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Intensive forestry filters understory plant traits over time and space in boreal forests

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Because of their scarcity, protected areas alone cannot maintain biodiversity. Therefore, it is necessary to create conditions appropriate for plants and wildlife in managed landscapes. We compared the effects of different intensities of forest management on functional responses of vascular understory plants using the fourth-corner method. We analysed functional community composition along a management gradient that spanned semi-natural forests to extensively managed forests (naturally regenerated cuts) to intensively managed forests (planted forests) in Canada. Results showed trait filtering along the gradient of forest management intensity. In natural and extensively managed forests, where forest retention was high in time and space, persistence traits (e.g. perennial geophytes or chamaephytes, non-leafy stem foliage structure) were maintained. At the opposite end of the gradient, in intensively managed plantations where forest retention elements (e.g. amount of dead wood) were reduced, trait filtering led to species associated with colonization, such as tall species with limited lateral extension. These results suggest that intensive forestry conducted over a large extent may change the functional composition of understory plants.

Introduction

The historical extent and intensity of boreal forest exploitation varies greatly between North America and Europe. Most European boreal forests have been exploited for centuries, which has led to simplification in forest structure and composition (Shorohova *et al.*, 2011). As a result, the majority of northern European boreal forests are relatively young and even-aged (Kouki *et al.*, 2001). At the same time the area of natural forests, which were historically dominant in the Fennoscandian forest, has diminished (Kuuluvainen and Siitonen, 2013). In contrast, some boreal forests in Russia and North America still possess many characteristics of primary forests, due to their more recent history of anthropogenic use and less intensive utilization (Gustafsson *et al.*, 2010).

Similar trends as in Fennoscandia are emerging in the boreal forests of Canada. For example, the proportion of young forest is much greater than historically (Cyr *et al.*, 2009) and coarse woody debris (CWD) has been reduced by 30 per cent of its historical levels (Pedlar *et al.*, 2002). Tree species composition has also been changing with greater proportions of pioneer species (such as poplars), species with advance regeneration strategies (such as balsam fir (*Abies balsamea* (L.) Miller)) (Carleton and MacLellan, 1994) in extensively managed forests or of commercially planted species where operations to control vegetation are intensive.

Structural and compositional changes caused by intensive forestry may adversely affect biodiversity (Hanski, 2000) and forest processes (Bengston *et al.*, 2000; Cardinal and Andrew, 2000). For example, in intensively managed Finnish forests, ~31 herbaceous species are classified as threatened by forest management practices (Rassi *et al.*, 2010) and are recorded on the Red List for Finland. However, the number of threatened species varies greatly depending on forest management intensity. To date, no threatened vascular plant species have been associated with forest management practices in boreal forests in North America (Venier *et al.*, 2014).

A taxonomic approach has traditionally been used to evaluate the effects of forest management intensification on biodiversity (Díaz and Cabido, 2001). At the site level, the species richness of understory plants following management can equal or exceed that of pre-management conditions, although species composition is often modified (Peltzer *et al.*, 2000; Hasenauer and Kindermann, 2002; Haeussler and Bergeron, 2004; Newmaster *et al.*, 2007; Kembel *et al.*, 2008). More recently, a functional trait approach has been proposed as a complement to the taxonomic approach allowing for a mechanistic understanding of the processes involved in vegetation change (Lavorel and Garnier, 2002; Naeem *et al.*, 2012). Further, the use of functional traits may provide advanced warning of potential community changes prior to actual species losses (Mouillot *et al.*, 2012).

A functional trait approach also permits comparison of different ecosystems with similar underlying processes, but potentially dissimilar species compositions (Aubin *et al.*, 2007; Bernhardt-Römermann *et al.*, 2011). Many researchers used this premise to compare changes in biodiversity across a gradient of land use (Stofer *et al.*, 2006; Aubin *et al.*, 2008; Philpott *et al.*, 2008). Within an ecosystem, environmental pressures act as a filter upon the species pool and, consequently, their response will be determined by a given species' trait regardless of the geographic location (Keddy, 1992). This process is called trait filtering and can be defined as 'the process by which abiotic variables determine whether a species has the requisite traits to colonize, establish, and persist in a given environment' (Mouillot *et al.*, 2012).

The objective of this study was to investigate how the gradient of forest management intensity at both stand and landscape levels affected the composition of functional traits within understory vascular plant communities. We hypothesized that traits related to processes such as dispersal and persistence would be filtered differently by the environment along the gradient of forest management intensity, resulting in a dissimilar trait syndrome, i.e. a set of traits selected by environmental conditions as described by Lloret *et al.* (2005). Within intensively managed forests, the prevalence of traits related to colonization was expected to increase while those related to persistence were expected to decrease. Conversely if the extensively managed forest was resilient to forest management, traits related to a persistence syndrome should be maintained.

Methods

Land use history

Industrial exploitation of the Canadian boreal forest only began in the early twentieth century, with a focus on harvesting spruce for pulp and paper (Bouthillier, 2011). Large-scale intensive management of monospecific forests in Canada is mainly carried out on private lands in New Brunswick (Park and Wilson, 2007). On public lands, the main forestry activity has been clear-cut logging of natural forests (Bock and Van Rees, 2002). These areas are sometimes replanted but most often they are left to naturally regenerate. Application of herbicide and thinning is rarely used in Canada except on intensively managed private lands.

The intensity of forest management can be defined by the amount of retention elements (stand and landscape scales) that are kept through time, as well as by other factors such as site preparation and rotation length. We define a retention element as any *natural feature that is maintained for a given time period after harvesting or natural disturbance at one or multiple spatial scales*. These elements include CWD, snags, individual or patches of green trees, forested corridors, riparian buffers, old forest, and large forest patches. In this study, three forest management intensities were compared: (1) high forest retention, which was maintained in naturally regenerated forests following a natural disturbance (semi-natural forest); (2) high forest retention which was maintained in naturally regenerated forests following partial or total cuts (extensively managed forests) and (3) low stand-level forest retention in intensively managed plantations, which were thinned once or twice (intensively managed). These planted forests received two applications of herbicide shortly after trees were planted and after one or two subsequent thinnings. It should be noted that 20 per cent of the landscape around these plantations was protected from harvesting. Under extensive management, no further silvicultural activities occurred after cutting and a greater amount of retention was left, as dead wood and green trees. In general, harvest rotations under intensive management were shorter (~20–30 years) than in extensively managed forests (~70–80 years) (Forestry Development Centre Tapio, 2006).

Site description

Study sites (n = 32) were located in the boreal or hemi-boreal zone of Quebec and New Brunswick, Canada (Brandt, 2009): in the upper Mauricie of Quebec (72.62 W, 47.60 N) for the semi-natural (n = 10) and extensive treatments (n = 10); and in northeastern New Brunswick on private land (67.64 W, 47.34 N) for the intensive plantations (n = 12). All sites aged 30 and 70 years old were randomly selected from a list of potential sites and sampled in 2010. Many criteria were used to define the potential sites (slope, time since the last disturbance, intensity of the disturbance, forest type, naturally regenerated, hydrology, etc.). All sample sites were located within a radius of 300 km, on mesic till soils and historically covered by mixed hardwood-conifer forests. In naturally regenerated sites, stands were dominated by balsam fir, trembling aspen (*Populus tremuloides* Michaux), white birch (*Betula papyrifera* Marshall) and black spruce (*Picea mariana* (Miller) BSP). Most of the planted sites were pure stands of white spruce (*Picea glauca* (Moench) Voss), but some were mixed with naturally regenerated black spruce or red spruce (*Picea rubens* Sargent). Annual precipitation ranged between 900 and 1100 mm, with an annual mean temperature of 3.3°C (Environment Canada, 2012).

Previous to extensive anthropogenic use, forests in the study region were dominated by mature and old-growth stands resulting from rare large-scale disturbances (Ostlund *et al.*, 1997; Kuuluvainen, 2009; Kneeshaw *et al.*, 2011). Available studies suggest that the mean fire interval was at least 200 years in spruce-dominated forests of sampled regions (Mosseler *et al.*, 2003; Alvarez *et al.*, 2011). Also, historically, all sampled forests were dominated by mixed hardwood-conifer stands.

Field sampling

In each of the 32 sites, a sample plot (26 m radius) was positioned more than 20 m from an edge to avoid edge effects. The minimum distance between sites was 2 km. Within the plot, four 26 m long transects were placed in a cross along cardinal compass points. Canopy openness was measured every 2 m along the four transects using a spherical crown densiometer (Ben Meadows Company, Janesville, WI). All trees with a diameter at breast height (DBH, 1.3 m) >10 cm and within 2 m of both sides of the transect were measured to determine stand basal area (m^2/ha). To determine the volume of dead logs (V, m^3/ha), line intersect sampling (Van Wagner, 1982) was performed along each transect. Cross-sectional diameters (cm) were measured at the line intercepts for all logs >5-cm diameter (Angers *et al.*, 2005). The volume of dead logs was then estimated using Van Wagner's formula (Van Wagner, 1982):

$$V = K/L*\Sigma d^2 \quad (1)$$

where K is a constant (1.234), d is the cross-section diameter of each log (cm) and L is the transect length (m). To calculate the volume of dead snags and stumps we measured the diameter and height of all snags (≥1.3 m tall, DBH ≥ 5 cm) and stumps (diameters ≥ 5 cm at 30 cm above the soil surface) within 2 m of the transect line. The total CWD volume was estimated on a per hectare basis for each site based on cross-sections of downed logs and the volumes of stumps and snags, calculated as cylinders.

A landscape analysis was performed using Geobase Land Cover Circa 2000 (Geobase, 2011). The percentage of forest and agricultural fields was determined within a 2 km radius of each site. The age of the surrounding forest was not considered as the objective was to compare whether species can disperse into the surrounding environment. Since the possibility of dispersion of species at the landscape scale is the same for young and old forest differences in forest, age were not taken into account.

Ten volumetric samples from both the organic layer and the first 15 cm of mineral soil were randomly sampled along the four transects at each site. We used the methods described by Thiffault *et al.* (2007) to measure soil pH, texture (granulometry) (sand = 53 μm–2 mm, silt = 2 μm–53 mm and clay = <2 μm), Ca, Na and K (cmol/kg) concentrations of each sample of mineral soil.

Vascular plant species, including woody species ≤5 cm DBH, were identified within a sampling area of 15-cm radius located every 2 m along the four transects (*N* = 52 points per site). In addition, species that were absent from the sample points, but that were present within 2 m of the transect were recorded. Species occurring at a sample point were assigned a value of 1 and species that were absent from the point but present in the plot were given a value of 0.5. The frequency of occurrence (per cent) for each species was determined as the proportion of points where the species was present, divided by the total number of sample points (52) per site. Calculations included the species scores for those that were present in the plot, but not in the sample points.

Traits

We selected nine traits and one ecological performance metric (light requirement) (*sensu*, Violle *et al*., 2007) that are related to colonization capacity and plant persistence and that are typical of disturbed sites (Table 1). A colonization syndrome is defined as a set of traits (e.g. small seeds, dispersed by wind or animals, tall plant, etc.: Table 1) that make a species more apt to colonize new areas than continued persistence in an area through time. To persist, species require a different set of traits (e.g. geophyte, perennial, big seeds, etc. Table 1) called the persistence syndrome. The concept of 'syndromes' has been underused in applied forest ecology but could be of use to managers to understand the potential response of vegetation to different types of forest management. Most information on traits was found in the TOPIC (Aubin *et al*., 2012), LEDA (Kleyer *et al*., 2008) and BIOFLOR (Klotz *et al*., 2002) databases. When the information was not available in these databases, a literature search was undertaken.

Statistical analysis

We used a *t*-test and a one-way analysis of variance, followed by Tukey means comparison, to determine if environmental factors varied among the different levels of forest management intensity. We used fourth-corner analysis (Dray and Legendre, 2008) to identify the functional trait significantly associated with each level of forest management intensity. This is a 'direct' approach to relate plant traits to environmental variables by simultaneously analysing three matrices: L= species occurrences measured in the field per plot; Q= species by functional traits; and R= plot by level of forest management intensity gradient. Dray and Legendre (2008) presented five permutation models. We used their first model (permute presence–absence values for each species independently), where the cell values were permuted within the columns of matrix L. This model tested the null hypothesis that the species were randomly distributed with respect to site characteristics. As with Aubin *et al*. (2009), we used a Holm's procedure to adjust the probabilities that resulted from overall significance tests in the fourth-corner matrix (Dray and Legendre, 2008).

Species richness and Simpson's diversity index were calculated for vascular plants and phanerophytes by level of forest management intensity. We used JMP 5.1 (Sas Institute, 2003) to perform ANOVA and *t*-tests, followed by Tukey tests. The fourth-corner analysis was performed in R (version 2.14.1) using the Vegan package.

Results

Differences in environmental factors along a gradient of forest management intensity

Environmental factors were similar in semi-natural and extensive forests at the landscape and the stand scales. However, at the landscape scale planted forests had a significantly greater proportion of agricultural fields (0.2 per cent compared with >0.01 per cent for semi-natural and extensive) and a smaller proportion of forest (75 per cent compared with 87 per cent for semi-natural and 90 per cent for extensive) (Table 2).

At the stand scale, planted forests had lower volumes of CWD (28 m^3 ha^{-1}) than in extensively managed (90 m^3 ha^{-1}) and semi-natural forests (123 m^3 ha^{-1}), but a higher per cent of conifers (96 per cent). Also, the soils in the planted forest sites were more fertile, had significantly higher base cations (K, Na and Mg), pH and per cent clay (37 per cent) than the other sites (Table 2).

Plant response

One hundred fifteen species were found in the survey. Of these, 75 species were associated with semi-natural forests, 81 with extensively managed forests and 71 with planted forests. More than twenty species were specific to semi-natural and extensively managed forests, including orchids such as *Corallorhiza maculata* Raf., *Cypripedium calceolus* L., *Goodyera repens* (L.) R. Br., *Habenaria* sp. Several less common species were also found in semi-natural and extensively managed forests: *Chimaphila umbellata* (L.) Barton, *Gaultheria hispidula* (L.) Muhl. ex Bigelow, *Gaultheria procumbens* L., *Monotropa hypopithys* L., *Monotropa uniflora* L., and *Trillium undulatum* Willd. In planted forests, we also found ~20 species that were not encountered in other sites. Most of these were sedges or grasses, such as *Carex intumescens* Rudge and *Cinna latifolia* (Trevis. ex Goepp.) Griseb. and early successional species, such as *Circaea* sp., *Hieracium* sp., *Impatiens capensis* Meerb., *Lactuca biennis* (Moench) Fernald, and *Valeriana officinalis* L.

Diversity indices (species richness and Simpson) were not significantly different among levels of forest management intensity (Table 2), but composition was different and this led to significant differences in functional traits. Traits related to a syndrome of colonization were favoured in plantations.

Influence of a gradient of forest management intensity

Occurrences of functional traits were similar between semi-natural and extensively managed stands, but different from the planted forests (Table 3). Most traits, with the exception of light requirement and traits related to seeds, exhibited significant differences among sites (Table 3). Occurrence of geophytes, chamaephytes, and micro-phanerophytes were reduced as well as perennials in planted forests. Also, phanerophytes with limited, compacted lateral extension or with multiple stems were less abundant in plantations than in the semi-natural and extensively managed forests. Among non-phanerophytes,

Table 1 Description and literature review of traits positively (+) or negatively (–) associated with forest management intensity

Traits	Class		References
Raunkiaer life form	Chamaephyte (herb/shrub, bud 1 mm to 25 cm above ground)	–	Hermy *et al.* (1999), Royo and Carlson (2006), Aubin *et al.* (2007)
	Geophyte (herb with underground bud)	–	
	Hemicryptophyte (herb with bud at the ground surface)	–	
	Mega or meso-phanerophyte (≥8 m in height)	–	
	Micro or nan-phanerophyte (25 cm to 8 m in height)	+	
	Therophyte (annual)	+	
Light requirement	Shade intolerant	+	Macdonald and Fenniak (2007), Craig and Macdonald (2009)
	Shade mid-tolerant		
	Shade tolerant	–	
Life cycle	Perennial and biannual	–	Brumelis and Carleton (1989), Peltzer *et al.* (2000)
	Annual	+	
Flowering phenology	Spring	–	Graae and Sunde (2000), Gachet *et al.* (2007)
	Summer/fall	+	
Height	Numerical values (cm)	+	Brumelis and Carleton (1989), Bock and Van Rees (2002)
Foliage structure	*Non-phanerophyte*		Mcintyre *et al.* (1995), Aubin *et al.* (2007)
	Decumbent stem	–	
	Erect leaves	–	
	Erect leafy stem	–	
	Stem bent in an arch-shaped	–	
	Non-leafy stem	–	
	Umbel-shaped stem	–	
	Rosette	+	
	Semi-rosette	+	
	Graminoid	+	
	Phanerophyte		
	Multi-stemmed	–	
	One stem	–	
Lateral extension	*Non-phanerophyte*		Brumelis and Carleton (1989), Peltzer *et al.* (2000), Haeussler *et al.* (2002)
	Limited (annuals and biennials, but also perennials not propagating vegetatively)	+	
	Clonal compact (perennials growing in dense tufts from buds on a rhizome or a root storage organ. Horizontal propagation is possible but not extensive)	+	
	Clonal extensive (perennials with obvious horizontal propagation, either above or below ground.)	–	
	Phanerophyte		
	Limited (no vegetative propagation)	+	
	Clonal compact (Vegetative propagation by sprouting or root collar sprouts)	–	
	Clonal intermediate (may include preceding forms, but also layering and low levels of horizontal propagation by root suckers or rhizomes)	–	
	Clonal extensive (may include preceding forms, but also high levels of horizontal propagation by root suckers or rhizomes)		
Seed length	Very small, <0.1 mm	+	Aubin *et al.* (2009)
	Small, 0.1–1.99 mm	+	
	Medium, 2–2.99 mm		
	Large, 3–4.99 mm	–	
	Very large, 5–40 mm	–	
Seed production	Abundant (>1000 seeds per shoot)	+	Rowe (1983)
	Semi-abundant (20–1000 seeds per shoot)	–	
	Few (1–20)	–	
Seed dispersal	Endozoochorous (animal ingestion including bird)	–	Mclachlan and Bazely (2001), Bradbury (2004), Aubin *et al.* (2007)
	Epizoochorous (carried externally by animals)	+	
	Anemochorous (wind)	+	

Positive sign (+) indicates a trait favoured by intensification in forest management (colonization trait). Conversely, a negative sign (–) means a trait is negatively associated with forest management intensity (persistence trait). For the seed dispersal vector, species can have more than one class.

Table 2 Mean values of environmental factors, species richness and Simpson's diversity indices by level of forest management intensity for two spatial scales

Variable	Semi-natural	Extensive	Intensive
	N = 10	*N* = 10	*N* = 12
LANDSCAPE			
% Agriculture	0 ± 0.06^{A}	0 ± 0.04^{A}	0.2 ± 0.05^{B}
% Forest	87 ± 3^{A}	90 ± 2^{A}	75 ± 3^{B}
STAND			
Basal area (m^2/ha)	33 ± 3^{A}	36 ± 2^{A}	36 ± 2^{A}
% Conifer	75 ± 5^{A}	67 ± 4^{A}	96 ± 5^{B}
% Openess	12 ± 1^{A}	10 ± 1^{A}	11 ± 1^{A}
CWD (m^3/ha)	123 ± 14^{A}	90 ± 10^{A}	28 ± 13^{B}
pH	3.86 ± 0.1^{AB}	3.72 ± 0.1^{A}	4.12 ± 0.1^{B}
SB (cmol/kg)	2.50 ± 4^{A}	1.91 ± 3^{A}	13.38 ± 4^{A}
% Clay	14 ± 1^{A}	12 ± 1^{A}	37 ± 1^{B}
% Sand	54 ± 2^{A}	57 ± 1^{A}	23 ± 2^{B}
DIVERSITY			
Richness	29 ± 2.0^{A}	30 ± 14^{A}	33 ± 1.8^{A}
Simpson	0.95 ± 0.003^{A}	0.95 ± 0.003^{A}	0.95 ± 0.003^{A}

The compares sites; semi-natural forests, extensively managed forests and intensively managed forests. A different letter indicates a significant difference at $P<0.05$ (one-way ANOVA followed by Tukey tests). Means are presented with their standard error (±); SB = sum of base.

plants with non-leafy stems and semi-rosettes were also less frequent, while hemicryptophytes and summer flowering species were more abundant within planted forests. Species were also generally taller in plantations compared with extensively managed forests. Decumbent, rosette and erect leaves were more prevalent in planted stands. Species with foliage arranged in rosettes were also abundant in semi-natural forests. In addition, non-woody species with a limited compact lateral extension occurred more frequently in planted forests.

Discussion

Syndrome of colonization traits in intensively managed forests

The comparison of a broad gradient of forest management intensity allowed us to identify broad patterns of long-term vegetation response to forest management practices. Although we did not asses within site variability in response, our results suggested trait filtering occurred along a management gradient.

As hypothesised, we found colonization traits associated with intensively managed forests (Table 1). Frequent silvicultural interventions in planted forests modify light, temperature and humidity (Gray and Spies, 1997), which filter persistence traits differently than conditions found in extensively managed and semi-natural forests. Frequent forest disturbance allows shade-intolerant species to dominate and compete for light with shade-tolerant ones (De Grandpré *et al.*, 2000; Bartemucci *et al.*, 2006). In areas under intensive management, both pre-commercial and commercial thinning removes ~20–30 per cent of the canopy every 20 years with a final cut after ~70–80 years. Under this regime, planted forests undergo a treatment almost every 30 years, which does not leave enough time for the canopy to close completely (Valverde and Silvertown, 1997). Aubin *et al.* (2014) observed delayed maturing of the understory of a plantation, characterized by a higher prevalence of traits and species typically associated with younger stands.

Changes expected (Table 1), but not observed in plantations (i.e., epizoochorous, shade-intolerant, small seeds wind-dispersed, therophytes and graminoid foliage structure) could also be due to a lag in compositional shifts of the understory vegetation at our study plots (Bartemucci *et al.*, 2006). Indeed, the majority of understory boreal species have the capacity to persist in disturbed sites through clonal growth, meaning that current composition is a function of past establishment opportunities (De Grandpré *et al.*, 1993). We therefore hypothesize that the currently observed relative resilience of understory communities in planted forests may be reduced after multiple forest rotations due to both the cumulative impacts of management actions and the larger proportion of the forest that may be managed under intensive management such as short rotations and frequent thinning. Indeed, in plantations, where short rotations are practiced, traits such as graminoid foliage structure (Liira *et al.*, 2007), therophytes, shade intolerant, epizoochorous and species limited to compact lateral extension were favoured (Patry *et al.*, 2014). These differences between short-rotation plantations such as found in Fennoscandia and the plantations that we studied suggest a stronger positive filtering of colonization traits in more intensively managed landscapes. Unlike Fenoscandinavian however, plantations in Canada are more recent and are dominated by continuous forest with a relatively large proportion of natural forests in the surrounding landscape. We speculate that high forest retention around plantations could help to offset effects of frequent canopy opening on environmental conditions and, therefore, on trait filtering.

Syndrome of persistence traits in natural and extensively managed forest

This study suggests that important functional changes have likely started to occur in intensively managed forests of Canada. We propose that an examination of the traits characterizing threatened species in other boreal countries be used to determine which Canadian understory species might be at risk in the future. For example, many orchids and mycoheterotrophic species with many traits characterizing the persistence syndrome are found on the Red List of threatened species of other boreal countries. Those species are also found naturally across the Canadian boreal forest (Rassi *et al.*, 2010; Mouillot *et al.*, 2012).

In contrast to planted forests, natural and extensively managed forests are less frequently and less severely disturbed. The need to disperse over long distances is thus reduced as shown by the higher number of a persistence traits observed in such forests (i.e. geophytes and perennials). In these stable environments, we found more geophytes and chamaephytes, which have slow growth rates limiting their capacity to quickly colonize new disturbed areas (Ramovs and Roberts, 2005). They are also more sensitive to management intensity as soil disturbance can damage vegetative reproductive organs (rhizomes, bulbs, tubers and corms) (Haeussler *et al.*, 2002). Furthermore, many mycoheterotrophic

Table 3 Influence of the gradient of forest management intensity on the occurrence of functional traits

Traits	Class	Fourth corner ($n = 32$)		
		Semi-natural ($n = 10$)	Extensive ($n = 10$)	Plantation ($n = 12$)
Raunkiaer	Chamaephyte		+	−
	Geophyte		+	−
	Hemicryptophyte	−	−	+
	Micro-phanerophyte			−
	Therophyte			
Light requirement	Shade intolerant			
	Shade mid-tolerant			
	Shade tolerant			
Life cycle	Perenial	+	+	−
	Annual			
Flowering phenology	Spring			
	Summer		−	+
Height herbaceous	Tall (>50 cm)		−	+
Foliage structure	Decumbent	−	−	+
	Erect leaves	−		+
	Erect leafy stem			
	Stem arch-shaped			
	Non-leafy stem		+	−
	Umbel-shaped stem			
	Rosette	+	−	+
	Semi-rosette	+		−
	Graminoid			
	Multi-stemmed			−
		CN (10)	**CE (10)**	**CP (12)**
Lateral extension	Limited		−	+
	Compact	−		+
	Extensive			
	Phanerophyte – limited		+	−
	Phanerophyte – compact			−
	Phanerophyte – intermediate			+
	Phanerophyte – extensive		+	−
Seed length	Large seeds (>3 mm)			
Seed production	Abundant (>1000)			
	Semi-abundant (20–1000)			
	Few (1–20)			
Seed dispersal	Endozoochorous			
	Epizoochorous			
	Anemochorous			
	Entomochorous			

The fourth corner analysis compared semi-natural forests, extensively managed forests and planted forests. A positive sign (+) or negative sign (−) assigned to a level of forest management intensity indicates that this trait is positively or negatively influenced relative to other levels of the gradient. Only significant differences at the 5 per cent level after Holm correction are shown for both analyses. Blank: non-significant relationship and/or mean not evaluated. Numbers in parentheses are the number of sites and the number of species in each group

species (e.g., *C. maculata*) are sensitive to forest management because of poor seed dispersal, their use of decaying dead wood for rooting and their intolerance to full sunlight (Haeussler *et al*., 2002). Mycoheterotrophic species were found in semi-natural and extensively managed forests, but not in the planted forests in this study.

Conclusion

Our study using syndrome in an innovative way suggests that persistence traits were negatively filtered and colonization traits were positively filtered with intensification in forest management. Conversely, no significant differences were observed between natural and extensively managed forests despite greater amounts of forest retention and the absence of thinning. However, the relative resilience of the understory vegetation in Canadian boreal forest could be reduced if the intensity of silvicultural interventions increases in conjunction with insufficient retention of forest in time and space. Our data suggest that intensively managed forests have started to undergo important changes in the occurrence of the functional traits of understory vegetation. Traits that were lost in intensive plantations in Canada are the same as those documented threatened species in other boreal countries. Our results should be seen as an early indication of the long-term cumulative effects of increasing management intensity across a portion of the boreal forest in Canada.

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