

Restoration of floral diversity through plantations on abandoned agricultural land

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Abstract: Plantations have been claimed to be “monocultures”, or “biological deserts”. We investigated these claims in the context of a long-term study on plant diversity within plantations with different indigenous tree species, spacings, and soil types that were compared with 410 native stands. Soil type had no influence on plantation species diversity or abundance, and wider spacing resulted in higher richness, lower woody plant abundance, slightly higher cover of herbaceous plants, and large increases in cryptogam cover. We also found a canopy species \times spacing interaction effect, where the impact of increased spacing on understory vegetation was more pronounced in spruce than in pine plantations. The dynamic community interactions among species of feathermoss appear to be in response to the physical impediment from varying amounts of needle rain from the different tree species. High light interception and needle fall were negatively correlated with understory plant diversity, as was lack of structural diversity. This study indicates that through afforestation efforts agricultural lands can be restored to productive forests that can harbour nearly one-half of the plant species found in equivalent natural forests within the same geographic region in as little as 50 years. We recommend applying afforestation using indigenous conifer species as a first step towards rehabilitating conifer forests that have been converted to agriculture and subsequently abandoned.

Résumé : Les plantations ont été considérées comme des monocultures ou des déserts biologiques. Les auteurs ont examiné ces prétentions dans le contexte d'une étude à long terme sur la diversité des plantes dans des plantations réalisées avec différentes espèces d'arbres indigènes, ainsi que différents espacements et types de sol, en les comparant à 410 peuplements naturels. Le type de sol n'avait pas d'influence sur la diversité ou l'abondance des espèces dans les plantations. Un espacement plus grand engendrait une plus grande richesse, une plus faible abondance de plantes ligneuses, un couvert de plantes herbacées légèrement plus important et une forte augmentation du couvert de cryptogames. Ils ont également observé une interaction entre l'espacement et les espèces de la canopée; l'impact d'une augmentation de l'espacement sur la végétation du sous-bois était plus prononcé dans les plantations d'épinette que dans les plantations de pin. Les interactions communautaires dynamiques entre les espèces de mousses semblent provoquées par les contraintes physiques engendrées par différentes quantités de pluie d'aiguilles provenant des différentes espèces d'arbres. Une forte interception de lumière et la chute des aiguilles étaient négativement corrélées avec la diversité des plantes en sous-étage, de même que le manque de diversité structurale. Cette étude montre que des efforts de reboisement permettent de reconvertir, en aussi peu que 50 ans, des terres agricoles en forêts productives qui peuvent contenir près de la moitié des espèces de plantes retrouvées dans les forêts naturelles équivalentes situées dans la même région géographique. Ils recommandent de reboiser avec des espèces indigènes comme première étape dans la restauration des forêts de conifères converties en terres agricoles puis abandonnées.

[Traduit par la Rédaction]

Introduction

The establishment of industrial forest plantations through afforestation efforts is increasing at a nearly exponential rate. In the 1980s, Mather (1990) estimated an increase in the planted area of approximately 1.0×10^6 to 1.2×10^6 ha·year⁻¹. By the early 1990s plantations occupied about 100×10^6 ha of land worldwide (Sutton 1993). More re-

cently, Leslie (1999) estimated new plantation establishment globally at 5×10^6 to 8×10^6 ha·year⁻¹. One of the foremost reasons for establishing plantations is the large quantities of fibre from relatively small land areas (Sedjo 1999; Bowyer 2001) and the need for sequestering carbon to meet obligations under the Kyoto Protocol. In Canada, plantations are deemed central to the Forest 2020 Strategy (CCFM 2001), and \$20 million is being invested by the federal government

Received 12 July 2005. Accepted 20 December 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 29 April 2006.

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to establish plantations on private lands across the country by 2005. While these plantations are expected to enhance fibre production and sequester carbon, there remain unanswered questions about their contribution to sustaining biodiversity under the Convention on Biological Diversity (CBD 1992).

There is a genuine concern by society at large that the forest industry may embrace single-species monoculture (plantations), a system claimed to negatively affect biodiversity (Whitehead 1982; Kirby 1988; Swindel and Grosenbaugh 1988). These concerns are founded on the fact that the worldwide area of plantation forests is increasing (FAO 2001; Roberts and Gilliam 1995a, 1995b) without considering the cost to biodiversity (Brockerhoff et al. 2003; Betts et al. 2005). Environmentalists, ecologists, and wildlife biologists claim that plantations are the most intensive form of forest management and a major contributor to the establishment of exotic species, loss of native species from forest communities, and the creation of single-layered monocultures, or "biological deserts" (Conde et al. 1983; Mosquin et al. 1995; Smith et al. 1997). Single-species plantations may result from afforestation of farm fields and wastelands or via reforestation through the combination of many silvicultural interventions (i.e., clear-cutting, site preparation, planting a single species, tending, and thinning). Managed plantations may lack the tree species diversity, the multilayered canopy (Kimball and Hunter 1990; Oswald 1990), and the number of indigenous plant species that exist in natural forests (Mosquin et al. 1995; Erdle and Pollard 2002). These claims are alarming given that maintaining native biodiversity in planted forests is of global interest and a legislative requirement for many forest ecosystem managers (Stanturf and Madsen 2002; Zerbe 2002).

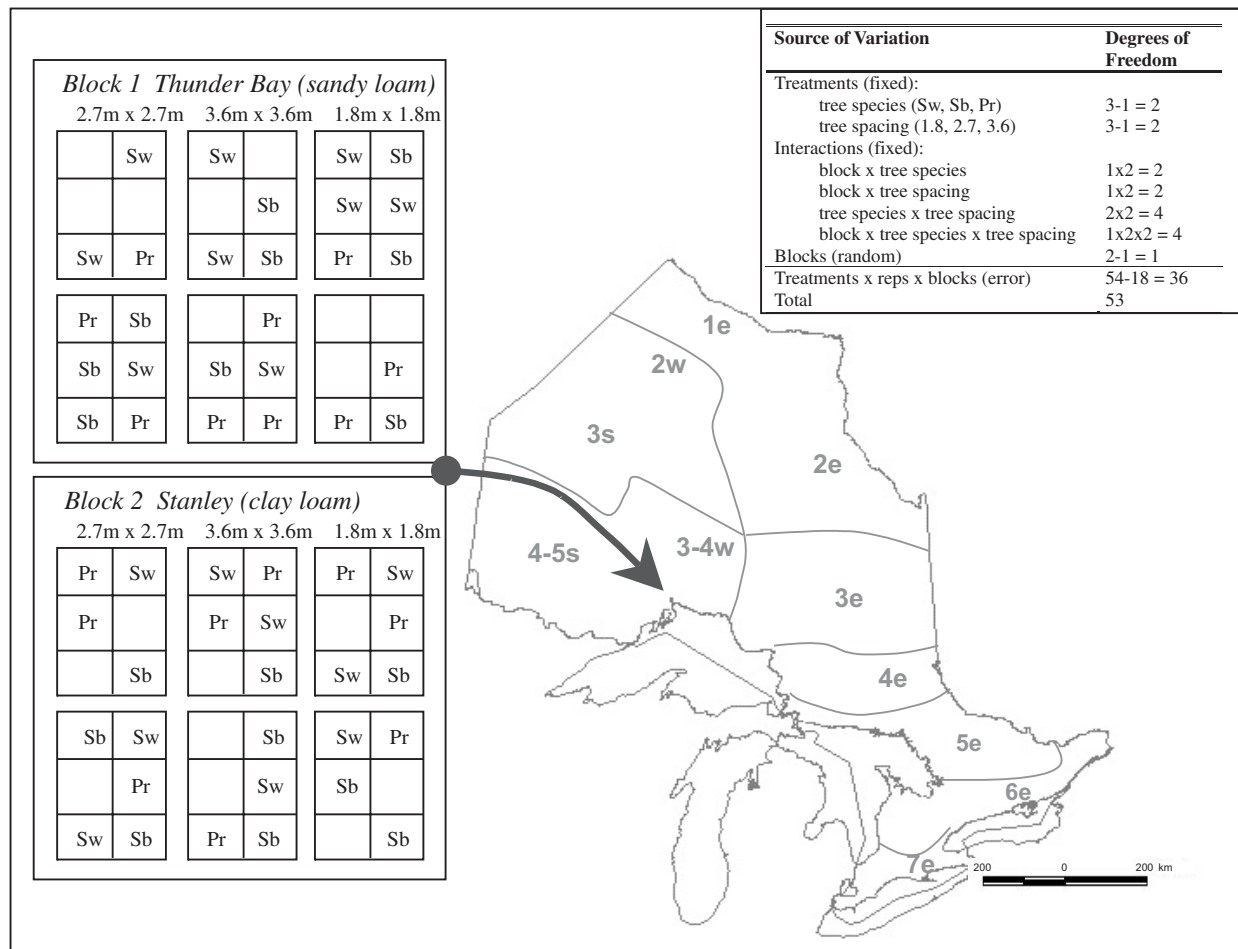
The aforementioned claims are largely based on qualitative evidence, as there is a lack of scientific literature on the topic of plantation biodiversity. Surprisingly, plantations offer refuge to more than just a handful of species. Research in red pine (*Pinus resinosa* Ait.) plantations recorded 113 understory plant species, of which 75% are native species (Parker et al. 2001). Many research projects have recorded higher herb diversity in plantations than in natural forests during the first few years following establishment (Schoonmaker and McKee 1988; Roberts 2002). Furthermore, young plantations are richer than old plantations (Nieppola 1992; Hannerz and Hånell 1997; Nagaike et al. 2003), and plantations with higher levels of disturbance support higher richness than do undisturbed plantations (Thomas et al. 1999). Many of the colonizing herbs following forest management treatments are ruderal or weedy species, defined here as invasive alien species (IAS), common to agricultural systems (Halpern and Spies 1995; Miller et al. 1995; Roberts and Zhu 2002). A comprehensive survey of invasive alien plants across Ontario presents empirical data to support the claim that there are more IAS in plantations (12%–25% IAS) than in native forests (1%–3% IAS) (Newmaster et al. 2005b). Research also exists to support the claim that IAS may displace or reduce populations of native species, significantly impeding the goal of conserving native biodiversity (Hobbs and Huenneke 1992; Hannerz and Hånell 1993). Forest management is responsible for the loss or reduced abundance of some native species due to distur-

bance of the forest floor (Martin 1988) and changes in microclimate (Hungerford and Babbitt 1987; McInnis and Roberts 1995). However, these claims have not been tested within plantations and need to be quantified with repeated measures with respect to changes in community measures of diversity over time.

Although plantation biodiversity may sound like somewhat of an oxymoron, it is an area studied by restoration ecologists. There is currently great interest in managing the succession of plantations to accelerate their conversion to more natural forest types (Parker et al. 2001). Tree monocultures may be used for restoration of native forests on degraded land, an apparent paradox (Lugo 1997; Oberhauser 1997) that comes as a trade-off between species diversity and the gross stem volume of a particular species (Jobidon et al. 2004). The identity of the dominant canopy species may be of less importance than stand age and site factors (Geldenhuys 1997; Brockerhoff et al. 2003). Many approaches focus on the restoration of planted tree species composition and structure, with the expectation that other components (i.e., taxonomic diversity) of biodiversity will follow (Allen et al. 2002; Schuler et al. 2002; Vallauri et al. 2002). Extending rotation age in plantations allows significant "old-growth" habitats and forest structure to be created that may foster species diversity (Fleming and Freedman 1998; Cameron 2002). Silvicultural techniques, such as thinning in conifer plantations, is often associated with increased diversity and abundance of understory flora (Bender et al. 1997; Dickmann et al. 1987; Thysell and Carey 2000). Parker et al. (2001) found that in older pine plantations, thinning and natural disturbances that opened the canopy encouraged the development of an understory of native forest species. Recent studies have just started to look at the dynamic interactions between planted trees and the ground vegetation within large experimental field trials manipulating factors such as tree spacing and fertilization that are known to impact vegetation (Otsamo 2002). These studies have been set up to manipulate several variables that are characteristic to monocultures; namely the tree species, spacing, and site conditions (often soil type) (McClain et al. 1994; Pearson et al. 1995). The development of such studies require long-term planning, as the plantations would need a researcher's lifetime to mature (80–100 years). It is necessary to test which characteristics of monocultures have an impact on biodiversity to support or refute the general claims made earlier.

The objective of this paper is to investigate to what degree and why monocultures (plantations) have considerably less diversity than native forests (fire origin). This study is designed to contrast the number of plant species present and their relative abundance within plantations having different indigenous tree species, spacings, and soil types. More specifically, species diversity (alpha (α) diversity, gamma (γ) diversity, beta (β) diversity) and abundance are assessed among (1) plantation blocks based on soil type (sandy loam and clay loam sites), (2) tree species (red pine (*Pinus resinosa* Ait.), black spruce (*Picea mariana* (Mill.) BSP), and white spruce (*Picea glauca* (Moench) Voss)), (3) tree spacings (1.8, 2.7, and 3.6 m), (4) tree species, spacing, and soils (block) interactions, and (5) temporal changes followed over 10 years. We hypothesize that plantations lack the diversity

Fig. 1. Experimental design and location of the research site with reference to Ontario's native ecoelements. Pr, red pine; Sb, black spruce; Sw, white spruce.



in the floristic habitats needed to support a rich flora because of the effects of forest management practices that favour increased timber harvest. To test this hypothesis, we compared these plantations to natural forests in the context of merchantable timber and floristic diversity (richness: α , γ , and β diversity). We discuss the results of this research in the context of whether plantation operations (1) result in single-layered species monocultures, (2) provide opportunities for the establishment of IAS, or (3) lead to the loss of indigenous plant species.

Materials and methods

Field site

The study sites are located within 20 km of Thunder Bay, Ontario, Canada (48°22'N, 89°23'W) (McClain et al. 1994) (Fig. 1). Two 8 ha spacing trials were established in 1950 by the research branch of the Ontario Ministry of Natural Resources (OMNR). The Thunder Bay Spacing Trial (block 1), located at the Northwest Science and Technology office (OMNR), is dominated by well-drained sandy loam soils. The Stanley Spacing Trial (block 2), located in Stanley Township (10 km west of block 1), is dominated by poorly drained clay loam soils. Both trials were established on abandoned farmland (old fields) and contained plantings of

red pine, black spruce, and white spruce established at three initial spacings (1.8, 2.7, and 3.6 m), based on a range of silvicultural standards used in forest management. The adjacent plant communities at both trials are old abandoned farm fields dominated by colonizing grasses (*Phalaris arundinacea* L., *Agrostis* spp., and *Calamagrostis canadensis* (Michx.) P. Beauv.), perennial herbs (*Hieracium* spp., *Taraxacum officinale* G. Weber, *Aster* spp., *Solidago* spp., and *Achillea millefolium* L.), and colonizing cryptogams (*Ceratodon purpureus* (Hedw.) Brid., *Brachythecium oxycladon* (Brid.) Jaeg., *Bryum* spp., *Marchantia polymorpha* L., and *Equisetum arvense* L.). Twenty-four environmental variables were measured at every plot: stand age, gross stem volume, light (photosynthetic photon flux density), crown closure, litter-fabric depth, conifer litter, broadleaf litter, soil cover, soil type, moisture regime, rock cover, coarse woody debris, shrub cover, herb cover, moss cover, elevation, slope position, aspect, latitude, longitude, degree-days, rainfall, mean annual temperature, and the number of microhabitats. Three diversity measures were derived from variables measured at each plot: α , β , and γ diversity.

Both sites were used for agricultural purposes prior to the establishment of the spacing trial. The surrounding forests are botanically diverse, bordering both the Great Lakes – St. Lawrence and Boreal forest regions.

Treatments and experimental design

The project uses a randomized complete block design with two blocks (8 ha each with three replicates of 2.67 ha) and the following treatments (Fig. 1): (1) three plantation tree species (Pr, red pine; Sb, black spruce; Sw, white spruce), (2) three plantation tree spacings (1.8, 2.7, and 3.6 m), and (3) two plantation blocks based on soil type (sandy loam and clay loam sites). Three replicates for each tree species (Pr, Sb, and Sw) per spacing regime (1.8, 2.7, and 3.6 m) were included in the trial. This resulted in 27 (9 treatments \times 3 replicates) treatment plots in block 1 (Thunder Bay trial) and 24 treatment plots in block 2 (Stanley trial). Unfortunately, the black spruce 3.6 m spacing treatments were harvested from the Stanley site before plant diversity and abundance was recorded (loss of three plots).

Subplot layout and data collection

Subplots were established for collecting vegetation data to determine plant diversity and abundance. Six 10 m \times 10 m (100 m²) subplots were established in each of the 51 treatment plots on the 2 blocks (306 plots). Species–area curves were plotted to check that this was an appropriate number of subplots to capture the treatment diversity. Subplots were randomly selected from all possible locations within the treatment plots that met the following predetermined criteria: (1) located >10 m away from other active experiment stations, pathways, and treatment boundaries and (2) representative of the surrounding vegetation community (species composition and physiognomy).

Environmental data were collected in the treatment subplots. In each treatment plot all tree diameters and heights were measured at a stand age of 46 years (1996). Site variables collected for each subplot include the ground cover (ocular estimate to the nearest 5%) for soil exposure (mineral and humus), moss, coarse woody debris, rocks, and broadleaf and needle litter.

Botanical surveys were conducted in late summer 1995 and 2004. Each of the plant species identified was given a percent cover estimate (ocular estimate) within the gridded 10 m \times 10 m subplot. Common bryophytes and lichens were identified in the field, but many specimens were collected as vouchers for laboratory identifications. A pre-project survey was conducted on all types of microhabitats (FHS methodology; see Newmaster et al. 2005a) in the entire research area to establish a base-line species list for the project. This list was used to reference species by microhabitat and was very helpful with field identifications and collections. This list also provided a means for evaluating the efficacy of the 306 sample plots (51 treatments and 6 subplots) in representing the project species richness and abundance. Exotic status of individual plants, species nomenclature, and coding follow *Ontario Flora* (Newmaster and Ragupathy 2005; Newmaster et al. 1998). Voucher specimens are deposited in the Ontario Forest Research Institute herbarium in Sault Ste. Marie, Ontario.

Forest ecosystem classification data

Forest ecosystem classification (FEC) data were provided by the Ecological Land Classification Program.² Methodol-

ogies for data collection, including site descriptions (V-type and ecoelement), are directly compared with those used in our study (Racey et al. 1996; Sims et al. 1989, 1997). A random set ($n = 410$ from a pool of 500) of FEC ecoelements (V-types) was measured and recorded for comparison with the plantation species (Pr, Sb, and Sw) at either end of the wet–dry site gradient (sandy vs. clay soils). The stands' ages ranged between 50 and 70 years. The following V-types were included in the FEC data set: V27 and V13 (Pr); V33, V19, and V35 (Sb); V15 and V24 (Sw). A data set of 410 FEC plots was used to compare and contrast species diversity between native forest ecoelements and our respective plantation treatments. The FEC plot size and sampling protocols are identical to that used in our plantation surveys. Furthermore, our crews were involved in the natural forest FEC data collection.

Diversity analysis

Species richness (γ and α diversity) was used to compare changes in stand diversity within the spacing and species treatments and between plantations and their corresponding ecoelements (natural forest types). Whittaker's (1965) terminology and concepts are used to describe diversity at different scales. Inventory diversity is simply species richness and is defined as either total richness (γ diversity) or mean stand richness (mean α diversity). In the present study, γ diversity is the total number of species within a plantation treatment (i.e., three tree species and three spacings) and within the corresponding native forest ecoelements for northwestern Ontario. Mean stand species richness, or α diversity, is the mean number of species within a stand for either the plantation treatments or native forest ecoelements. Beta diversity (species turnover) was also evaluated within plantation treatments and native forest ecoelements. Beta diversity was calculated directly using Whittaker's (1965) β diversity measure (eq. 1). Furthermore, species turnover between all stands was compared in our multivariate analysis (see next section).

$$[1] \quad \beta_w = \left(\frac{\gamma}{\alpha} \right)^{-1}$$

where γ is gamma diversity (total species richness per age-class) and α is alpha diversity (mean species richness per stand).

Biometric statistical analysis

Species richness (Fisher et al. 1942; McIntosh 1967) has the statistical weakness of a potentially large sampling bias, in that rare species often will be absent even in large samples or exhaustive surveys (Lande 1996). However, it is the oldest and most fundamental and widely used concept of diversity and is thus adopted in our research (Pielou 1966; Peet 1974). Species richness and abundance were calculated for each of the nine treatment areas (each with three replicates) in both blocks within three life forms (woody plants, herbs including forbs, and cryptogams). Richness and abundance were analyzed using analysis of variance (ANOVA) and least significant difference (LSD) tests across the two blocks, nine treatments, and three replicates, with a model

²Ecological Land Classification Program, Ontario Forest Research Institute, Ontario Ministry of Natural Resources.

Table 1. Summary of analysis of variance results (*p* values) for species richness and abundance.

| Source or contrast | Richness | | | Abundance | | |
|-------------------------------------|----------|--------|------------|-----------|--------|------------|
| | Woody | Herbs | Cryptogams | Woody | Herbs | Cryptogams |
| Block | 0.638 | 0.966 | 0.914 | 0.950 | 0.666 | 0.633 |
| Tree species | 0.241 | 0.402 | <0.001 | 0.953 | 0.614 | <0.001 |
| Spacing | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| Block vs. tree species | 0.722 | 0.959 | 0.746 | 0.715 | 0.913 | 0.500 |
| Block vs. spacing | 0.967 | 0.976 | 0.978 | 0.947 | 0.834 | 0.873 |
| Tree species vs. spacing | 0.768 | 0.697 | 0.872 | 0.633 | 0.734 | <0.001 |
| Block vs. tree species plus spacing | 0.967 | 0.978 | 0.976 | 0.805 | 0.947 | 0.297 |

appropriate for a randomized complete block design. A priori comparisons were made between treatments for each block in a full factorial design including treatment contrasts. Restrictions for ANOVA (Zar 1984) were met and the analyses were run in SPSS 9.0 (1999). In all cases, model residuals were examined to verify that the assumptions of homogeneity of variance and normality were met. In these analyses, planned comparisons of species richness and abundance, that is, (1) plantation blocks based on soil type (sandy loam and clay loam sites), (2) tree species (red pine, black spruce, and white spruce), (3) tree spacing (1.8, 2.7, and 3.6 m) and (4) tree species, spacing, and soils (block) contrasts, were used to answer specific questions posed in the study objectives. Richness and abundance of plant life forms and three feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*) were quantified over time (1995–2004) using repeated measures ANOVA (RMANOVA). Orthogonal polynomial response functions were fit to the repeated measures of each experimental unit and the estimated coefficients (mean, linear, quadratic) used as primary data in the underlying ANOVA structure (Meredith and Stehman 1991). Sources of variation in richness and abundance were considered as being an interaction term with time. An LSD test was used to identify significant differences among treatments over time (Pitt et al. 2000).

Multivariate ordination analysis

A multivariate analysis was used to compare the species data for the six site preparation treatments and their respective native forest ecoelements. The relationship of community structure in the species data to the major environmental gradients was analyzed with nonmetric multidimensional scaling (NMS; Kruskal 1964; McCune and Mefford 1997). In NMS, the Bray Curtis distance measure was used because of its robustness for both large and small ecological gradients (Minchin 1987). Data were standardized by species maxima. Two-dimensional solutions were appropriately chosen based on plotting a measure of fit ("stress") to the number of dimensions. One hundred iterations were used for each NMS run, using random start coordinates. The first two ordination axes were rotated to enhance interpretability with the environmental gradients. Beta diversity is a measure of heterogeneity in the species plot data and is expressed as a 50% change in species composition (half change) on the NMS ordinations. The 27 environmental variables measured were used to constrain the ordination. These variables were considered for all plantations and native stands together and then with plantations and native forests independently of one

another. Pearson correlations (*r*) and *p* values were calculated for all environmental variables.

Plantations versus native forests

FEC data from northwestern Ontario were compared with the plantation treatment data from both the Thunder Bay and Stanley spacing trials. Environmental variables were recorded from both spacing trials and compared with the FEC data. Mean gross stem volume (m³/ha) and mean ground cover (mineral soil, humus, broadleaf litter, conifer litter, coarse woody debris, rock, moss) were calculated for each plantation treatment and native forest ecoelement. Mean richness and abundance including standard errors (SE) were calculated for all treatments, blocks, and ecoelement for each group of plants (woody plants, herbs, and cryptogams). Species turnover was compared between plantations and native forests using β diversity calculations and ordination techniques as described in our analysis methodologies previously. A list of species including their abundance for each plantation treatment and native forest ecoelement was used to compare the groups of species associated with either plantations or native forests.

Results

Plantation soil type

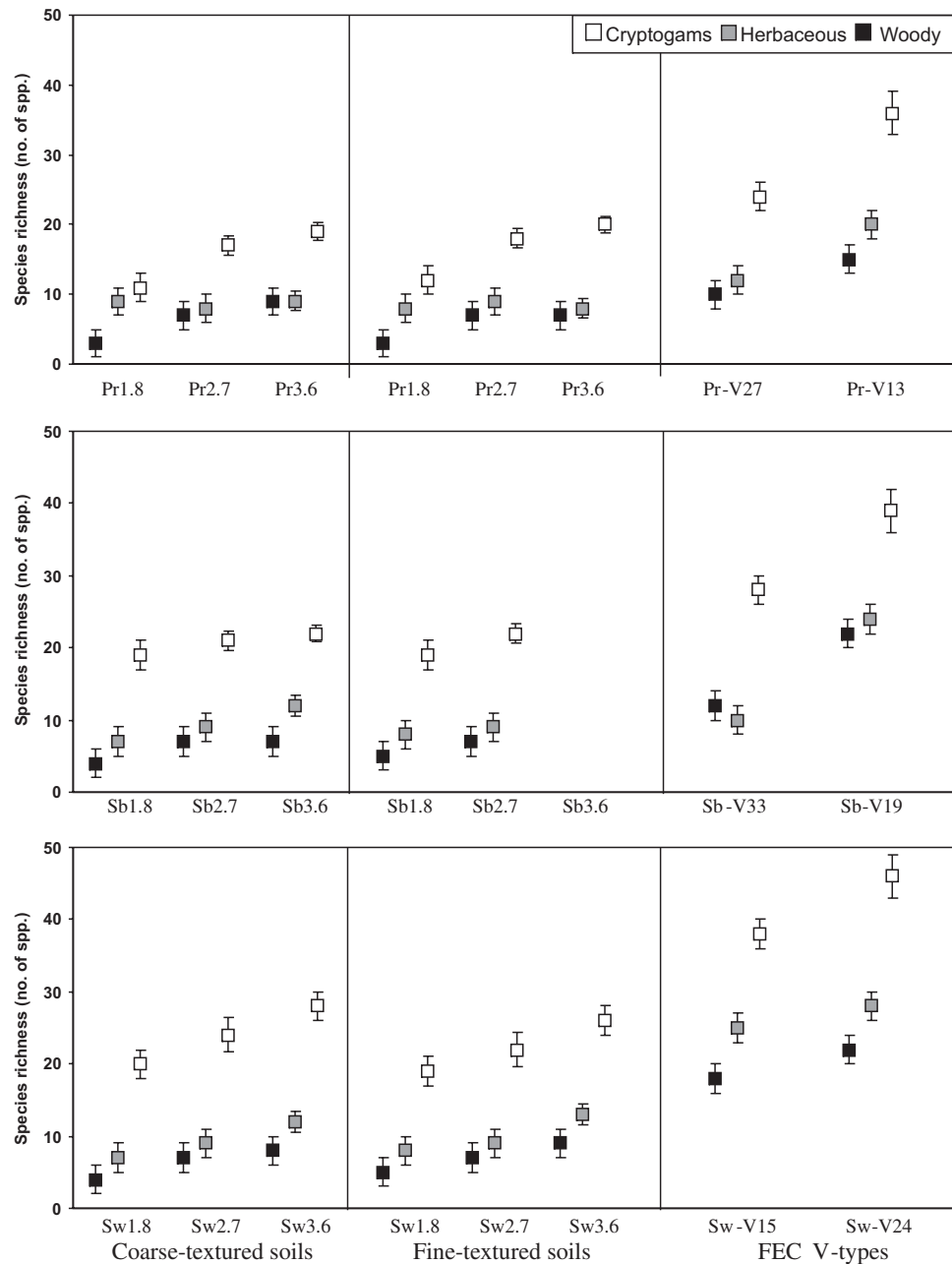
Plantation diversity was similar for research sites on fine- and coarse-textured soils. Sandy loam soils characterized the soil profile in the Thunder Bay spacing trial (block 1); the Stanley spacing trial (block 2) was dominated by clay loam soils. Species richness and abundance for woody species, herbs, and cryptogams were not significantly different (*p* > 0.633) between the blocks (Table 1; Fig. 2).

Plantation tree species

Phanerogam diversity

Phanerogam diversity was similar between the different plantation tree species: red pine, black spruce, and white spruce. Herbaceous and woody mean species abundance and richness were not significantly different (*p* = 0.241) for each of the plantation tree species (Table 2). Woody species abundance (71%–73% cover) was high and species richness (3–9 species) was low (Figs. 2 and 3). Herb species richness was slightly higher (8–12 species), but abundance (3%–4% cover) was low.

Fig. 2. Mean richness for plantations and native forest ecoelements. The values 1.8, 2.7, and 3.6 indicate the spacing in metres. Pr, red pine; Sb, black spruce; Sw, white spruce.



Cryptogam species diversity

Cryptogam diversity differed between the three plantation tree species (Table 1). Mean species richness was significantly higher ($p < 0.001$) in spruce (22 ± 4 species; mean \pm SE) than in red pine (14 ± 3 species) plantation plots (Table 2; Fig. 2). Species richness was not significantly different ($p = 0.841$) between black spruce (21 ± 3 species) and white spruce (23 ± 3 species) plantation plots. Species abundance was significantly different ($p < 0.001$) between the plantation tree species (Table 1). Cryptogam abundance was lowest (22 ± 18 species) in red pine plots and highest in the black spruce (49 ± 31 species) and white spruce (52 ± 34 species) plots. There was no significant difference ($p = 0.632$) in species abundance between black spruce and white spruce plantation plots (Table 3).

Plantation tree spacings

Woody species diversity

Woody species diversity differed among the three tree spacings (1.8, 2.7, and 3.6 m) in the plantation. Species richness and abundance was significantly different ($p < 0.001$) among different tree spacings (Table 1). Species richness at the 1.8 m spacing was lower (3 ± 1 species) than species richness at the wider spacing (7 ± 2 species) (Table 3; Fig. 2). Richness between 2.7 and 3.6 m spacing plots was not significantly different ($p = 0.079$). Species abundance was significantly ($p < 0.001$) different among each of the plantation spacings (Table 3). Woody abundance was $81\% \pm 3\%$ at 1.8 m spacing, but decreased to $72\% \pm 5\%$ at 2.7 m spacing and $65\% \pm 3\%$ at 3.6 m spacing (Table 3; Fig. 3).

Table 2. Comparisons of mean species richness and abundance including post hoc test (least significant difference (LSD) test) between forest tree species.

| Group | Tree species | Richness | | | Abundance | | |
|------------|--------------|-----------|----------|--------|-----------|----------|--------|
| | | Mean | LSD test | | Mean | LSD test | |
| | | | Sb | Sw | | Sb | Sw |
| Woody | Pr | 4 | 0.171 | 0.425 | 71 | 0.172 | 0.897 |
| | Sb | 5 | — | 0.112 | 73 | — | 0.137 |
| | Sw | 6 | — | — | 72 | — | — |
| Herbs | Pr | 8 | 0.933 | 0.208 | 3 | 0.895 | 0.672 |
| | Sb | 9 | — | 0.262 | 3 | — | 0.335 |
| | Sw | 9 | — | — | 4 | — | — |
| Cryptogams | Pr | 14 | <0.001 | <0.001 | 22 | <0.001 | <0.001 |
| | Sb | 21 | — | 0.841 | 49 | — | 0.632 |
| | Sw | 23 | — | — | 52 | — | — |

Note: Means in bold are significantly different ($p < 0.05$). Pr, red pine; Sb, black spruce; Sw, white spruce.

Table 3. Comparisons of mean species richness and abundance including post hoc test (least significant difference (LSD) test) between three tree spacings.

| Group | Spacing (m) | Richness | | | Abundance | | |
|------------|-------------|-----------|----------|--------------|-----------|----------|--------------|
| | | Mean | LSD test | | Mean | LSD test | |
| | | | 2.7 m | 3.6 m | | 2.7 m | 3.6 m |
| Woody | 1.8 | 3 | 0.022 | 0.022 | 81 | 0.031 | 0.011 |
| | 2.7 | 7 | — | 0.879 | 72 | — | 0.028 |
| | 3.6 | 7 | — | — | 65 | — | — |
| Herbs | 1.8 | 8 | 0.061 | 0.021 | 3 | 0.869 | 0.014 |
| | 2.7 | 10 | — | 0.073 | 4 | — | 0.023 |
| | 3.6 | 12 | — | — | 9 | — | — |
| Cryptogams | 1.8 | 16 | 0.010 | 0.007 | 11 | <0.001 | <0.001 |
| | 2.7 | 23 | — | 0.201 | 51 | — | 0.061 |
| | 3.6 | 24 | — | — | 58 | — | — |

Note: Means in bold are significantly different ($p < 0.05$).

Herb species diversity

Herbaceous species diversity differed among the tree spacings. Species richness was significantly lower ($p = 0.021$) at closer spacing (1.8 m: 8 ± 2 species) than at wider spacing (3.6 m: 12 ± 2 species) (Table 3; Fig. 2). Species abundance was also significantly different ($p < 0.001$) among the plantation spacing (Table 1). Herb abundance was higher ($9\% \pm 2\%$ cover) at the wider spacing (3.6 m) than at either the 1.8 m ($3\% \pm 1\%$ cover) or 2.7 m ($4\% \pm 1\%$ cover) spacing (Table 3; Fig. 3).

Cryptogam species diversity

Cryptogam diversity was different among the three-tree spacings. Species richness was significantly lower ($p < 0.001$) at the 1.8 m spacing (16 ± 4 species) than at either the 2.7 m (23 ± 3 species) or 3.6 m (24 ± 3 species) spacing (Table 3; Fig. 2). Species abundance was significantly different ($p < 0.001$) among the tree spacings (Table 3). Cryptogam abundance was $15\% \pm 8\%$ cover at 1.8 m spacing, but increased dramatically to $52\% \pm 26\%$ at 2.7 m spacing and $56\% \pm 28\%$ at 3.6 m spacing (Table 3; Fig. 3).

Tree species, spacing, and soils interactions

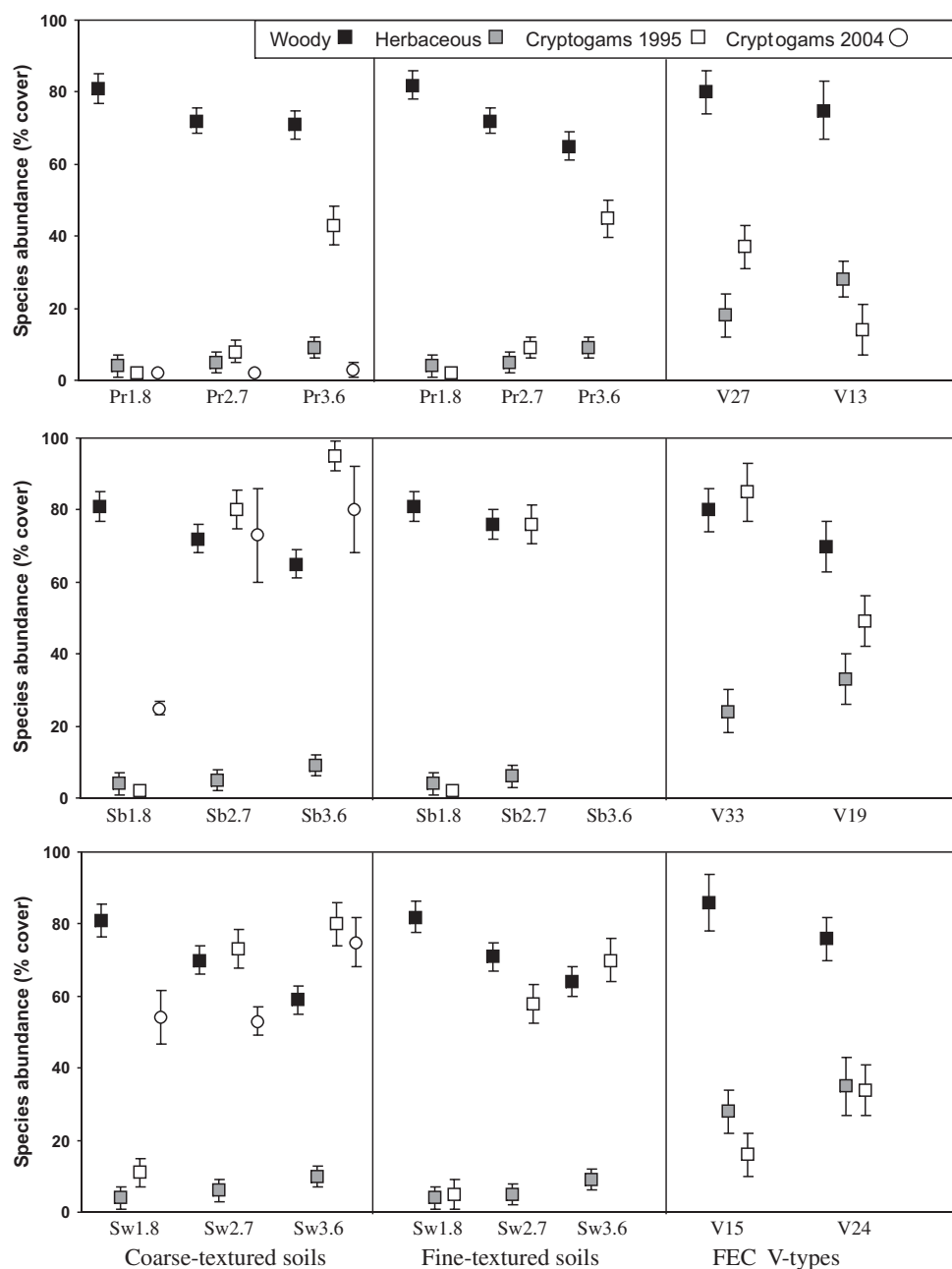
Interactions between tree species, spacing, and soils were

tested for both species richness and abundance. Soil type had no influence on richness or abundance interactions with tree spacing or tree species. There were no significant ($p > 0.697$) species richness interactions between tree species and spacing (Table 1). Furthermore, there were no species abundance interactions for the phanerogams. However, there were significant abundance interactions between species and spacing for the cryptogams (Table 1). This interaction can be explained by the differential increase in cryptogam abundance with spacing for red pine and spruce (Fig. 3). Abundance of cryptogams in red pine plots increased with spacing from 4% cover (1.8 m), to 18% cover (2.7 m), to 38% (3.6 m). Abundance increased much more quickly in spruce (black or white) with spacing from 20% cover (1.8 m), to 65% (2.7 m), to 82% (3.6 m) (Fig. 3).

Temporal patterns

Patterns in diversity were evident within a 10-year window where detailed community data were collected. Phanerogam diversity did not change ($p > 0.441$) with time (10 years). Cryptogam richness did not change significantly ($p > 0.191$), but abundance did change, particularly in red pine plots, where cryptogam abundance dropped significantly ($p < 0.022$) to almost zero (Fig. 3). Mean cryptogam

Fig. 3. Mean abundance for plantations and native forest ecoelements. The values 1.8, 2.7, and 3.6 indicate the spacing in metres. Pr, red pine; Sb, black spruce; Sw, white spruce.



abundance did not change in spruce plots; however, there were changes in the cover of feathermoss. In all plots, feathermoss (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*) accounts for over 95% of the total cryptogam abundance. Patterns among the species and spacings are quite striking, and the temporal aspect provides further evidence to define the dynamic nature of these feathermoss communities. First, it is evident that all plantation plots were dominated by *Pleurozium schreberi* (Fig. 4). However, the cover of *Pleurozium schreberi* dropped significantly ($p < 0.034$) over 10 years. During this time abundance increased significantly ($p < 0.031$) for both *Hylocomium splendens* and *Ptilium crista-castrensis* in all the spruce stands. Regardless of time, all species increased

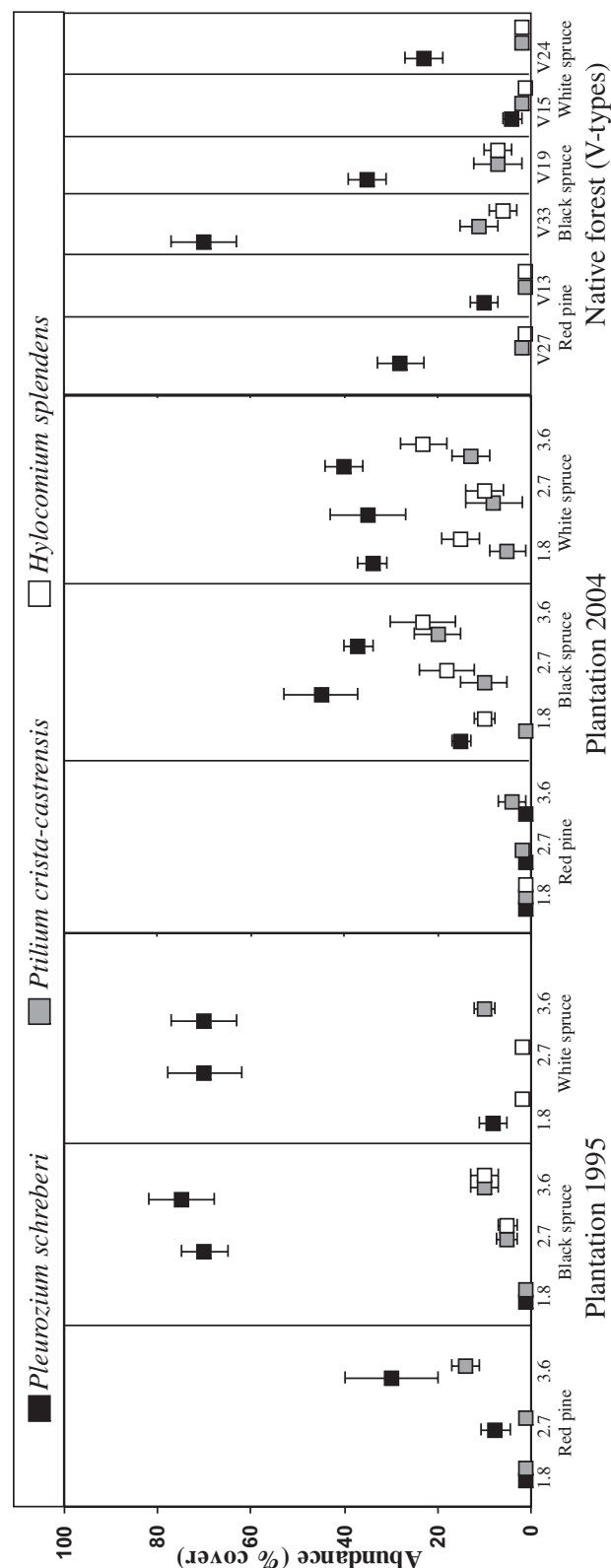
significantly ($p < 0.04$) in cover from the narrowest (1.8 m) to the widest (3.6 m) spacing.

Plantations versus natural forests

Merchantable timber

Gross stem volume (m^3/ha) is higher in plantations than in the respective native ecoelement. Red pine plantations have higher gross total stem volumes ($645 \text{ m}^3/\text{ha}$) at close spacing (1.8 m) than native red pine forest ($V13 = 388 \text{ m}^3/\text{ha}$; $V27 = 638 \text{ m}^3/\text{ha}$). Volumes in black spruce plantations also increase with closer spacing. At 1.8 m spacing, black spruce plantations have higher volumes ($296 \text{ m}^3/\text{ha}$) than native black spruce ecoelements ($V35 = 246 \text{ m}^3/\text{ha}$). Similarly, vol-

Fig. 4. Abundance of the three most dominant mosses in plantations and relevant native forests. The values 1.8, 2.7, and 3.6 indicate the spacing in metres.



umes in native white spruce forest (V15 = 268 m³/ha) are lower than those in white spruce plantations at 1.8 m spacing (332 m³/ha).

Species abundance

Comparisons of abundance suggest some differences between native forests and plantations. Woody species in plantations regardless of spacing have similar abundance to that of native forests. However, herbs have higher abundance in native forests than in plantations with wide or narrow spacing (Fig. 3). Red pine plantations have similar cryptogam abundance to that of native forest. Black spruce plantations with spacing >2.7 m have similar abundance to that of native black spruce ecoelements (Fig. 3). White spruce plantations have higher cryptogam abundance at wide spacing (>2.7 m) than do native white spruce forests (Figs. 3 and 4).

Species richness

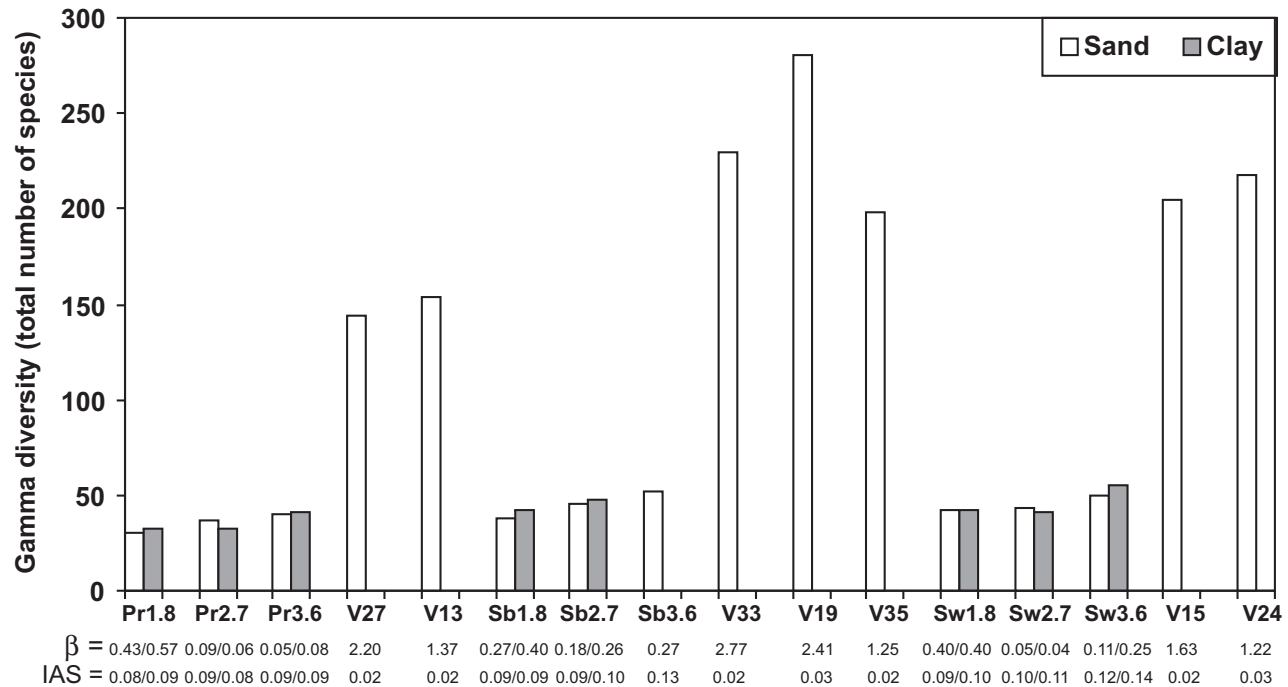
Native forests have much higher α (mean richness) and γ (total richness) diversity than plantations. At the widest spacing, red pine plantations have fewer cryptogams, herbs, and woody plants than do their native ecoelements (i.e., V27 and V13) (Fig. 2). Gamma diversity is higher (150 species) in the native red pine forest when compared to red pine plantations (<50 species) (Fig. 5). Black spruce plantations also have lower mean richness (α diversity) in the research plots when compared to black spruce ecoelements (Fig. 2). Gamma diversity is much higher (>250 species) in native black spruce forest than in its plantation counterpart (<50 species). Alpha diversity is higher in native white spruce forest than in white spruce plantations. This is quite evident in the cryptogams (Fig. 1). The total number of species (γ diversity) is much lower in white spruce plantations than in native white spruce forest (<50 species vs. >200 species) (Fig. 5).

Beta diversity

Beta diversity within plantations is low when compared to the species turnover within native forests. Within a plantation, β diversity drops with an increase in spacing (Fig. 5). All plantations had higher β diversity at closer spacing ($\beta = 0.27$ – 0.57) than at wider spacing ($\beta = 0.04$ – 0.26). Beta diversity was much higher in the native forests ($\beta = 1.22$ – 2.77) than within the plantations ($\beta = 0.04$ – 0.57). In native forests, β diversity decreased within each pair of V-types (i.e., red pine, white spruce, and black spruce) (Fig. 5). In red pine stands, β diversity is lower in the drier V27 ecoelement than in the V13 ecoelement. This pattern is similar for both white spruce and black spruce (Fig. 5).

Species turnover was observed in the NMS ordinations of plantations and native ecoelements. Plantations are arranged on the left side of the ordination and native forests on the right (Fig. 6). Habitat diversity was most strongly positively correlated ($r = 0.843$; $p < 0.001$) with the x -axis, as were other physiographic variables such as increasing rock cover and coarse woody debris cover (Table 4). Plant diversity, including shrub–herb–moss cover and α and γ diversity, also increased with these physiographic variables. The increasing cover of soil and broadleaf or needle cover was negatively correlated with the x -axis. Red pine plantations and ecoelements are arranged near the top of the ordination. White

Fig. 5. Gamma diversity (total number of species), beta diversity (β , species turnover), and the percentage of invasive alien plants (IAS) for plantations and ecoelements in northwestern Ontario. The values 1.8, 2.7, and 3.6 indicate the spacing in metres. Pr, red pine; Sb, black spruce; Sw, white spruce.



spruce plantations and ecoelements are grouped in the middle, while black spruce plantations and ecoelements are found at the bottom of the ordination (Fig. 6). Litter depth was most strongly positively correlated ($r = 0.838$; $p < 0.001$) with the y-axis. Related variables that also strongly correlated with the x-axis include gross stem volume, canopy light, and crown closure (negative correlation, see Table 4). Moss cover was negatively correlated with the y-axis. Plantations with wide spacing (3.6 m) are the most similar to the native forests. This is true for red pine, white spruce, and black spruce plantations and forests. Plantations with close spacing (1.8 m) are quite different. Red pine plantations with 1.8 m spacing share less than one-quarter of the species found in native red pine forests (Fig. 6). White spruce and black spruce plantations at 1.8 m spacing share less than half of the species found in native spruce forests (Fig. 6). The environmental variables constraining the ordination of just the native forests were also dominated by diverse physiognomy on the x-axis and litter depth along the y-axis (Table 4).

Environmental gradients (bi-plot correlations) were also considered for the plantations and the native forests. The native forest bi-plots were no different when considering all the native forests and plantation plots together, as described previously. However, in the plantation bi-plots, sunlight (photosynthetic photon flux density) was most strongly positively correlated with the x-axis ($r = 0.6754$; $p < 0.001$), and crown closure was strongly negatively correlated ($r = -0.674$; $p < 0.001$). Plant diversity, including shrub–herb–moss cover and α , β , and γ diversity, was also positively correlated with the x-axis. Litter depth ($r = 0.975$; $p < 0.001$) and conifer litter cover ($r = 0.842$; $p < 0.001$) were most strongly positively correlated with the y-axis. Soil cover was negatively correlated with the y-axis ($r = -0.922$; $p < 0.001$).

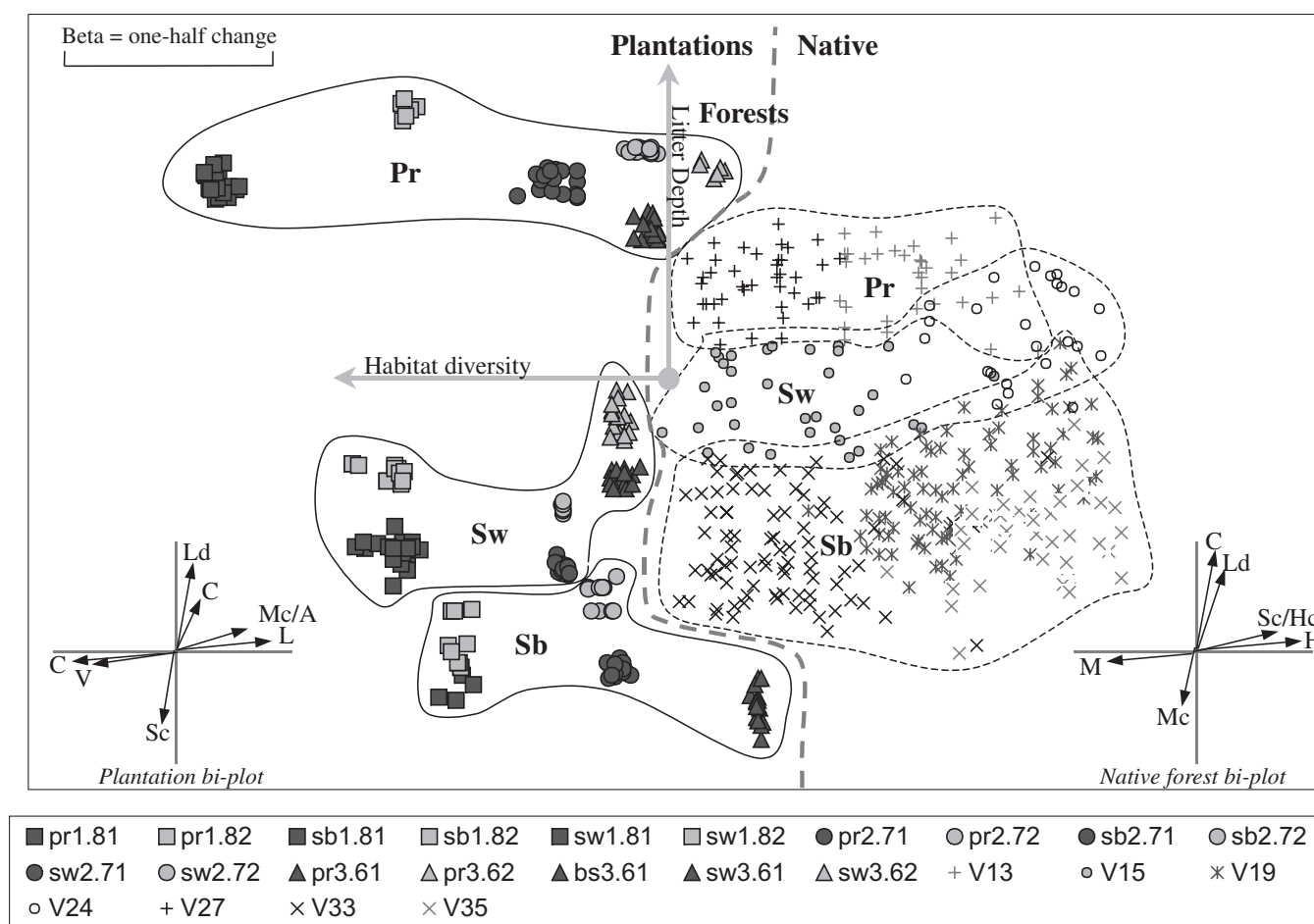
Plant diversity, including shrub–herb–moss cover and α , β , and γ diversity, was negatively correlated with the y-axis (Table 4).

Community composition

Plantations have a different community of species than do their respective native forest ecoelements. Native forests have a layered canopy consisting of several tree species (i.e., V15 = *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb., and *Acer rubrum* L.). The plantations in our study were single-species monocultures (i.e., red pine, black spruce, or white spruce). Few shrubs were found in the plantations, which is in sharp contrast to the diverse and abundant shrub layer found in the native forests (e.g., *Corylus cornuta* Marsh., *Acer spicatum* Lamb., *Lonicera canadensis* Bart., *Cornus stolonifera* Michx., and *Alnus viridis* (Chaix) DC. subsp. *crispa* (Ait.) Turr.).

The herb layer within the plantation consisted of only a few common forest species (e.g., *Maianthemum canadense* Desf., *Trientalis borealis* Raf. subsp. *borealis*, *Clintonia borealis* (Ait.) Raf., *Streptopus roseus* Michx., *Actaea pachypoda* Elliott, *Fragaria virginiana* Mill. subsp. *virginiana*, *Aster macrophyllus* L., and *Aralia nudicaulis* L.). Herbaceous exotics dominated the herb communities in the plantations (e.g., *Taraxacum officinale* G. Weber). The lack of herbaceous species in the plantations was the greatest contrast to the respective native forest ecoelements. The native forests contained many indigenous species that were not in the plantations (e.g., *Pyrola elliptica* Nutt., *Goodyera pubescens* (Willd.) R. Br., *Mertensia virginica* (L.) Pers. ex Link, *Goodyera tessellata* Lodd., *Coptis trifolia* (L.) Salisb.,

Fig. 6. Nonmetric multidimensional scaling ordination of 306 plantation and 410 forest ecoelement plots. Pr, red pine; Sb, black spruce; Sw, white spruce. See Table 4 for definition of symbols. (Note: The codes identify the tree species, spacing, and block (different soil types); e.g., pr1.81 means red pine at 1.8 m spacing on block 1 – sandy loam soils; pr1.82 means red pine at 1.8 m spacing on block 2 – poorly drained clay loam soils.)



Anemone quiquefolia L., *Melampyrum lineare* Desr., and *Orthilia secunda* (L.) House).

The cryptogam communities displayed the most striking contrasts between plantations and native forests. Feather-mosses, colonizing bryophytes, and lichens dominated the plantation cryptogam community (e.g., *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp. in B.S.G., *Polytrichum juniperinum* Hedw., *Polytrichum commune* Hedw., *Brachythecium oxycladon* (Brid.) Jaeger, *Ceratodon purpureus* (Hedw.) Brid., *Dicranum fuscescens* Turn., *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb., *Brachythecium salebrosum* (Webb & Mohr) Schimp. in B.S.G., *Cladonia coniocraea* (Korke) Spreng., and *Peltigera canina* (L.) Willd.). The most obvious contrast between the plantations and native forests was the lack of forest mesophytes (e.g., *Plagiommium cuspidatum* (Hedw.) T. Kop., *Gymnocarpium dryopteris* (L.) Newman, *Rhizomnium punctatum* (Hedw.) T. Kop., *Lycopodium clavatum* L., *Dryopteris expansa* (C. Presl.) Fraser-Jenk. & Jermy, *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Bazzania trilobata* (L.) Gray var. *trilobata*, and *Hypnum pratense* (Rabenh.) W. Koch ex Spruce), particularly those species associated with logs (*Lophozia*

longidens (Lindb.) Macoun, *Barbilophozia barbata* (Schmid. ex Schreb.) Loeske, *Calypogeja neesiana* (Massales & Carest.) K. Mull., *Dicranum montanum* Hedw., and *Hypnum pallescens* (Hedw.) P. Beauv.) and rocks (e.g., *Dicranum scoparium* Hedw., *Hedwigia ciliata* (Hedw.) P. Beauv., and *Polypodium virginianum* L.). Furthermore, the native forest had a diversity of pteridophytes, whereas the plantations had only a few weedy horsetails (e.g., *Equisetum arvense* L., *Equisetum hyemale* L. subsp. *affine* (Engelm.) Calder & Roy).

Discussion

Influence of plantation variables (soils, canopy species, and spacing) for restoring floral diversity in abandoned fields

There is great potential to develop forest restoration plans on abandoned farmland using several environmental variables: soils, canopy species, spacings, and microhabitats. Our research indicates that native plant diversity can be recovered in the most extreme forest management scenario, that is, agricultural cultivation followed by plantations with little variability in structure. In our study, we found that soil type (clay vs. sand) had no influence on plantation species

Table 4. Pearson correlations (*r*) and significance for 27 environmental variables used to constrain two nonmetric multidimensional scaling axes (*x* and *y*).

| Environmental variable | Symbol | Plantations | | | Native forests | | | Plantations and native forests | | | | | | | |
|-------------------------|--------|--------------|--------|--------------|----------------|--------|--------------|--------------------------------|--------------|--------|--------|--------------|--------|--------------|--------|
| | | x-axis | | y-axis | x-axis | | y-axis | x-axis | | y-axis | | | | | |
| | | r | p | r | p | r | P | r | p | r | p | | | | |
| Stand age | Ag | 0.029 | 0.657 | -0.056 | 0.382 | 0.672 | 0.023 | 0.672 | 0.061 | 0.100 | 0.061 | 0.603 | <0.001 | 0.003 | 0.935 |
| Gross stem volume | V | -0.624 | <0.001 | 0.845 | <0.001 | <0.001 | -0.390 | <0.001 | <0.001 | 0.655 | <0.001 | -0.461 | <0.001 | 0.737 | <0.001 |
| Light (PPFD) | L | 0.675 | <0.001 | 0.435 | <0.001 | <0.001 | -0.252 | <0.001 | <0.001 | 0.746 | <0.001 | -0.022 | 0.591 | 0.465 | <0.001 |
| Crown closure | C | -0.674 | <0.001 | -0.432 | <0.001 | <0.001 | 0.252 | <0.001 | <0.001 | -0.747 | <0.001 | -0.157 | 0.002 | -0.514 | <0.001 |
| Litter or fibric depth | Ld | -0.342 | <0.001 | 0.975 | <0.001 | <0.001 | -0.321 | <0.001 | <0.001 | 0.822 | <0.001 | -0.547 | <0.001 | 0.838 | <0.001 |
| Conifer litter | Cl | -0.669 | <0.001 | 0.842 | <0.001 | 0.035 | -0.112 | 0.035 | 0.879 | <0.001 | <0.001 | -0.775 | <0.001 | 0.372 | <0.001 |
| Broad leaf litter | Bl | 0.091 | 0.158 | -0.107 | 0.097 | 0.001 | 0.181 | 0.001 | 0.280 | 0.280 | <0.001 | 0.521 | <0.001 | 0.103 | 0.012 |
| Soil cover | Sc | 0.207 | 0.001 | -0.922 | <0.001 | <0.001 | -0.252 | <0.001 | <0.001 | 0.746 | <0.001 | -0.615 | <0.001 | -0.306 | <0.001 |
| Soil type | St | 0.073 | 0.257 | 0.094 | 0.143 | <0.001 | 0.582 | <0.001 | <0.001 | -0.163 | 0.002 | 0.437 | <0.001 | -0.049 | 0.235 |
| Moisture regime | M | -0.080 | 0.217 | -0.081 | 0.207 | <0.001 | -0.537 | <0.001 | <0.001 | 0.539 | <0.001 | -0.602 | <0.001 | 0.181 | 0.001 |
| Rock cover | Rc | 0.156 | 0.015 | -0.148 | 0.021 | 0.038 | 0.116 | 0.038 | 0.210 | 0.582 | <0.001 | 0.776 | <0.001 | -0.078 | 0.056 |
| Coarse woody debris | W | -0.066 | 0.309 | 0.001 | 0.993 | 0.001 | 0.183 | 0.001 | 0.585 | <0.001 | <0.001 | 0.688 | <0.001 | 0.149 | <0.001 |
| Habitat diversity | H | 0.085 | 0.188 | -0.015 | 0.813 | <0.001 | 0.665 | <0.001 | -0.045 | 0.395 | 0.395 | 0.843 | <0.001 | -0.049 | 0.232 |
| Alpha diversity | A | 0.632 | <0.001 | -0.415 | <0.001 | <0.001 | 0.422 | <0.001 | 0.156 | 0.003 | 0.003 | 0.778 | <0.001 | -0.079 | 0.055 |
| Beta diversity | B | 0.489 | <0.001 | -0.576 | <0.001 | <0.001 | -0.440 | <0.001 | -0.456 | <0.001 | <0.001 | 0.650 | <0.001 | -0.172 | 0.001 |
| Gamma diversity | G | 0.639 | <0.001 | -0.676 | <0.001 | <0.001 | 0.310 | <0.001 | -0.620 | <0.001 | <0.001 | 0.796 | <0.001 | -0.198 | 0.001 |
| Shrub cover | Sc | 0.469 | <0.001 | -0.279 | <0.001 | <0.001 | 0.631 | <0.001 | -0.226 | <0.001 | <0.001 | 0.791 | <0.001 | -0.180 | 0.002 |
| Herb cover | Hc | 0.461 | <0.001 | -0.280 | <0.001 | <0.001 | 0.626 | <0.001 | -0.069 | 0.195 | 0.195 | 0.650 | <0.001 | -0.109 | 0.008 |
| Moss cover | Mc | 0.672 | <0.001 | -0.767 | <0.001 | <0.001 | -0.095 | <0.001 | -0.770 | <0.001 | <0.001 | 0.488 | <0.001 | -0.425 | <0.001 |
| Elevation | Elv | -0.073 | 0.257 | -0.094 | 0.143 | 0.138 | -0.079 | 0.138 | 0.046 | 0.388 | 0.388 | 0.161 | <0.001 | -0.014 | 0.727 |
| Slope position | SP | 0.083 | 0.197 | 0.001 | 0.990 | 0.085 | 0.092 | 0.085 | -0.029 | 0.593 | 0.593 | 0.431 | <0.001 | -0.031 | 0.456 |
| Aspect | As | 0.066 | 0.309 | -0.009 | 0.885 | 0.349 | 0.050 | 0.349 | 0.060 | 0.264 | 0.264 | 0.480 | <0.001 | -0.007 | 0.856 |
| Latitude | Lt | 0.001 | 0.997 | 0.003 | 0.957 | 0.920 | -0.005 | 0.920 | 0.046 | 0.390 | 0.390 | 0.502 | <0.001 | -0.008 | 0.854 |
| Longitude | Ln | -0.132 | 0.041 | 0.127 | 0.049 | 0.067 | -0.098 | 0.067 | 0.066 | 0.216 | 0.216 | 0.629 | <0.001 | -0.014 | 0.730 |
| Degree-days | Dd | 0.098 | 0.127 | -0.095 | 0.141 | 0.180 | -0.071 | 0.180 | 0.035 | 0.507 | 0.507 | 0.072 | 0.079 | 0.013 | 0.751 |
| Rainfall | Rn | 0.152 | 0.018 | -0.141 | 0.028 | 0.411 | -0.044 | 0.411 | 0.107 | 0.044 | 0.044 | 0.422 | <0.001 | 0.025 | 0.544 |
| Mean annual temperature | Ta | -0.159 | 0.013 | 0.147 | 0.022 | <0.001 | -0.073 | <0.001 | 0.050 | 0.348 | 0.348 | -0.231 | <0.001 | 0.044 | 0.279 |

Note: PPFD, photosynthetic photon flux density.

Note: PPFD, photosynthetic photon flux density.

diversity or abundance, including interaction with canopy species type or spacing. This is surprising because many forest ecosystem classifications are built on predefined associations between soil characteristics (moisture and nutrient capacity) and vegetation types (Racey et al. 1996; Sims et al. 1997). However, we are not the first to show that soils are not driving mechanisms in experimental field studies where heterogeneity in physiognomy and physiography are controlled. Pearson et al. (1995) has shown that more productive soils influence early-successional plant communities within plantations, but differences in understory vegetation were not significant 3 years after regeneration. These results are supported by several other research experiments blocked by soil type that have followed plant successional patterns over 10 years postregeneration (Bell and Newmaster 2002; Newmaster and Bell 2002). Our analysis of native vegetation suggests the contrary; vegetation is closely associated with soil characteristics. We suspect that soils in the native forest are more diverse than those of plantations, and consequently microhabitat diversity is also higher in native forest.

Patterns in plantation plant diversity are apparent when specific ecological variables are manipulated. The diversity and composition of understory vegetation in our plantations differed with stand canopy species and spacing treatments. We found that wider spacing resulted in higher richness, lower woody plant abundance, slightly higher cover of herbaceous plants, and large increases in cryptogam cover. The largest differences were from 1.8 to 2.7 m spacing, with no differences from 2.7 to 3.6 m spacing. Pearson et al. (1995) conducted plantation spacing field experiments and did not find any differences in the understory herbaceous vegetation, which they attributed to the confounding effects of an abundant shrub and vine layer. We had very few shrubs and no vines in our study. Thinning research trials have found small changes in the herbaceous layer, as we did in our study (Alaback and Herman 1988; He and Barclay 2000). A closer look at herb abundance in these studies and in ours reveals the dynamic nature of forest plant communities. Some forest generalist species appear to tolerate treatments such as canopy spacing through the allocation of resources to growth, reproduction, or survival (Eriksson 1993; Damman and Cain 1998). Other forest species are absent because of the lack of forest structure (Boudreault et al. 2002; Bell and Newmaster 2002). In some thinning studies, understory vegetation increased significantly for long periods of time after treatment (McKenzie et al. 2000; Thysell and Carey 2001). These species are identified collectively in these studies as release species (species that are released after overstory removal), and in our study these were IAS common to roadside flora or agricultural systems. Parker et al. (2001) also found that this flora existed after treatment and that it was strongly correlated to the proximity of neighboring plant communities (e.g., a propagule source from an adjacent old field or roadside). Otsamo (2002) found dramatic changes in understory vegetation in a spacing trial, which he attributed to differences in light intensity under different canopies including a canopy species \times spacing interaction.

We also found a canopy species \times spacing interaction effect, where the impact of increased spacing on understory vegetation was more pronounced in spruce than in pine plan-

tations. The most dramatic change in understory vegetation was observed for the bryophyte layer, which increased from low cover (<10%) at close spacing to almost complete cover of the forest floor (>80% cover) at wide spacing treatments. This result has not been recorded in the literature, which is probably due to the lack of this type of large field research experiment. However, there are several feathermoss studies that have found high correlations between leaf area index and moss abundance, which may appear to contradict our findings (Vogel and Gower 1998; Bisbee et al. 2001). A physiological explanation does exist to explain this discrepancy. High solar radiation (open sites) desiccates moss (Oechel and Van Cleve 1986), because it causes photo-inhibition (Murray et al. 1993). However, under the shade of the forest canopy, feathermosses do extremely well because they have particularly low light saturation points ($300\text{--}500\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Hoddington and Bain 1979; Bubier et al. 1997; Bergamini and Peintinger 2002). In our study, feathermoss abundance increased dramatically, as predicted, with canopy spacing (light), where the widest spacing allowed the most optimal amount of light ($500\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to reach the forest floor. However, we did not expect to see such dynamic community interactions among species of feathermoss over the 10-year study.

In northern forests, bryophytes are the dominating constituents of forest floor vegetation (Hägglund and Lundmark 1977; Bonan and Korzukhin 1989) and play an important role in biomass production (Carleton and Dunham 2003; O'Connell et al. 2003) that may even exceed that of the tree species present (Romell 1939; Havas and Kubin 1983). Bryophyte diversity in forests often exceeds that of other plant groups (Newmaster and Bell 2002) and significantly affects forest management (Newmaster et al. 1999, 2003). Several species dominate this terricolous community: *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*, *Polytrichum commune*, and *Dicranum polysetum* (Esseen et al. 1997). In our plantation study, only three feathermosses dominated the forest floor: *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*. *Pleurozium schreberi* dominated all our plantation sites, but decreased with cover over the 10-year study period. Several early-successional studies have noted that *Pleurozium schreberi* is a pioneer species that quickly invades sites following silvicultural disturbance (Johnson 1981; Foster 1985). Boudreault et al. (2002) found in a study of 22 black spruce stands that *Pleurozium schreberi* also dominated the ground cover in mature stands (80–120 years). Tamm (1953), in a comprehensive survey of boreal forest feathermosses, found that *Hylocomium splendens* is a late-successional species that increases in cover with time. We found that both *Hylocomium splendens* and *Ptilium crista-castrensis* increased in abundance over time and noted that both of these species grew overtop of populations of *Pleurozium schreberi*. This was most pronounced at wider plantation spacing. Furthermore, both *Hylocomium splendens* and *Ptilium crista-castrensis* have a growth form that promotes upward growth. Perhaps this growth form allows these species to have at least two advantages over *Pleurozium schreberi*. First, it allows them to physically outcompete (grow overtop of) *Pleurozium schreberi*. Second, it allows them to push up through the rain of needles that accumulates

over time as the canopy matures. We could see evidence of this in remeasurement plots over time, where *Pleurozium schreberi* populations decreased because the needles buried them. This was most pronounced in the red pine plantation at close spacing, where almost all the feathermosses were buried under the large red pine needles, which overlap, creating a deep needle layer. Perhaps these species of feathermoss have competitive advantages under different canopy conditions, including species-specific variability to use light as a resource and deal with the physical impediment from needle rain. Given that bryophytes are largely thought to be opportunistic and facilitate the cycling of resources (Økland 1994, 1995), this is quantitative evidence to suggest that competition may be a strong mechanism in controlling the community dynamics of bryophytes. This hypothesis needs to be tested in controlled competition experiments and related to patterns of diversity observed in natural northern forests.

In a plantation we have control over the forest canopy, which appears to be mechanistic in controlling understory community composition. Light is more available in young plantations and supports a flora of ruderal species. Brockerhoff et al. (2003) found that the community dynamics of understory species is most related to temporal changes in the structure of the canopy. Similarly, Roberts (2002) found in a detrended correspondence analysis ordination that native stands were clearly separated from the plantations, particularly the young plantations, just as we found in our ordination. We measured the possible environmental variables that might constrain the ordination and found (as did Brockerhoff et al. 2003) in our ordination of plantations that canopy-related factors (i.e., light, needle input) were most strongly correlated with the composition of understory communities. Parker et al. (2001) showed that plantations could be converted to native forests types (including the understory) by thinning and underplanting. Perhaps this is because the canopy influences the understory environment, buffering temperature extremes, reducing light intensity, altering solar radiation, and intercepting precipitation (Aussenac 2000). The establishment, growth, and abundance of understory vegetation are limited by needle rain, heavy shade, reduced precipitation inputs, and root competition for moisture with overstory trees (Canham et al. 1990; Zackerissson et al. 1997). Controlling spacing to increase light, soil moisture, and nutrient availability promotes understory succession, which is dependent on the intensity of disturbance (Bazzaz and Wayne 1994; Coates and Burton 1997). Roberts (2002) noted that older plantations have increasing shade and belowground competition, which supports the reinvasion of native species (Schoonmaker and McKee 1988; Hong et al. 1997). Although many native species may reinvade as the forest returns to its native environment, the limited dispersal and slow rate of growth of these species may prevent their recovery (Bierzzychudek 1982; Roberts 2002). There is a lack of research that investigates the habitat and dispersal requirements of native species with respect to the size of fragmented forest (Radtke and Burkhart 1998). This movement towards restoration of native forest could use such a tool in conjunction with fostering old growth structure (Lindh and Muir 2004) and the addition of microhabitats such as logs to encourage the establishment of native bryophytes (Newmaster and Bell 2002; Newmaster et al. 2003).

Dealing with the claims about plantations and biodiversity

Do plantations cause single-species or single-layered monocultures, or “biological deserts”? Obviously, the answer is no, because there were over 100 species found in each of several plantation studies (176 species in our plantation study), including many subcanopy trees and shrubs, creating variability in forest physiognomy (Pearson et al. 1995; Otsamo et al. 2002).

Are plantations a major contributor to the establishment of invasive alien plant species? Our study had significantly more IAS (10%–14%) than did native forests (2%–3%) of similar sites and canopy species. Parker et al. (2001) found even higher percentages (25%) of IAS in southern Ontario. A recent review of IAS in Ontario provides quantitative evidence to support this claim (Newmaster et al. 2005b). Northern Ontario plantations have 10%–14% IAS, and southern Ontario plantations have even more IAS (20%–27%). NMS ordinations constrained by a plethora of environmental variables revealed that a disturbance gradient was strongly associated with the composition of IAS at multiple landscape scales (Newmaster et al. 2005b). Plantation management practices set the plant community back to a previous stage of succession, one dominated by ruderals (Swindel et al. 1986; Moore and Allen 1999). The invasion of IAS in plantations should be considered in the context of the intensity of forest management (Busing and Garman 2002; Newmaster et al. 2005b). Many of these species are common agricultural weeds found along roadsides, and the concern that these species will invade forest communities is justified, but further research is needed to validate that concern.

Are plantations a major contributor to the loss of native species? Both Conde et al. (1983) and Roberts (2002) stated that there is no loss of native herbs in plantations, but there is a significant drop in abundance of many native species. Our result for just the herb layer supports their research. However, we compared plantations with native forests on similar sites and dominant canopy species for all groups of plants, including bryophytes and lichens. If all plant groups are considered, our results showed that native forests are much more diverse (three to four times α , γ , or β diversity), have complex physiognomy, and more abundance of native species than plantations. Northern plantations are particularly devoid of woody plants and herbs. Feathermoss abundance was similar in plantations and native forests, but species richness was much higher in native forests. This was attributed to the lack of microhabitats in plantations, which support complex communities of bryophytes. Patterns of bryophyte diversity in forested ecosystems are closely related to the number and type of microhabitats (Vitt and Belland 1997; Newmaster et al. 2003; Gignac and Dale 2005). The impact of these species on native diversity has been studied in qualitative surveys, but no conclusive evidence has been presented to show that IAS displace native species (Newmaster et al. 2005b). Other mechanisms may be responsible for the loss of native diversity in plantations, such as dispersal limitations, deficient source of propagules, or the lack of interactions between plants and soil microbes (Klironomos 2002). Our research is the first step in understanding the relative diversity and abundance of species in

plantations, but in general this is largely an unsolved problem in community ecology.

The loss of native species abundance also appears to be as important as the loss of species in our study and those of others (Gilliam 2002; Roberts 2002). Finally, there is research to support the hypothesis that plantations lack the diversity in microhabitats needed to support a rich fauna. Older plantations and native forests contain more plant species used by wildlife: bird-dispersed seeds, including fleshy-fruit species that attract frugivorous birds (Kollmann and Grubb 1999; Alcántara et al. 2000); mammal-dispersed seeds (Parrotta 1995; Parrotta et al. 1997); endozoochory and ant-dispersed seeds (Bossuyt et al. 1999; Graae 2000); and plants that provide habitat for wildlife (Gjerde and Saetersdal 1997; Díaz et al. 1998; Moore and Allen 1999). Increasing the diversity of microhabitats is a positive step towards restoring native plant diversity and the many corresponding elements of biodiversity.

Conclusions and management recommendations

Although monocultures are deemed to be “biological deserts” by some, we must acknowledge the fact that many of these monocultures were formerly abandoned agricultural lands. This study indicates that through restoration efforts agricultural lands can be converted to productive forests that can harbour nearly one-half of the plant species found in equivalent natural forests within the same geographic region in as little as 50 years.

In this study, conifer plantations, regardless of species or initial planting density, did have significantly lower native plant diversity and higher IAS diversity than did natural forests. High densities of a long-needled conifer such as red pine had a greater effect on plant diversity than did shorter needled conifers such as spruce. High light interception and needle fall were negatively correlated with understory plant diversity, as was lack of structural diversity.

We recommend applying restoration using indigenous conifer species as a first step towards rehabilitating conifer forests that have been converted to agricultural lands and subsequently abandoned.

Intensive forest management may lead to the use of plantations to regenerate forests after harvesting. Ecological variation (e.g., habitat, soil, physiognomy) within these plantations would probably be even higher than in plantations established on farmland. At worst, these plantations would be expected to have plant diversity somewhere between plantations established on farmland and native forests. A next step would be to compare different types of plantations to evaluate this hypothesis and to further address the general claim that plantations are biological deserts.

Acknowledgements

The Ontario Ministry of Natural Resources and a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to Dr. S.G. Newmaster supported this study and publication. Colin Bowling and the staff at Northwest Science and Technology (OMNR) provided valuable field support. We would like to thank Peter Uhlig and Sean

McMurray of the Ecological Land Classification program (Ontario Forest Research Institute) for providing FEC data. Annabel Newmaster, Lisa Buse, and John Winters provided appreciated editorial work.

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