Recovery of plant community functional traits following severe soil perturbation in plantations: a case-study

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**ABSTRACT**

We present a case study in which we assessed the effects of a severe soil perturbation on the plant community and soil variables in young hybrid poplar (\emph{Populus} sp.) plantations of southern Québec (Canada). Our overall goal was to test if soil perturbation and planting fast-growing species could promote the reestablishment of a relatively diverse plant community. A chronosequence that included three plantations (4, 8, and 12-year old) established after soil scarification, paired with three natural stands representative of the local temperate mixedwood forest comprising both pioneer and late-successional tree species, was implemented. Vegetation surveys and soil collection were performed in 2012 and species traits were provided by the Traits Of Plants In Canada and TRY databases. Principal response curve analyses showed species and functional trait divergence between treated and natural stands at ages 4 and 8, but that those divergences were less at age 12. Species and trait convergences were slower in the scarification furrows than in the scarification berms (mounds between furrows). However, severe site preparation did not appear to affect soil variables on the study sites. Our results suggest that even following severe site preparation, gradual recovery of species and trait composition similar to that of natural stands appears possible in the long term, mainly through fast canopy development by hybrid poplar. However, organic material export and soil erosion risks associated with this type of site preparation need to be evaluated.

1. **Introduction**

Intensive forestry practices used to achieve high-timber production rates are often viewed as being incompatible with promoting biodiversity. However, severe soil perturbation and planting of fast-growing species could, in some contexts, promote the reestablishment of a relatively diverse plant community, with possible synergy between these objectives. Using both taxonomic and functional approaches to plant diversity, this case study assessed the effects of severe mechanical scarification prior to tree plantation establishment on species diversity and soil during the first 12 post-planting years. The establishment phase of hybrid poplar (\emph{Populus} sp.) plantations was studied on former natural forest sites. Intensively managed plantations such as those of this study are designed to reduce the structural variability of the stands, improve the predictability of expected yields, and enhance the efficiency of establishment, tending, and harvesting operations (Savill et al. 1997). We thus wanted to evaluate how the species composition and functional traits of the plant community diverged or converged compared to uncut control stands. We also aimed to assess whether the changes in major soil properties following scarification are related to changes in plant/trait composition.

The increased productivity of exotic plantations compared to natural forests is of particular interest in boreal ecosystems where natural productivity is inherently low (Kjær et al. 2014). The silviculture used in such plantations is generally based on agricultural practices in order to produce more wood over the shortest possible rotation (Paquette & Messier 2010); for example, hybrid poplar plantations in southeastern Québec (Canada) are harvested after 20–25 years (Messier et al. 2003). When compared to native stands, exotic plantations established on similar sites initially show a lower plant diversity that generally tends to increase with time, due to the influence of the planted species on the understory environment, variation in germination of seed-banking species, and the development of a humus layer that favors plant establishment (Carnus et al. 2006).

Biodiversity can be described on taxonomic, phylogenetic, or functional bases; the latter is defined as the variation of a function at different levels of...
biological organization (Garnier & Navas 2013). Functional biodiversity can be assessed at the plant level by measuring plant functional traits (plant characteristics related to functions). By simplifying taxonomic diversity to functional diversity, traits provide a process-oriented representation of the plant community (Lavorel et al. 1997) to help identify the mechanisms that drive community change, which, in turn, influence ecosystem functioning (Lavorel & Garnier 2002; Lavorel 2013; Soudzilovskaia et al. 2013). This approach is useful for studying the effect of environmental processes that operate at different scales, influencing local species assemblages and inducing non-random plant community structures (Aubin et al. 2014).

Silvicultural practices related to plantations, like scarification, are expected to affect biodiversity, which in turn influences ecosystem resilience (Archaux et al. 2010; Tomimatsu et al. 2013). Scarification involves breaking up soil to a specified depth. It is effective in stimulating tree growth, especially for fast-growing tree species such as hybrid poplar that have a low tolerance for root competition and that are planted in contexts where herbicide use is restricted or prohibited (Bilodeau-Gauthier et al. 2011, 2013; Thiffault & Roy 2011). However, scarification severity influences plant community composition by modifying the type and the amount of available substrates for plant colonization, and through its effect on residual propagules and availability of resources such as water and nutrients (Newmaster et al. 2007). Whereas treatments of low-to-moderate severity can perpetuate the presence of established species, severe mechanical scarification can negatively affect the existing vegetation through vegetation removal or by destroying vegetative reproductive organs; severe scarification can also favor the establishment of ruderal and invasive species (Jobidon 1990; Haeussler et al. 2002). Changes in the abundance of certain species may affect functional trait variation and therefore biogeochemical cycling and nutrient turnover (Van Bodegom et al. 2012).

Based on previous studies that have documented plant diversity in plantations and unmanaged forest stands (e.g., Aubin et al. 2008), we predicted that the composition of the plant and trait communities would initially diverge in hybrid poplar plantations compared to the natural forest. However, the plant and trait communities were expected to gradually converge between the treated and natural sites over the following years (Irwin et al. 2014). We also predicted that the community convergence with natural conditions would be faster in the scarification berms (mound between furrows, with a mix of organic/mineral material) compared to the scarification furrows (exposed mineral soil) (Newmaster et al. 2007). Indices of soil fertility were expected to be lowest in the younger plantations and to increase with plantation age and higher seasonal litter production. We further posited that berms would present higher carbon and nutrient concentrations compared to furrows.

2. Material and methods

2.1. Study sites and experimental design

This study is based on a non-replicated chronosequence of hybrid poplar plantations. This restriction is due to the lack of available sites replicating the appropriate disturbance severity in the study region. Although such a design does not permit generalization of its results (hence, we avoided performing inferential statistics), this approach has been used in the past to elucidate mechanisms like plant succession or soil carbon storage (Diöchon et al. 2009; Chen et al. 2013; Shiflett et al. 2014).

The experiment was implemented in three hybrid poplar plantations established with clones of *Populus maximowiczii × P. deltoides × P. trichocarpa*. The plantations were located about 30 km SW of the municipality of Cabano, Quebec (Canada) (47°29′48″N, 68°57′16″W), in the temperate mixedwood region described by Saucier et al. (2009). Elevation ranges between 240 and 360 m. Mean annual temperature for this region is 3.1°C (±0.9°C) and total annual precipitation is 1012 mm, of which 28% falls as snow (Environment Canada 2013). Soils are gleyed podzols formed from a moderate (50 cm—1 m)–deep (>1 m) coarse glacial till deposit (Soil Classification Working Group 1998). The studied plantations were 4, 8, and 12-year old in 2012, and covered 3.14, 88.4, and 11.45 ha, respectively. Each plantation was paired with a nearby uncut natural stand, representative of the tree composition of the planted sites before harvest (hereafter, referred to as ‘natural stand’).

Double-blade site preparation was performed the fall prior to planting to expose the mineral soil. The first scarification pass, performed with a 'V-blade' mounted in front of a bulldozer, created a 2.7 m wide × 0.47 m deep furrow entirely exposing the mineral soil (Figure 1). To further increase furrow depth at its center, a second pass was performed with a smaller V-blade (back hoe) mounted at the back of the bulldozer. In the spring following scarification, 1-year-old unrooted hybrid poplar cuttings (approx. height = 100 cm) were planted 30 cm deep in the hinge position of the scarification furrow (Figure 1), using a metallic rod to create a planting hole. Planting spacing was 4 m × 3 m (approx. density = 833 tree ha⁻¹). One year after planting, cuttings were each fertilized with 460 g of a 15–30–5 ammonium nitrate granular fertilizer. For the two older sites, mechanical release from competing vegetation was performed at year 5 by manual cutting with
brushsaws. The other commercial species on the site was balsam fir (*Abies balsamea* (L.) Mill.). All balsam fir seedlings and saplings that established naturally following site preparation were preserved on microsites where planted poplar cuttings had failed.

### 2.2. Vegetation sampling

We used a space-for-time substitution for serial succession (Foster & Tilman 2000), represented by plantations of 4, 8, and 12 years. Vegetation surveys were performed in September 2012. At each site, four plots (20 m²) were randomly distributed; three of them were located in the plantation and the fourth one (control) was placed in the paired natural stand.

In the natural stands only, we further established a 400 m² circular sample plot centered on the 20-m² vegetation plot to describe the original tree cover of the area (Table 1). Sampling plots on all sites were located a minimum of 100 m from the forest edge. All trees with a diameter $\geq$ 1 cm at 1.3 m were measured for their diameter at 1.3 m. In each 400 m² plot, we also randomly selected and measured the height of three to four trees from the dominant layer and cored them at 1.3 m to determine their age. Stand age of the three natural stands ranged between 51 and 68 years; dominant height was 19–21 m, and total basal area varied between 23.6 and 33 m² ha⁻¹ (Table 1).

The natural stands and plantations had two distinct vegetation layers: a dominant tree layer forming the canopy, and an understory layer of small woody vegetation, herbaceous species, graminoids, and ferns. In the 20-m² plots, woody species $\geq$2.5 m were included in the tree layer and woody species <2.5 m in height were included in the understory layer. Planted hybrid poplars were measured at 1.3 m to determine their diameter in the 20-m² plots and total height was measured on 7–9 individuals randomly selected in each plot. Tree and understory layers were separately evaluated for percent cover class (1%, 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 95%, and 100%) using visual assessment of the entire 20-m² plot surface.
Table 1. Characteristics of the uncut natural stands paired with each plantation site.

| Sampling site | Unnatural stand age (year at 1.3 m) | Dominant species | Mean height (m) | Mean DBH (cm) | Basal area (m² ha⁻¹) |
|---------------|-------------------------------------|------------------|----------------|---------------|---------------------|
| Plantation year 4 | 51 | Populus balsamifera, Thuya occidentalis, Picea glauca | 21.1 (0.5) | 18.7 (9.2) | 29.9 |
| Plantation year 8 | 68 | Acer rubrum, Betula papyrifera, Acer saccharum | 20.9 (0.2) | 12.1 (7.5) | 33.0 |
| Plantation year 12 | 68 | Acer rubrum, Betula papyrifera, Acer saccharum | 18.7 (5.3) | 8.6 (7.0) | 23.6 |

Notes: Based on data obtained from a 400 m² circular sampling plot per stand. Natural stand age and height of dominant trees forming the upper continuous canopy (as described by Oliver & Larson 1996) were measured on three to four trees per plot. Dominant species are those with the highest basal area in each plot (presented in descending order). DBH: diameter at breast height (1.3 m). Mean DBH and basal area were calculated using all trees with a DBH > 1.0 cm. Dominant height and DBH values are presented as mean (SD).

Table 2. Species encountered during the vegetation surveys with their corresponding codes.

| Code | Species |
|------|---------|
| ABIBAL | Abies balsamea (Linnaeus) Miller |
| ACENEG | Acer negundo Linnaeus |
| ACENEP | Acer papyrophyllum Linnaeus |
| ACERUB | Acer rubrum Linnaeus |
| ACESSAC | Acer saccharum Marshall |
| ACESPI | Acer spicatum Lamark |
| ALNURUG | Alnus incana subsp. rugosa (Du Roi) R.T. Clausen |
| ANAMAR | Anaphalis margaritacea (Linnaeus) Bentham & Hooker f. |
| ARANUD | Aralia nudicaulis Linnaeus |
| ASTACU | Oclema acuminata (Michaux) Greene |
| ASTESP | Aster spp. |
| ASTMAC | Aster macrophyllus Linnaeus |
| BETALL | Betula alleghaniensis Britton |
| BETPAP | Betula papyrifera Marshall |
| CARESP | Carex spp. |
| CIRCEE | Cirsium spp. |
| CLIBOR | Clintonia borealis (Aiton) Rafinesque |
| CPGP | Coptis groenlandica (Oeder) Fernald |
| CORCAN | Cornus canadensis Linnaeus |
| CORCOR | Corvus corax Marshall |
| CORSTO | Cornus stolonifera Michaux |
| DIELON | Dievilia lonicera Miller |
| DRYINT | Dryopteris intermedia (Muhlenberg ex Willdenow) A Gray |
| DRYSPI | Dryopteris carthusiana (Villars) H.P. Fuchs |
| EPIANG | Epianthus angustifolium (Linnaeus) Holub |
| EPIHEL | Epilobium hirsutum Linnaeus (Linnaeus) Crantz |
| FAGGA | Fagopyrum glabrum Ehrl. |
| FRAVIR | Fragaria virginiana Miller |
| GALTRI | Galium triflorum Michaux |
| GEUESP | Geum spp. |
| GRAESP | Gramineae spp. |
| GYMDRY | Gymnocarpium dryopteris (Linnaeus) Newman |
| HIEESP | Hieracium spp. |
| ILEX | Ilex verticillata (Linnaeus) A. Gray |
| LINBOR | Linnaea borealis Linnaeus |
| LONCAN | Loniceria canadensis Bartram |
| LYCLUC | Lycopus lucidulum (Michaux) Trevisan |
| LYCBOB | Lycopodium obscurum Linnaeus |
| MAICAN | Mainsthemum canadense Desfontaines |
| MITNUD | Micella nuda Linnaeus |
| MOUSSES | Mosses |
| OSMREG | Osmunda regalis Linnaeus |
| OXAMON | Oxaíis montana Rafinesque |
| PETPAL | Petasites palustris Linnaeus |
| PHECON | Phegopteris connectilis (Michaux) Watt |
| PICGLA | Picea glauca (Moench) Voss |
| PPHYB | Populus maximowiczii × P. deltoides × P. trichocarpa |
| POPTPRE | Populus tremuloides Michaux |
| PRUPEN | Prunus perysylvanica Linnaeus f. |
| PRUVIR | Prunus virginiana Linnaeus |
| PTEAQU | Pteridium aquilinum (Linnaeus) Kuhn |
| PYRESP | Pyrola spp. |
| RIBLAC | Ribes lacustre (Pers.) Poir. |
| RUBIDA | Rubus idaeus Linnaeus |
| RUBPUB | Rubus pubescens Rafinesque |
| SALESPP | Salix spp. |
| SAMSPUB | Sambucus racemosa subsp. pubens (Michaux) Trautvetter & C.A. Meyer var. pubens |
| SOLNLL | Bare soil |
| SOLRUG | Solidago rugosa Miller |
| SORAME | Sorbus americana Marshall |
| SPHESP | Sphagnum spp. |
| STRROS | Streptopus roseus (Aiton) Reveal |
| TAROFF | Taraxacum officinale F.H. Wiggers |
| THUOCJ | Thuja occidentalis Linnaeus |
| TRIBOR | Trisetum borealis Rafinesque |
| TRIERE | Trillium erectum Linnaeus |
| TUSFAR | Tussilago farfara Linnaeus |
| VEROFF | Veronica officinalis Linnaeus |
| VIBALN | Viburnum lantanoides Michaux |
| VICCRA | Vicia cracca Linnaeus |
| VIOESP | Viola spp. |

In each 20-m² plot, four 1-m² quadrats were randomly installed in the scarification furrows and four on the berms between scarification furrows to survey the vegetation cover of individual species less than 2.5 m in height. Four 1-m² quadrats were also randomly installed in the natural stand plots (Figure 1). We used the point-intercept method with a grid divided into 100 squares of 10 cm each. For each quadrat, we randomly selected 20 intersection points on the grid. At each of the selected intersection point, a cylindrical rod (3-mm diameter) was planted in the ground and every plant that touched the rod was counted and identified to species. Bare soil was also identified if the rod touched it. We identified plant functional traits for each species surveyed by the point-intercept method. Table 2 presents the complete list of species encountered on all sites. Traits (Table 3) were obtained from the Traits Of Plants In Canada (Aubin et al. 2012) and the TRY (Atkin et al. 1997; Díaz et al. 2004; Enquist et al. 2007; Kattge et al. 2011) databases. Traits were numerically codified to perform statistical analyses (Table 3). For groups identified to genus (e.g., ASTESP; Table 2), traits scores were averaged across species likely to have been encountered in that genus.

2.3. Litterfall and soil measurements

Litterfall was collected using 40 cm × 60 cm litter traps that were visited and emptied every 2 weeks between 24 September and 25 November 2012. We randomly placed three traps at the bottom of the scarification furrow, three at mid location between the bottom and the top of the scarification furrow, and three on the
berm, for a total of nine traps per plot (Figure 1). We also randomly positioned 12 traps in every natural stand. Harvested litter was then sorted by species, dried at 55°C until constant mass, weighted, and summed for the entire growing season (g m⁻²).

Six soil cores were collected in each plantation plot in November 2012: three in the furrow and three at the top of the berm (Figure 1). One composite soil sample was collected in each natural stand. Soil cores were collected in the top 20 cm of the soil profile using a 4.8-cm diameter cylinder. Samples were dried to 5% mass-based humidity at ambient temperature and ground to pass through a 2-mm mesh screen. Extraction of inorganic N was made with a 2 mol L⁻¹ KCl solution and measured colorimetrically by spectrophotometry (Lachat Quickchem 8000, method No. 13-107-06-2-C; Zwellenger Instruments, Milwaukee, WI, USA). Extractable P, K, Ca, and Mg were extracted with a Mehlich-III solution (Simard & Sen Tran 1993) and measured colorimetrically by spectrophotometry (Optima 4300 DV; Perkin-Elmer, Norwalk, CT, USA). The pH was determined following mixing of a 10 g subsample with KCl solution and measured colorimetrically by spectrophotometry (Lachat Quickchem 8000, method No. 33-08-01-19; Zwellenger Instruments, Milwaukee, WI, USA). The NPK content in soil was determined following mixing of a 10 g subsample with a 2 mol L⁻¹ Demineralized water using a Fisher Scientific Accumet 50 (Denver Instrument, Bohemia, NY, USA).

### 2.4. Statistical analyses

We used principal response curves analysis (PRC) to determine if understory species, plant traits, and soil characteristics in the scarified furrows and berms converged toward the natural stand conditions over time. A PRC is a kind of redundancy analysis where response variables are expressed by a deviation curve from a reference line (Van den Brink & Ter Braak 1999). In our study, the PRC expressed the differences in species, trait, or soil characteristics between a disturbed ecosystem (hybrid plantation) and its reference state (uncut natural stand) along the chronosequence. For the PRC conducted on traits, we combined the trait matrix with the understory species abundance matrix to generate a community-weighted mean value trait matrix (CWM) (Garnier et al. 2004).

We performed a co-inertia analysis (Dolédec & Chessel 1994) to evaluate the degree of association between (i) matrices of species and soil variables and (ii) matrices of CWM and soil variables, for each site. The analysis first produced a principal component analysis (PCA) for each matrix pair in which the principal axes were selected to reduce dimensionality. Through a rotation in multidimensional space, the concordance between pairs of datasets was maximized and new axes were generated. We used the RV-coefficients (i.e., the coefficient of correlation between the two tables) to assess the global similarity between datasets (0–1; 1 indicating perfect similarity) and performed a Monte-Carlo permutation test (9999 permutations) to evaluate the strength of those similarities (Aubin et al. 2013). All PRC and co-inertia analyses were executed using the R. 3.0.2 package (R Core Team 2013) with the ‘vegan’ (Oksanen et al. 2013) and ‘ade4’ (Dray & Dufour 2007) packages.

#### 3. Results

### 3.1. Hybrid poplar dimensions, understory species richness, and percent cover

Four years after planting, hybrid poplars were more than 5 m tall (Table 4), and had a percent cover of 30%. In the 8-year-old plantation, the planted trees were twice as tall as the trees on the younger site. After 12 years, hybrid poplars reached ~14 m and a commercial diameter (defined as ≥9.1 cm at 1.3 m).

The number of understory species (<2.5 m in height) was similar across plantation ages and natural stands, and percent cover of the understory layer varied between 33% (natural stands) and 67% (8-year-old plantation; Table 4).

### Table 3. Functional plant trait description and codification used for statistical analyses.

| Trait                  | Code | Type      | Description                                                                 |
|------------------------|------|-----------|-----------------------------------------------------------------------------|
| Foliage structure      | SF0  | Ordinal   | 1. Rosette, 2. Graminoid, 3. Erected leaves, 4. Vine, 5. Umbell-shaped stem, 6. Decumbent, 7. Semi-rosette, 8. Erected leafy stem, 9. Non-leafy stem, 10. Intermediary, 11. Multi-stemmed |
| Growth rate            | PGR  | Ordinal   | 1. Slow, 2. Moderate, 3. Fast                                               |
| Minimum root depth     | MRD  | Quantitative | 1. Seeds only, 2. Vegetative propagation possible but mostly by seeds, 3. Mainly vegetative propagation |
| Main reproduction      | REP  | Ordinal   | 1. Short viability (≤1 year), 2. Semi-permanent bank (1–5 years), 3. Seed bank (≥5 years), 4. Aboveground seed bank |
| Persistence            | SPE  | Ordinal   | 1. Non-dormant, 2. Physiological dormancy not deep (cyclic), 3. Physiological or morphophysiological dormancy (implies stratification of inhibitor leaching) |
| Seed dormancy          | SDO  | Ordinal   | 1. Shade tolerant (<2 h direct sun), 2. Mid-tolerant (2–5 h direct sun), 3. Shade intolerant (>5 h direct sun) |
| Light requirement      | LIG  | Ordinal   | 1. Wet, 2. Mesic, 3. Xeric                                                  |
| Water preference       | XER  | Ordinal   |                                                                              |

### Table 4. Mean (SD) hybrid poplar dimensions in plantations of various ages.

| Plantation age | n (height) | Height (m) | n (DBH) | DBH (cm) |
|----------------|------------|------------|---------|----------|
| 4              | 7          | 5.5 (0.6)  | 140     | 3.2 (1.6) |
| 8              | 9          | 10.4 (0.7) | 66      | 7.4 (2.9) |
| 12             | 7          | 13.8 (1.8) | 161     | 10.3 (5.6) |

Notes: DBH = diameter at breast height (1.3 m).
Table 5. Mean (SD) species richness and percent cover of the shrub and tree layers in natural stands and hybrid poplar plantations of various ages.

| Treatments       | Shrub layer (<2.5 m in height) | Tree layer (≥2.5 m in height) |
|------------------|---------------------------------|--------------------------------|
|                  | Number of species | Percent cover | Number of species | Percent cover |
| Natural stands   | 6 (3)               | 33 (15)       | 5 (1)              | 77 (15)       |
| Plantation year 4| 6 (1)               | 40 (10)       | 3 (1)              | 23 (15)       |
| Plantation year 8| 8 (2)               | 67 (12)       | 2 (1)              | 13 (6)        |
| Plantation year 12| 7 (2)              | 37 (15)       | 3 (1)              | 46 (15)       |

Table 5). The number and percent cover of tree species (≥2.5 m in height) tended to be higher in natural stands than in plantations (Table 5). The percent cover of the tree layer of the oldest plantation was twice that of the youngest plantation, but was least in the 8-year-old plantation (Table 5); all plantation ages were dominated by hybrid poplars. A full list of species count by treatment can be found in supplemental data.

3.2. Species

The PRC analysis revealed a greater difference in species composition between natural stands and plantations at years 4 and 8 than at year 12, especially in the furrows, where the scarification exposed the bedrock in certain locations. The left-side plot of the PRC (Figure 2a) explained 52% of the total variance in species composition between natural stands (reference line) and plantations (p < 0.01), of which 48% was associated with the scarification treatment (p < 0.01) and 28% with time (p < 0.01).

Variable scores on the right-side vertical plot (Figure 2b) indicate how strongly each species, traits, or
soil parameters is associated with the natural forest (larger positive values) or plantation (larger negative values). Positive values for *Clintonia borealis*, *Acer saccharum*, *Maianthemum canadense*, *Rubus pubescens*, *Abies balsamea*, *Acer spicatum*, *Acer rubrum*, *Cornus canadensis*, *Mitella nuda*, and *Carex* sp. (Table 2; Figure 2b) indicated that those species were still more abundant in the natural stands than in the plantations after 12 years. Conversely, species with negative values, such as *Rubus idaeus*, *Prunus pensylvanica*, *Diervilla lonicera*, *Hieracium* sp., and *Betula papyrifera* were more abundant in the plantations than in the natural stands at 12 years.

### 3.3. Traits

In the PRC analysis of community-weighted traits (CWM; Table 3), the first plot explained 60% of the total variance in CWM between natural stands (reference line) and plantations (*p* < 0.01), 32% of which was explained by the scarification treatment (*p* < 0.01) and 9% by time (*p* < 0.01) (Figure 3a). PRC showed a greater difference in trait composition between natural stands and plantations at year 8 than at year 4 or 12. The convergence from year 8 to year 12 seemed faster in the berms than in the furrows (Figure 3a). Species associated with scarification plots were shade intolerant, had fast growth rates, reproduced asexually, and lacked a buried seed bank (Figure 3b, Table 3). Inversely, species with deep rooting habits, seed dormancy, and erect-leaf foliage were associated with natural stands (Figure 3b, Table 3). Species encountered on berms shared more of the traits associated with natural stands than the species found in furrows.

### 3.4. Soil

Table 6 summarizes soil parameter values for the various combinations of site and positions within the scarified trenches. For example, pH varied from...
4.9 in the natural stands to 5.6 in the furrows of the youngest plantation. Percent total carbon was highly variable across treatments and sites, ranging from <1% up to 11.7%. The highest value for percent total N was measured in the berms of the oldest plantation, whereas the lowest value was found in the furrows of the youngest plantation. Furrows in the 4-year-old plantation presented the highest C/N ratio among sites and treatments. The PRC analysis for soil parameters was not significant ($p = 0.43$), which indicates that soil variables were influenced neither by scarification nor by time.

### 3.5. Co-inertia analyses

We found a significant association between the species and the soil matrices (RV = 0.4682, $p = 0.002$) (Figure 4), and the strength of the association decreased with time. The results of co-inertia analyses are presented in Figure 4, with sites represented by arrows that describe the degree of association of species or traits with soil variables. A shorter arrow indicates a stronger association between matrices. At year 4, the strong association between the soil variables and species was higher in the furrows than in the berms (Figure 4). In the 12-year-old plantation, the strength of the association between the matrices was weaker and similar to that of the natural stands. No association was found between the CWM and soil matrices (RV = 0.1016, $p = 0.43$).

### 3.6. Litter

Although litter data could not be submitted to formal statistical analysis due to the lack of appropriate replication, there was a clear pattern of increased total litter production with increasing plantation age (Figure 5). Whereas litter from the planted hybrid poplars represented a small fraction of the collected material in the 4-year-old plantation, it dominated litter production in the oldest plantation, with total litter production in the 12-year-old plantation similar to that the mean litter production of the natural stands over the 75-day sampling period (Figure 5).

### Table 6. Mean (SD) values for soil parameters in natural stands and hybrid poplar plantations at 4, 8, and 12 years at the berm and furrow positions.

| Treatments       | C total (%) | N total (%) | pH (water) | P (cmol+/kg) | K (cmol+/kg) | Ca (cmol+/kg) | Mg (cmol+/kg) | CEC (cmol+/kg) | C/N |
|------------------|-------------|-------------|------------|--------------|--------------|---------------|---------------|---------------|------|
| Natural stands   | 4.77 (1.99) | 0.29 (0.12) | 4.93 (0.89) | 30.38 (26.98) | 0.33 (0.11)  | 6.03 (7.35)   | 1.35 (1.41)   | 7.87 (8.86)   | 16.72 (1.71) |
| Year 4 – berm     | 5.84 (3.80) | 0.31 (0.21) | 5.03 (0.02) | 7.08 (2.85)   | 0.38 (0.28)  | 6.61 (4.88)   | 1.38 (0.88)   | 8.51 (6.04)   | 18.63 (1.40) |
| Year 4 – furrow   | 0.60 (0.27) | 0.02 (0.01) | 5.59 (0.27) | 9.53 (2.92)   | 0.11 (0.04)  | 1.24 (0.34)   | 0.38 (0.10)   | 1.82 (0.43)   | 28.43 (11.86) |
| Year 8 – berm     | 2.37 (0.66) | 0.18 (0.04) | 5.03 (0.01) | 7.65 (2.38)   | 0.17 (0.06)  | 2.23 (1.98)   | 0.35 (0.16)   | 3.00 (1.98)   | 13.54 (1.59) |
| Year 8 – furrow   | 0.92 (0.25) | 0.10 (0.02) | 5.15 (0.08) | 37.02 (41.70) | 0.15 (0.05)  | 0.45 (0.10)   | 0.14 (0.15)   | 0.87 (0.15)   | 8.94 (1.52)   |
| Year 12 – berm    | 11.67 (14.23) | 0.71 (0.45) | 5.00 (0.06) | 20.30 (32.12) | 0.41 (0.15)  | 11.65 (7.14)  | 1.54 (1.06)   | 13.31 (8.48)  | 16.47 (7.92)  |
| Year 12 – furrow  | 5.24 (5.27) | 0.32 (0.30) | 5.30 (0.31) | 9.74 (8.25)   | 0.27 (0.18)  | 6.19 (6.61)   | 1.03 (0.94)   | 7.71 (7.64)   | 16.37 (1.59)  |

Notes: For the natural stands, means are based on one composite sample per stand.

### Figure 4. Co-inertia analysis comparing the degree of association between matrices of species and soil variables for different berm (B) and furrow (F) plots within the 4, 8, and 12-year-old hybrid poplar plantations and referenced natural forest stands (Forest). Numbers indicate plantation age. Shorter arrows indicate stronger association between the matrices for a given plot. Consistency in arrow direction for a given treatment (e.g., furrows for the year 8 plantation or F8) would indicate an ecological pattern or environmental gradient (as in principal component analyses).

### 4. Discussion

In many parts of the world, forest plantations are relied on for high-wood production (Paquette & Messier 2010). High-yield plantations represent artificialization of natural forests (Brockerhoff et al. 2008), and the resulting stands are typically considered to be ‘biological deserts’ (Stephens & Wagner 2007). However, even intensively managed monocultures may provide opportunities for biodiversity conservation (Updegoff et al. 2004; Pawson et al. 2013). Moreover, the stand-level impacts of increased intensity of silvicultural treatments on plant diversity are not linear (Jobidon et al. 2004; this paper). Predicting plant community responses to environmental changes, such as those resulting from intensive plantation management, thus remains a challenge in...
ecosystem ecology. Traditionally, changes in a plant community are assessed by measuring variation in taxonomic biodiversity. It is presumed that a loss of biodiversity leads to changes in community assembly that, in turn, affect ecosystem functioning. However, this link between plant community assembly and its effect on ecosystem functioning is difficult to establish (Shipley 2010). Therefore, in this case-study, we examined impacts on both taxonomic and functional diversity.

In the furrows, the scarification treatment created local edaphic conditions, which we hypothesize, are typical of primary succession after deglaciation (Chapin et al. 1994), by exposing C soil horizons that have not undergone any pedological development. While plant communities on both berms and furrows seemed to gradually converge toward those of natural stands, convergence was faster in the berms than the furrows (Figure 2a), probably because the soil profile was deeper (Figure 1) and still contained reproductive propagules.

A possible explanation for the convergence by 12 years of the plant communities on plantation berms and furrows with that of natural stands is that rapid growth of hybrid poplar accelerated canopy development, creating favorable growing conditions for shade-tolerant species associated with natural stands (Boothroyd-Roberts et al. 2013). Indeed, canopy development is a main driver of change in vegetation communities (Tilman 1985). The abundant leaf litter production of planted hybrid poplar could also have favored convergence of understory species toward natural stand conditions by supplying the soil with fast cycling organic carbon and nutrients; litter input was similar between the 12-year-old hybrid poplar plantation and nearby natural stands (Figure 5).

Scarification often leads to colonization by shade-intolerant `ruderal’ species (Jeffries et al. 2010), as defined by Grime (1977). Instead, we observed that traits associated with scarification plots were representative of ‘competitive’ species. ‘Competitive’ species are usually found where disturbance severity is low. This might indicate that the ‘V-blade’ scarification treatment was not as severe as we expected, and/or that inherent soil fertility (after humus removal) was high enough so that ‘competitive’ species, such as Rubus idaeus (Figure 2a), could establish. This is supported by the apparent lack of treatment effect on soil properties (not statistically tested). In a study investigating floristic diversity in 7-to-8-year-old hybrid poplar plantations established on abandoned agricultural sites of Estonia and submitted to various site preparation methods, Soo et al. (2009) also reported that plant composition was dominated by ‘competitive’ species.

CWM for plantation berms and furrows in the 8-year-old plantation diverged more than CWM for the 4-year-old plantation from CWM observed in natural stands. By weighting traits with species abundance, one trait may have driven the PRC to diverge more due to a high abundance of a few species carrying the specific trait. In our study, it seems plausible that Rubus idaeus, a shade-intolerant species that was found at high densities in scarified plots, was favored during in the 8-year-old plantation due to limited development of the tree canopy, and hence, increased light availability and percent cover of the understory layer. Thus, this species probably had a strong influence on CWM, resulting in the inflection observed for the 8-year-old plantation in the PRC traits curve (Figure 3a), compared to the 4-year-old and 12-year-old plantations. The impact of R. idaeus would probably diminish as its density declined following canopy closure at approximately 10 years of age.

The lack of association between soil parameters and either scarification or time was unexpected, given the severity of the scarification treatment that could have promoted soil erosion, especially at the early stages of a plantation (Figueiredo et al. 2011). For example, Boothroyd-Roberts et al. (2013) measured lower C/N ratios in the soil of 10-year-old hybrid poplar plantations submitted to intensive silviculture compared to second growth forests. The apparent lack of treatment effects on soil parameters might be related to sampling variability, which was very high in our study. A more substantial soil sampling, especially in the berms where the mixing of the organic and the mineral horizons was inconsistent, might have resulted in clearer relationships between time and individual soil parameters.
The lack of association between the soil and CWM matrices does not imply that there is no link between all plant functional traits and soil processes. The main purpose of the functional trait approach for this study was to evaluate how the plant community responded to soil scarification and the planting of hybrid poplar. Therefore, most of the traits chosen were response traits. The results of the co-inertia analysis might have differed if additional response traits, like specific leaf area or leaf N, had been included; these traits are known to respond to soil resource availability (act as response traits) as well as influence soil fertility (act as effect traits) (Garnier & Navas 2013). Unfortunately, these traits were not available for all species in the databases.

5. Conclusion

Our results suggest that, even following a soil perturbation as severe as ‘V-blading’, if rapid canopy closure is achieved, the reestablishment of a plant community with species composition and traits converging to that of natural uncut stands is possible in subboreal mixedwoods. Plantations of fast-growing species such as hybrid poplar produce large amounts of litter and rapidly develop a canopy, probably favoring the reestablishment of species and traits typical of non-harvested conditions. This would help to reestablish the plant biodiversity typical of nearby natural stands, suggesting a potential synergy between timber management and plant diversity recovery following harvesting. Other studies have also found no link between severe scarification treatments and reduced site fertility in hybrid poplar plantations (e.g., mounding; Bilodeau-Gauthier et al. 2013). However, our case-study is based on a limited number of soil samples that did not allow statistical comparison of scarified plots and natural stands, and we did not examine the impact of scarification on soil erosion, and hence, on nutrient export. Such impacts might be especially important when scarification furrows are parallel to the slope. Moreover, although the natural stands were selected to represent ‘uncut controls’ for the plantations, they varied in terms of tree composition and dendrometric characteristics (Table 1). These differences influenced our comparisons between planted stands and their natural counterparts. Under the conditions of the present study, the impact of scarification appeared to have a short-term effect on soil and plant communities, potentially due to the rapid recovery of canopy closure and nutrient cycles typical of fast-growing tree plantations. The effect of V-blade scarification on plant community and ecosystem functions over time should be formally tested using replicated chronosequences.

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Disclosure statement

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