height, Rauk.cha, Repro.mse, Flower.sp, Shad.mid, Seed.semi-permanent, Seed.weight, Rhizome, Shad.int, Seed.permanent, Clone.guerilla; the abbreviations are defined in Table 3) was greater in both careful logging and clear-cut forests. On the contrary, the CWM of eight groups (Rauk.hem, Rauk.mcpha, Clone.phalanx, Non-rhizome, Repro.veg, Flower.sp, Shad.tol, Seed.short) was lower in both careful logging and clear-cut forests than in unharvested forests. Comparing the two retention patterns, the CWM of eight trait groups (Rauk.cha, Repro.mse, Flower.sp, Broad.humid, Shad.mid, Seed.semi-permanent, Non-rhizome, seed.short) were lower in CL than in CC forests, while the CWM of nine trait groups (Rauk.geo, Rhizome, Shad.int, Xeric, Seed.permanent, Clone.phalanx, Repro.veg, Flower.sp, Shad.tol) was greater in CL than in CC forests.

3.2. Best Model for Functional Diversity and Its Effect

Model comparison showed that compared to retention pattern and forest attributes (stand type, time since fire, or time since harvest), the combined effect of retention pattern and site preparation was the most important factor explaining the variability in all the three functional diversity indices (Table 4). When compared to unharvested forests, the functional richness (FRic) was significantly greater in forests with prescribed burning after clear cut (CCPB; Figure 2) and lower in forests with the two mechanical site preparation techniques: disk trenching (CLDT) and plowing (CLPL) after careful logging. Functional evenness (FEve) was significantly greater in CLDT, CLPL forests, and careful logging-only (CLOL) forests than in unharvested forests (Figure 2). For functional divergence (FDiv), it was lower in CLOL and CCPL forests than in unharvested forests (Figure 2). Furthermore, FRic was significantly greater in CCPB forests than in CLPL forests or CLDT forests but did not differ between CLPL and CLDT forests. For FDiv, it was significantly lower in CLPL forests than in CLDT or CCPB forests. Besides, no significant difference in FEve was found among CLPL, CLDT, and CPB forests.

3.3. RLQ Analysis

RLQ analysis was used to test the relationship between trait groups and forests under the combined disturbance of retention pattern and post-harvest site preparation. Among basic RLQ and partial RLQ analyses with co-variables of stand type (RLQ_{covSTP}), time since fire (RLQ_{covTSF}), or time since harvest (RLQ_{covTSH}), the first two axes of basic RLQ accounted for the highest percentage (93.27%, Table 5) of total co-inertia. The percentage captured by basic RLQ was higher than the partial RLQ on the first two axes, indicating the non-significant relevance of stand type (STP), time since fire (TSF), or time since harvest (TSH) gradient along the first axis of the partial RLQ compared to the basic RLQ. Thus, the following analysis of the first two axes of RLQ analysis was therefore based on basic RLQ rather than partial RLQ.

Table 4. Model selection results for the three functional diversity indices.

	Model	K	AICc	Delta_AICc
FRic	**Combined disturbance of retention pattern and site preparation**	**9**	**260.50**	**0.00**
	Retention pattern	6	285.08	24.58
	Time since harvest	5	302.28	41.78
	Time since fire	5	342.92	82.42
	Null model	4	348.13	87.63
	Stand type	5	349.76	89.26
FEve	**Combined disturbance of retention pattern and site preparation**	**9**	**350.48**	**0.00**
	Stand type	5	361.28	10.80
	Retention pattern	6	372.46	21.98
	Time since harvest	5	372.53	22.04
	Null model	4	380.08	29.6
	Time since fire	5	381.69	31.21
FDiv	**Combined disturbance of retention pattern and site preparation**	**9**	**428.72**	**0.00**
	Retention pattern	6	439.34	10.62
	Time since harvest	5	470.84	42.12
	Time since fire	5	485.98	57.25
	Null model	4	495.36	66.64
	Stand type	5	497.37	68.64

FRic: functional richness, FEve: functional evenness, FDiv: functional divergence. AICc: the second-order Akaike Information Criterion, Delta_AICc: the distance from the best model. The smaller the AICc, the better the model with respect to the others. The model with the smallest AICc is in bold for each functional diversity indices.

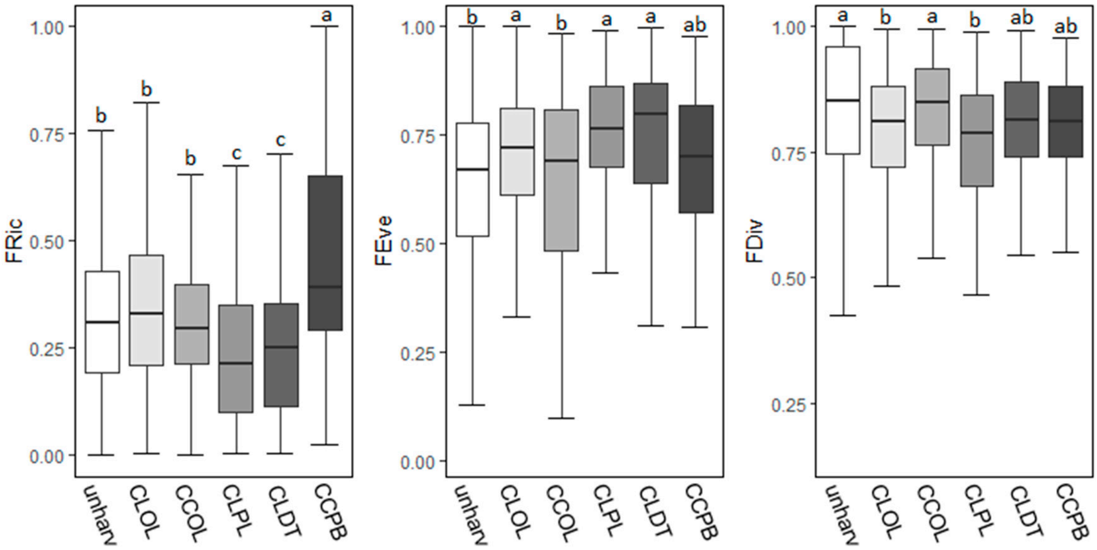

Figure 2. Distribution of functional diversity indices (FRic, FEve, and FDiv) depending on the combined disturbance of retention pattern and site preparation, ordered from lowest to highest soil disturbance degree. unharv: unharvest, CLOL: careful logging only, CLPL: plowing after careful logging, CLDT: disk trenching after careful logging, CCOL: clear cut only, CCPB: prescribed burning after clear cut. Values in each group with different letters denote a significant difference ($p < 0.05$).

The first axis of RLQ clearly separated forests with a distinction between unharvested and harvested forests (Figure 3). Regarding traits, the first axis divided species among trait groups of clonal compact species versus chamaephyte species (Figure 3). From unharvested forests to harvested forests, species changed from shade-tolerant species, clonal compact species, non-rhizome, and mega and meso phanerophytes, to mid-shade tolerant species, clonal guerilla species, non-rhizome species, and chamaephyte species. Furthermore, regarding the relationship between trait groups and the combined disturbance of retention pattern and site preparation (Figure 4), plow and disk trenching after careful logging were respectively favored by clonal guerilla species and geophytes, while prescribed burning (CCPB) was favored by higher seed weight. The results also showed that clear cut only (CCOL) and careful logging only (CLOL) forests were favored by mid-shade tolerant species, and unharvested forests were favored by mega and meso phanerophyte and shade-tolerant species.

Table 5. Eigenvalues, percentage, and cumulative percentage of variance explained by the first two axes of the basic RLQ and the partial RLQ at the fine scale.

	Axis 1		**Axis 2**		
	Eigenvalues	**%**	**Eigenvalues**	**%**	**Cum.%**
Basic RLQ	**0.24**	**75.40**	**0.04**	**17.87**	**93.27**
RLQ_{covSTP}	0.03	63.30	0.02	10.52	73.82
RLQ_{covTSF}	0.04	72.50	0.01	17.51	90.01
RLQ_{covTSH}	0.02	69.42	0.01	18.92	88.34

"RLQ_{covSTP}", "RLQ_{covTSF}", or "RLQ_{covTSH}" respectively mean partial RLQ analysis using stand type (STP), time since fire (TSF), or time since disturbance (TSH) as co-variable. The RLQ analysis with the highest cumulative percentage of variance is explained by the first two axes was in bold.

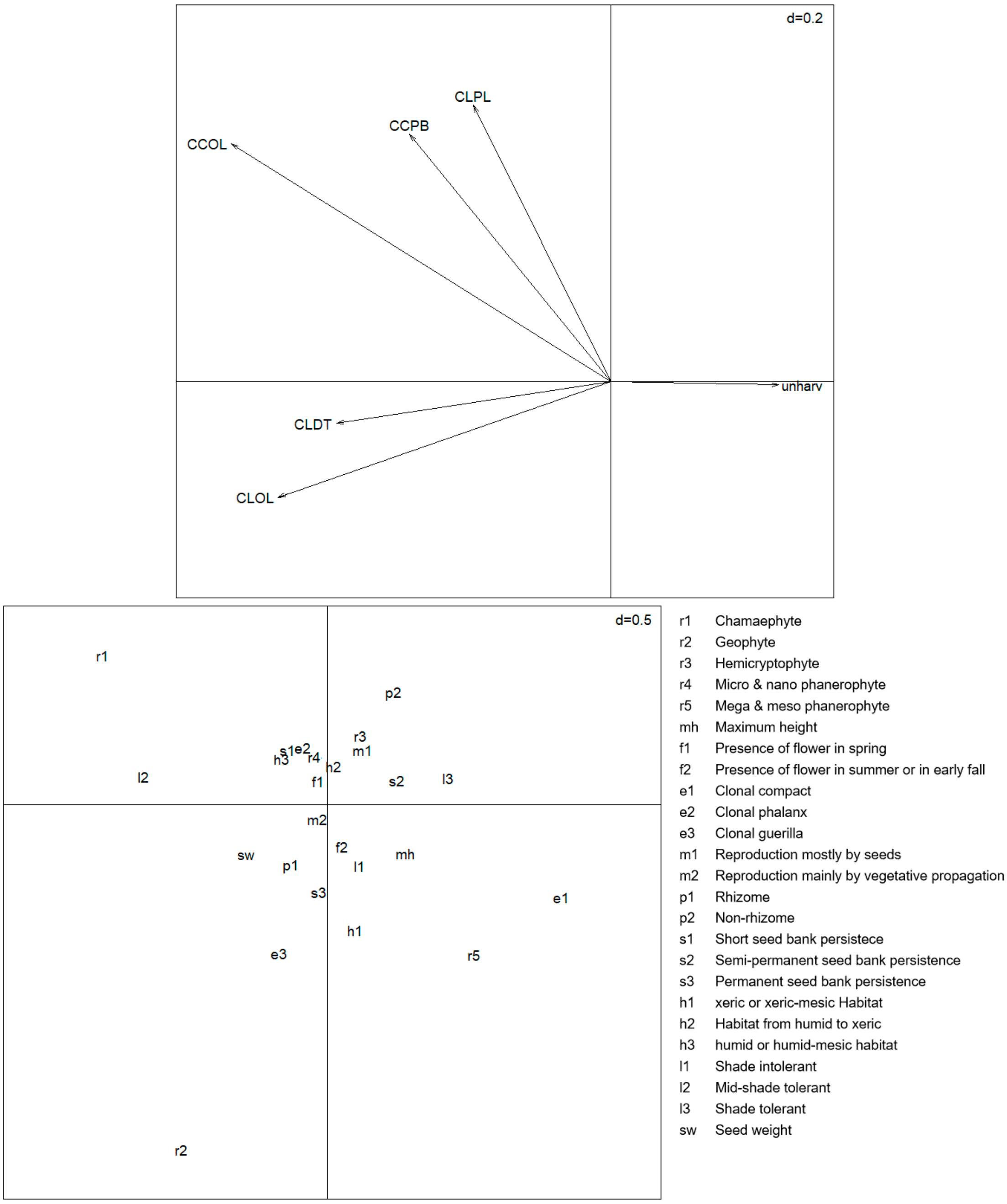

Figure 3. Result of basic RLQ indicating different combinations of retention pattern and site preparation (left), and trait groups (right) along the first two axes. unharv: unharvest, CLOL: careful logging only, CCOL: clear cut only, CLPL: plowing after careful logging, CLDT: disk trenching after careful logging, CCPB: prescribed burning after clear cut. Abbreviations for traits are defined in Table 3.

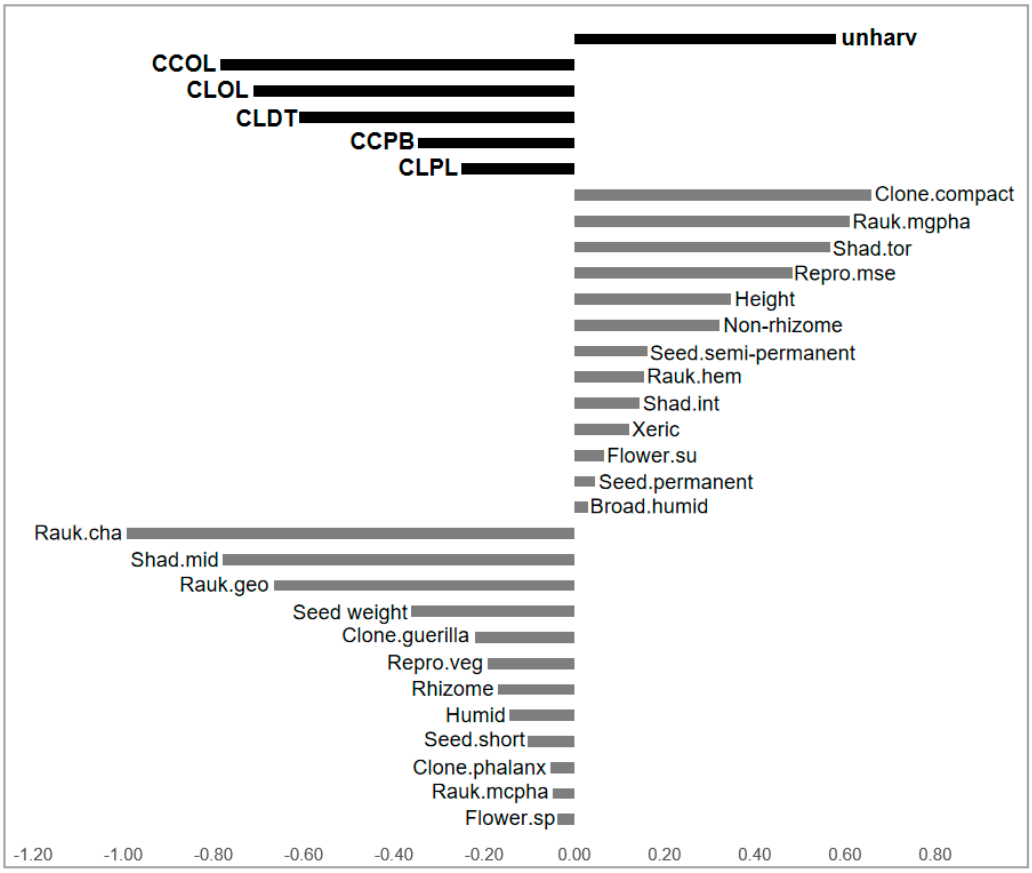

Figure 4. Plot of the eigenvalues along RLQ axis 1 relating different combinations of retention pattern and site preparation (black bars) and functional traits (grey bars). The combination and trait groups with similar positions along the axis co-vary. The different combinations were: CLPL: plowing after careful logging, CLDT: disk trenching after careful logging, CCPB: prescribed burning after clear cut, CLOL: careful logging only, CCOL: clear cut only, and unharv: unharvested. The abbreviations for traits are defined in Table 3.

4. Discussion

4.1. Variation in Functional Diversity among Retention Patterns

In our study, both community-weighted mean (CWM) and functional diversity indices (FRic, FEve, and FDiv) were different between harvested forests (careful logging or clear cut) and unharvested forests. Moreover, the variation of the three functional diversity indices or CWM in a large proportion of trait groups was consistent between the different retention patterns. Similarly, in previous studies, an increase in plant diversity after thinning was found in coniferous and temperate forests [60–63]. Both retention patterns in our study—careful logging and clear cut—increased the functional richness compared to unharvested forests, although functional richness did not differ between careful logging and clear cut. In contrast, Biswas and Mallik [18] found higher functional richness at moderate disturbances than at low (unharvested) or high disturbance (clear cut). As Pakeman [64] found, our sites included probably only part of the disturbance gradient described by Biswas and Mallik [18], so the results are probably not contradictory with this study. Furthermore, an increased functional evenness and decreased functional divergence in careful logging or clear-cut forests compared to unharvested forests suggests a more effective utilization of resources available within the niche space it encompasses, as well as higher degree of niche differentiation, and therefore, lower resource competition after harvest [65].

4.2. Best Model for Functional Diversity and Its Effect

Although functional diversity significantly varied among the retention patterns, our results of model comparison showed that the combined effect of retention pattern and site preparation better explained the understory functional diversity than retention pattern only and forest attributes (stand type, time since fire, time since harvest). The more important role of the combined effect of retention pattern and site preparation than retention pattern indicated that the compounding effects of light variation and soil disturbance mattered more than light variation alone for explaining understory functional diversity. Regarding the relationship between functional diversity and the combined disturbance of retention pattern and site preparation in our study, only prescribed fire after burning (CCPB), which emulates the effects of wildfire, can increase niche spaces and functional richness. Functional richness was significantly greater in CCPB forests than in forests under plowing or disk trenching after careful logging (CLPL and CLDT). We agree with Pidgen and Mallik [15] that this can be attributed to the compounding effects associated with the addition of prescribed fire to these previously clear-cut disturbed forests. In contrast, functional richness decreased in the two mechanical site preparation techniques: plowing (CLPL) and disk trenching (CLDT) after careful logging. However, an increased functional evenness in CLPL and CLDT forests compared to unhavested forests was found, indicating the increased efficiency of resource utilization. Thus, the two mechanical site preparation techniques might help maintain understory diversity at a relatively stable level under certain environmental conditions after harvest. Finally, functional divergence increased in forests with careful logging only or plow after careful logging (CLOL or CCPL) compared to unharvested stands, which might increase forest productivity and decrease resource opportunities for invaders in those forests [65].

4.3. Relationships between Site Preparation Techniques and Functional Trait Groups

In general, the first axis of basic RLQ separated forests according to their management history, with a distinction of unharvested versus harvested, despite the range in forest ages (time since fire) included in the unharvested forests. This indicated that the functional traits generated by all the variables related to the combined disturbance (retention pattern and site preparation) examined here differed from those found in natural forests at all stages of succession. However, lacking the very early successional stage (<45 yr) in natural forests might also induce some diversity differences between harvested and unharvested forests. In our study, both model comparisons and partial RLQ analysis indicated that the time since fire was not an important factor affecting understory diversity. Consequently, we are confident in our results despite the lack of very early post-fire forests.

Post-harvest site preparation affected the understory mainly by the resistance or resilience ability of plants after disturbance. Plow and disk trenching after careful logging favored respectively guerilla species that are burial-tolerant stabilizers [66–68] and geophytes that thrive under moderate to high disturbance [69]. Unharvested forests favored mega and meso phanerophytes and shade-tolerant species, which is consistent with the negative relationships between management intensity and mega/meso phanerophytes [70,71] and clonal compact species [72,73] found in previous studies. Moreover, in our study, prescribed burning after clear cut favored species with higher seed weights, because larger seeds have a higher chance of surviving wildfires and produce more vigorous seedlings with a lower death rate [74]. Finally, the retention pattern mainly changed the understory based on species light requirements, which followed the expected pattern with shade-tolerant species associated with unharvested forests, and careful logging and clear cut favored mid-shade tolerant species.

4.4. The Role of Forest Attributes

Compared to the retention patterns or their combined effect with site preparation, the forest attributes in our study (stand type, time since fire, and time since harvest) did not play a significant role in determining functional diversity (functional richness, functional evenness, or functional divergence), nor in affecting the relationships between trait groups and site preparation. We only found a slight effect of time since fire when studying the relationship between trait groups and the combined disturbance of retention pattern and site preparation. A weak effect of stand type or time since harvest may have been caused by the conifer forest focus of our study, and the range of years since harvesting disturbance (mean and SD were 14 years and 11 years, respectively) was relatively narrow among sites. Therefore, we infer that studies covering different types of forests, e.g., an aspen to conifer forest chronosequence, might show a non-negligible role of forest attributes on functional diversity. However, some workers have inferred that the weak role of time since harvest might be because of the relatively fast regeneration time of understory plant communities in boreal forests [75,76], especially after careful logging that protects the soil and promotes the rapid regeneration of native trees [77].

5. Conclusions

Our study systematically investigates the combined effect of retention pattern and post-harvest site preparation in understory community assembly using a functional trait approach in boreal forests. We found that strong trait filtering occurred, from broad-scale light environment filtering due to the retention pattern, to fine-scale niche partitioning due to the soil disturbance caused by site preparation for tree regeneration. However, the combined effect of retention pattern and post-harvest site preparation in our boreal ecosystem was the most powerful explanatory factor for understory functional diversity, when compared to retention pattern only and forest attributes (stand type, time since fire, and time since harvest). Our results indicate that the compounding effect of light variation and soil disturbance more than light alone best explains the functional trait diversity after disturbance. Among the three post-harvest site preparation techniques studied here, only prescribed burning after clear cut can achieve the goal of improving understory functional richness while promoting tree regeneration. The combined disturbance of retention pattern and site preparation affected the understory mainly by filtering for plant resistance or resilience abilities after disturbance. Yet harvested forests without subsequent site preparation mainly filtered species based on their light requirements. Finally, since our study is in boreal ecosystems, more studies on other ecosystems are needed for understanding the mechanisms behind the relationship between forest management operations and understory functional diversity.

Maintaining or improving biodiversity is an important goal of sustainable forest management. One of the forester's most fundamental acts is the choice of retention pattern. In our study, careful logging and clear cut respectively represent the recent and traditional harvesting choices, and the selection of either of those two retention patterns induces different degrees of variation in functional diversity. However, the trend in diversity variation caused by harvest management is more complicated when incorporating the role of post-harvest site preparation. Site preparation is often neglected in plant diversity study, due to its primary goal of promoting timber production. However, our results suggest that in a boreal forest ecosystem, the choice of post-harvest site preparation techniques, e.g., the prescribed fire or mechanical site preparation that applied to retention patterns, plays an important role in understory functional composition and diversity. For example, prescribed burning after clear cut maintains higher functional richness than the two mechanical site preparation techniques after careful logging. Meanwhile, the two mechanical site preparation techniques after careful logging increase the resource utilization efficiency compared to unharvested forests, which could not be achieved by prescribed burning after clear cut. Besides, by using trait-based approach, the "indicator" traits that are favored by a specific combination of site preparation techniques with retention pattern could be identified. For example, plow and disk trenching after careful logging were respectively favored by clonal guerilla species and geophytes, while prescribed burning was favored by higher seed weight. Therefore, the trait-based approach would help researchers or forest managers predict plant diversity patterns when planning which site preparation to select, or help assess the stability of understory communities under some specific forestry practices.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/11/1006/s1: Supplementary Materials: Figure S1. Distribution of functional diversity indices (FRic, FEve, and FDiv) depending on harvesting method (unharvested, CL, and CC). Figure S2. Distribution of the CWM of trait groups depending on harvesting methods (unharvested vs. CL and CC).

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