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# Fine-scale environmental variation and structure of understorey plant communities in two old-growth pine forests

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## Summary

**1** Although it is well established that nitrogen and light play major roles in structuring plant communities across the landscape, it is not as clear how they structure communities within forest stands. Virtually nothing is known about within-stand structure of understorey communities of herbs and small shrubs in near-boreal forests.

**2** We tested the hypothesis that fine-scale (5–20 m) variability in N and light structure forest-floor plant communities in two old-growth mixed *Pinus resinosa* and *Pinus strobus* forests in north-eastern Minnesota, USA.

**3** In each forest, all trees > 1.4 m tall were mapped on a 0.75–1.0 ha area. A grid of subplots 5–10 m apart was established (total $n = 147$), and N mineralization (µg $g^{-1}$ soil $day^{-1}$), soil depth (cm), light (% canopy openness), and percentage cover of all herbs and small shrubs were measured on each subplot.

**4** Cluster analysis showed that the dominant understorey species fall into three groups. Group 1 is unrelated to N and light, and is negatively associated with a midstorey of the small tree *Acer rubrum* and the most abundant tall shrub *Corylus cornuta*. Group 2 reaches maximum abundance in places (mostly gaps) with relatively high light, but is unrelated to within-stand variation in N availability. Group 3 consists of a single species, *Aster macrophyllus*, and reaches maximum abundance in areas with low N availability and low abundance of *Corylus*, but higher than average abundance of *P. strobus* and *Betula papyrifera* overstorey trees.

**5** N and light have a moderate influence on understorey plant community structure. The plant species do arrange themselves along N and light gradients, but the gradients are likely to be too narrow to allow the degree of differentiation seen at the landscape level. Spatial patterning of the species groups is probably influenced by other factors, including disturbance history, chance and neighbourhood effects such as clonal reproduction.

*Key-words*: *Aster macrophyllus*, boreal forest, Minnesota, nitrogen, light, understorey plant communities, white pine.

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## Introduction

It is clear that environmental gradients of nitrogen and light determine forest species distribution and thus are important in structuring communities across the landscape. In cold-temperate, near-boreal forests of North America, *Pinus* and *Picea*, with long-leaf lifespans, typically dominate forests on nutrient poor sites, whereas species with short leaf lifespans (*Populus*, *Betula*, and *Acer*) occupy progressively more nutrient rich sites (Curtis 1959; Grigal & Ohmann 1975; Pastor *et al.* 1984; Reich *et al.* 1997), and similar patterns are observed in all forested biomes (Reich *et al.* 1992). Across the temperate–boreal transition zone of eastern North America, there is also a gradient in species that cast progressively greater shade, which is associated with a successional gradient from *Betula papyrifera*, to *Quercus rubra*, *Pinus strobus*, *Acer rubrum* and, finally, to *Abies balsamea*, *Picea mariana*, *Acer saccharum* and *Tsuga canadensis* (Canham *et al.* 1994; Walters & Reich 1996). Under the canopy of many of these species light levels do not favour their own reproduction, but allow succession to any species later in the list. Hence the landscape is a mosaic, strongly related

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to light availability, of stands in different stages of succession.

At the landscape level, understorey plant communities in forests also respond to N and light (Carleton & Maycock 1980, 1981; Kurmis *et al.* 1986; Whitney & Foster 1988; Lichter 1998). Disturbance history is superimposed upon these environmental gradients, and succession in understorey plant communities often parallels that in the overstorey, although the short dispersal distances of herb propagules may delay recolonization of a disturbed site and thus limit the correlation (Whitney & Foster 1988; Matlack 1994; Lichter 1998). In boreal forests, there is significant, but not total correlation between canopy type and understorey composition (Reich *et al.* 2001), because of the presence of species with the same environmental preference (Carleton & Maycock 1980).

The well documented importance of N and light gradients at the landscape scale may or may not translate to other scales. The degree to which variation in N and light structures the distribution of understorey communities within a single forest stand is unclear. Within stands, variation is at a small spatial scale (on the order of tens of metres), and is also more limited in the total range of measured values than those measured across the landscape (Reich *et al.* 1997; Finzi *et al.* 1998; Ferrari 1999). Cold-temperate mixed deciduous–evergreen forests, such as those at our study site, clearly exhibit small-scale variation in N and light availability, which are sometimes higher under deciduous trees (here broadleaf species) in mixed stands than under evergreens (which are coniferous). This statement cannot, however, be generalized for all forest communities (Mladenoff 1987; Pastor *et al.* 1987; Boettcher & Kalisz 1990; Canham *et al.* 1994; Binkley 1995; Ferarri 1999).

The relationship between nutrients or light or overstorey structure and herb growth have been examined individually in boreal forests (Landhauser *et al.* 1997; Arii & Turkington 2002; Legare *et al.* 2002; Turkington *et al.* 2002), and the influence of fire history and forest type on herb communities at landscape scales has also been examined (Ahlgren 1960; Carleton & Maycock 1981). At this point, however, we are unaware of any studies that take the next step and link forest floor community composition with fine-scale variation in light and N in boreal forests.

A number of studies have looked at within-stand interactions between nutrients, light or overstorey trees and forest-floor herbs in more southerly forests dominated by genera such as *Quercus*, *Acer*, *Fagus*, *Tsuga*, *Tilia* and *Lirodendron* (Bratton 1976; Hicks 1980; Maguire & Forman 1983; Beatty 1984; Crozier & Boerner 1984; Marino *et al.* 1997; McKenzie *et al.* 2000; Lezberg *et al.* 2001; Rankin & Tramer 2002). These authors concluded that microhabitats are important and that there are some significant relationships between canopy type immediately overhead and herb composition, due to alteration of the nutrient, light and physical environment of the forest floor by the overstorey.

No clear patterns or principles emerge to allow us to predict the influence of N and light gradients on within-stand forest-floor community structure. Growth rates may be more affected than presence or absence of species at a given location on the forest floor, as many species can persist in what is, for them, a poor environment (Lezberg *et al.* 2001). Many herbs reproduce vegetatively, and/or have very short seed dispersal distances (Cain *et al.* 1998), or could expand in clonal fashion independently of small-scale variability of N and light within a stand.

One can therefore reasonably entertain alternative hypotheses that: (i) N and light, together with their complex relationship to canopy tree composition and soil, will explain much of the observed understorey community structure, or (ii) that colonies of forest-floor plants may form patches that are independent of small-scale environmental differences. We used spatial analyses to assess the relative importance of canopy, N and light for the structure of forest floor herb and small shrub communities in two near-boreal, old-growth *Pinus strobus* and *Pinus resinosa* stands. All trees were mapped and forest floor communities and environmental variables were measured on a systematic grid. Tree seedling dynamics and moss communities are considered as factors that could potentially affect the herb and small shrub community but their responses will be considered elsewhere. Our study sites are bedrock-controlled with shallow soils, whose moisture availability is linked with soil depth. Soil depth was therefore also characterized to investigate its interaction with N and light.

We considered the following questions: (i) do the understorey species arrange themselves according to local canopy composition, (ii) do they arrange themselves along N and light gradients, and (iii) are the understorey species individualistic, or are they arranged in definite communities?

## Methods

### FIELD AND LABORATORY METHODS

The study sites are in the Great Lakes Pine-Hardwood Forest/boreal forests transition zone of north-eastern Minnesota (92°00′ W, and 48°00′ N). They are covered by a mixture of *Pinus strobus*, *Pinus resinosa*, *Betula papyrifera* and *Acer rubrum*, representing the pine-hardwood forest, with *Abies balsamea* and *Picea mariana* representing the boreal element. Soils in the region are shallow and rocky, consisting of highly variable sandy to loamy glacial deposits from 0 to 0.5 m thick over granitic bedrock. The region has a continental boreal climate (Ahlgren 1969). Winters are long and cold (mean January temperature of −17 °C and snow covers the ground from mid-November to mid-April) and summers are short and cool (growing season length is < 100 days with a mean July temperature of 17 °C).

All trees > 1.4 m tall were mapped, measured for d.b.h., and species identified on two macroplots. Hegman Lake (0.76 ha, $n = 1248$ trees) was mapped in

1994 and Kawishiwi Pines (0.98 ha, $n = 1243$ trees) in 1996. The Hegman Lake stand is dominated by large *Pinus resinosa* and *P. strobus* that originated after a severe fire in 1822, while the Kawishiwi stand is dominated by *P. strobus* that recruited after a severe fire in 1854 (Heinselman 1973). Neither stand has experienced commercial logging, and both are old enough to have completed the stem-exclusion stage of development (Frelich 2002), and are now in the early and middle phases, respectively, of transition to multi-aged stands.

Within each macroplot, a grid of subplots, centred at 5-m intervals, was established during 1995–97. A subset of these subplots was chosen for detailed environmental measurements, including N mineralization rate, soil depth and light, which were carried out during the summers of 1995–97 (Machado 1999). This subset was randomly chosen at Hegman (94 subplots, with many subplots at both 5 and 10 m intervals), but every other subplot was chosen at Kawishiwi (53 subplots, creating a 10 m grid with only a few exceptions). Percentage cover was determined at mid-summer 1997 by an experienced field crew that had been doing similar work for at least 3 summers (Reich *et al.* 2001). There are no spring ephemerals in this area, and all work was done within 2 weeks to ensure comparable phenological stage among subplots. The subplots had nested radii of 1.1 m, within which cover of all shrub species was determined, and 0.75 m, within which cover of vascular herbaceous plants, mosses and tree seedlings was determined using Gleason & Cronquist (1991) as the source for taxonomic nomenclature of vascular plants. The vast majority of plants were identified to species although *Viola* spp., *Fragaria* spp. and some *Lycopodium* spp. had to be grouped on some occasions when early blooming season or lack of resolution of taxonomic status prevented identification. Ordinal cover classes were defined as follows: class 1, absent; class 2, < 1%; class 3, 1–5%; class 4, 6–25%; class 5, 26–50%; class 6, 51–75%; and class 7, 76–100% cover.

To evaluate the distribution of light environments on the two macroplots we measured percentage canopy openness using the LAI-2000 Plant Canopy Analyser (Li-Cor, Lincoln, Nebraska, USA) at 1.0 m above ground level on each subplot. Such measurements provide a good surrogate of mean daily percentage photosynthetic photon flux density in these forests (Machado & Reich 1999). Two canopy openness measurements were taken at the centre of each subplot when the sky was uniformly overcast or within 1 hour after dawn or 1 hour before dusk and compared with open sky values simultaneously measured with a second LAI 2000 in a large clearing less than 1 km away. The values reported here represent percentage open sky in an imaginary inverted cone with the vertex at the sensor and sides that extend upward through the forest canopy at an angle of 60% from vertical. Details of methodology are given by Machado & Reich (1999).

N mineralization was determined with a modified semi-open core *in-situ* incubation method (Grigal & Homann 1994) between July 1–8 and August 5–11, 1995. We sampled the 0–15 cm horizon since we found the majority of roots at this depth. At the beginning of the incubation period, PVC tubes were used to remove six 2.5 cm diameter × 15 cm deep cores at each subplot for determination of initial values. Simultaneously, six PVC tubes were pounded into the ground to a depth of no more than 15 cm, within 10 cm of the initial cores, and left to incubate for 34 or 35 days. The PVC tubes were covered with rubber corks to prevent water flow through the soil column and had air holes at the top to facilitate ventilation. At the end of the incubation period the cores were refrigerated and transported to the laboratory. The six cores from each subplot for each time point were pooled and cleaned of roots and woody debris. We oven-dried the soils at 105 °C to determine water content, after removal of a sample for determination of 2 M KCl extractable NH4-N and $NO_3$-N. $NH_4$-N and $NO_3$-N in the extract solutions were determined by the University of Minnesota Department of Soil Science Research Analytical Laboratory by conversion to nitrate with salicylic acid and subsequent copper cadmium reduction, followed by colorimetric analysis. N mineralization potential of each sample was calculated as $\mu g\ N\ g^{-1}\ soil\ day^{-1}$ using the difference in total N concentration between the initial and incubated core samples.

Soil depth was measured with a 50-cm probe at 5 points arranged at the corners and in the middle of a 50 × 50 cm square near the centre of each subplot. The sites are on bedrock of the Canadian Shield, and measurements, which reflect depth to bedrock or large boulder, were averaged to give an index of soil depth at each subplot. Those few subplots with deeper soil are entered into the data set as > 50 cm.

### STATISTICAL METHODS

Initial examination of the data showed that 58 species of herbs and small shrubs occurred on the two macroplots. Twenty-nine of these species occurred on a relatively large number of subplots, while the remainder were very rare (most occurring in low abundance only on 1 or 2 subplots), thus precluding any analysis of their response to environmental variables. These rare species collectively accounted for only 5.4% of cover, using the midpoints of the cover classes recorded in the field to convert values to percentages.

An overall description of the subplot data was achieved with non-metric multidimensional scaling (nMDS) ordination with PC-ORD software (McCune & Mefford 1999), using the relative abundance of each of the 29 important species on all 147 subplots. The 'slow and thorough' procedure, which carries out 40 runs with the real data, each of which steps though dimensions from 6 down to 1, and 50 runs with randomized data, was employed to determine the best solution. The best final configuration is that which has the highest number of dimensions but still has a stress statistic lower than in 95% of the randomized runs, and is also the lowest among the 40 runs with real data for the chosen number of dimensions (McCune & Mefford 1999). The resulting scatter plots were used to see if any structure exists among the 147 subplots, and whether the subplots cluster tightly for each macroplot, or form a continuum.

A hierarchical, agglomerative clustering method, using Ward's method for group linkage on the ordinal cover classes was employed to assign the 29 important species into groups (JMP software, version 3.2.2, SAS Institute, Cary, NC, USA). The percentage cover for all species within each group was then pooled for each subplot for further analysis. NMDS ordinations (using relative abundance of each species group in an analogous procedure to that for describing the two macroplots) were also done using the species groups as variables, to check the validity of the cluster analysis.

Ordinal logistic regression (Minitab Statistical Software, Release 12, 1998, State College, Pennsylvania, USA) was used to evaluate whether quantitative environmental factors play a significant role in determining the distribution of a given species group among ordered categorical levels of cover. This method assumes that samples are independent (i.e. that the plants on one subplot do not influence the plants on another subplot – see below for spatial autocorrelation tests). Percentages for species groups were calculated by converting the cover class of each species to a percentage and then summing for all species in the group. Five levels of abundance – level 1 (0–1% cover), level 2 (1.1–5% cover), level 3 (5.1–20% cover), level 4 (20.1–50% cover, and level 5 (> 50% cover) – were used in ordinal logistic regressions which were done separately for each species group, using N mineralization, light, soil depth, percentage cover of tree seedlings, percentage cover of mosses, basal area of each of six important tree species within 5 m of each plot centre (*Picea mariana*, *Pinus resinosa*, *P. strobus*, *Abies balsamea*, *Betula papyrifera* and *Acer rubrum*) and percentage cover of the predominant tall shrub species (*Corylus cornuta*) as variables.

A second method of examining the relationship between species groups and their environment, which we call maximum abundance analysis, was to compare the environment of subplots on which each species group was maximally abundant to all remaining subplots. We developed a two-step procedure to examine the correlation of each species group with each variable. First we examined a histogram of species group abundance among all subplots, and looked for a break in the distribution that separated subplots where the group was a minor component from those relatively few subplots where it achieved high cover. We then separated those subplots with high cover and used one-way ANOVA to test whether their environmental variables were significantly different from the other subplots. One can then, for example, characterize a given species group as reaching maximum abundance on sites with high, average or low N. The nonparametric Kruskal–Wallis ANOVA from Minitab Release 12 was used because all distributions were highly non-normal.

Moran's $I$ (Sokal & Oden 1978) was calculated at 5-m intervals to determine if the plant species groups on adjacent subplots were independent of one another. The computer program for Moran's $I$ was written by the senior author, following the formulas and significance tests from Sokal & Oden (1978). These spatial analyses were done separately for each macroplot, which have independent grid-coordinate systems. Analyses of spatial clustering of the environmental variables N, light and soil, had already been done for a previous study (Machado 1999), whose data are used for comparison to the species group data.

## Results

### GENERAL PATTERN OF FOREST FLOOR HERBS AND SMALL SHRUBS

Average aggregated cover for the 29 species of herbs and small shrubs studied was 22% for the two macroplots pooled. Cover was significantly different between the two macroplots (median 9.5% at Hegman, and 25.5% at Kawishiwi, Kruskal–Wallis $H = 31.5$, $P < 0.001$). The lower median cover at Hegman was due to some subplots having essentially no vascular plant community on the forest floor, either because they were located on two bedrock knobs, most of which were covered by mosses ($n = 15$), or because of very dense coniferous cover or dense clones of the tall shrub *Corylus* in addition to a coniferous tree canopy ($n = 8$ with less than 2.0% cover for the 29 species added together). An nMDS ordination showed that the bedrock plots were somewhat separate from the main cluster of points, within which representatives from the two macroplots were mixed together (Fig. 1).

The species richness of all forest floor vascular plants (species per 1.77 $m^2$ subplot), ranged from 1 to 19, and the distribution among subplots was normal with a mean of 9.9 and standard deviation of 3.2. Species richness for the 29 species studied in detail ranged from 1 to 13, and the distribution was also normal with a mean of 6.3 and standard deviation of 2.54. The only significant correlations with species richness (Pearson correlation, $n = 147$ subplots, for the 29 common species) were for N mineralization ($r = -0.265$, $P = 0.001$), light ($r = -0.221$, $P = 0.007$), and abundance of *Corylus* ($r = -0.186$, $P = 0.023$).

The 29 species studied in detail included 12 summer-green herbs, six small shrubs, five ferns and allies including clubmosses, two evergreen herbs, two miniature vines, one vine, and one grass. Summer-green herbs had the highest percentage cover of any growth form on 120 of the 147 subplots and were present on all but one subplot. One-way ANOVA revealed that N mineralization and light levels were higher on 10 subplots where small shrubs dominated than on subplots where other growth forms dominated (1.97 µg N $g^{-1}$ soil $day^{-1}$ vs. 0.76 for other growth forms, $F = 16.8$, d.f. 1,143, $P < 0.001$ and 21% canopy openness vs. 7.6% for other

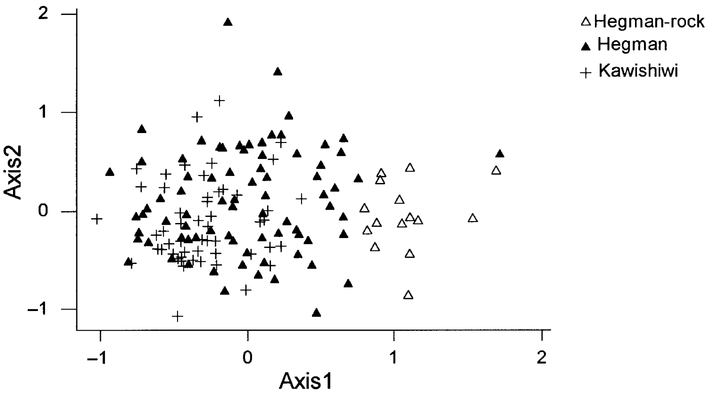

**Fig. 1** NMDS ordination of the 147 subplots using relative abundance of the 29 important species. Two axes are shown of the three retained by the NMDS procedure in PC-ORD. Subplot location: △, rock domes on the Hegman macroplot dominated by moss; ▲, rest of Hegman; +, Kawishiwi.

growth forms, $F = 51.2$, d.f. 1,145, $P < 0.001$). No other significant effects were detected, probably because the preponderance of summer-green herbs weakened any relationships between growth form and environmental variables.

Cluster analysis revealed that the 29 common species could be split into three (possibly five) groups (Fig. 2). To determine which grouping scheme worked best, nMDS ordinations were run using three and five species groups as variables. Relative abundance, based on total cover of all species within a group on each subplot, was used in the ordinations. For both ordinations PC-ORD recommended retaining two axes, and the resulting final plot of the axes revealed a triangular structure. For both ordinations the vertices of the triangle corresponded with subplots dominated by the three-species grouping, which was therefore used for subsequent analyses (Fig. 3).

Group 1 is a taxonomically and morphologically diverse group of six perennials including two summer-green herbs (*Aralia nudicaulis* and *Maianthemum canadense*), a grass (*Oryzopsis asperifolia*), a miniature vine in the rose family (*Rubus pubescens*), a miniature vine in the honeysuckle family (*Linnaea borealis*), and

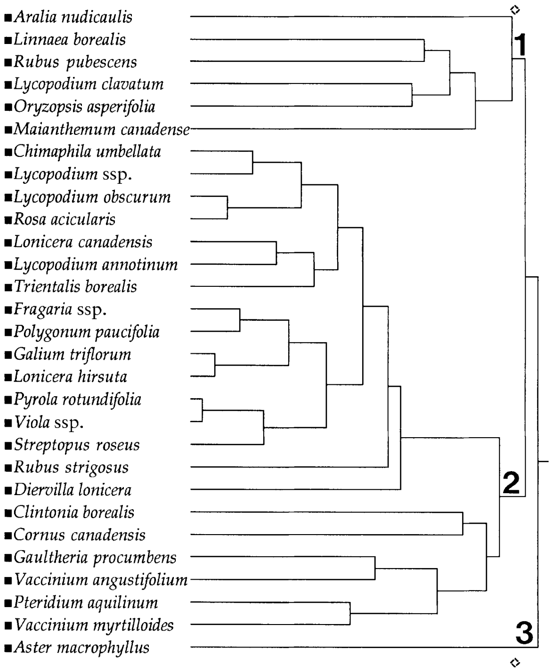

**Fig. 2** Dendrogram for the cluster analysis of species, showing how the 29 common species can be divided into three groups.

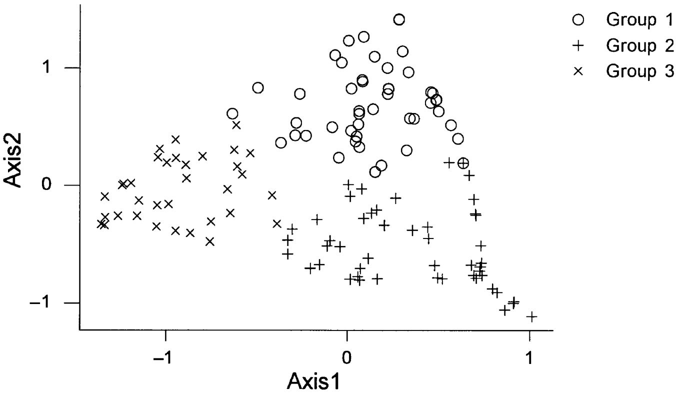

**Fig. 3** NMDS ordination based on relative abundance of three species groups on the 147 subplots: ○, group 1; +, group 2; ×, group 3.

a clubmoss (*Lycopodium clavatum*). Group 2 is the largest, with 22 species, and comprises several summer-green herbs (*Clintonia borealis*, *Trientalis borealis*, *Fragaria* spp., *Polygala paucifolia*, *Galium triflorum*, *Pyrola rotundifolia*, *Viola* spp., *Cornus canadensis* and *Streptopus roseus*), two evergreen herbs (*Chimaphilla umbellata* and *Gaultheria procumbens*), two small ericaceous shrubs (*Vaccinium myrtilloides* and *V. angustifolium*), two small honeysuckle-family shrubs (*Lonicera canadensis* and *Diervilla lonicera*), two small rosaceous shrubs (*Rosa acicularis* and *Rubus strigosus*), a fern (*Pteridium aquilinum*), three club mosses (*Lycopodium obscurum*, *L. annotinum* and *Lycopodium* sp.), and a vine in the honeysuckle family (*Lonicera hirsuta*). The third group consists of a single summer-green herb, *Aster macrophyllus*, commonly called large-leaved aster, whose dense clonal habit often excludes other species.

There was no significant spatial autocorrelation (using Moran's $I$ on percentage cover for each species group) for any of the three species groups, on either macroplot, for distance classes from 5 m to 45 m. Thus, it was valid to assume independence of plant communities on subplots for the logistic regression and Kruskal–Wallis tests. Subplots would be perfectly correlated with themselves, and the lack of a significant correlation at 5 m means that the correlation drops from 1.0 to 0.0 somewhere between 0 and 5 m. Our grid of sample points was not therefore fine enough to detect any spatial structure for each species group. Although there appeared to be no significant patch structure, subplots with maximum abundance of particular species groups occurred in spatially separated areas of both macroplots (Fig. 4). The nMDS ordination (Fig. 3) also showed separation of subplots with high abundance of the different species groups with a limited overlap, indicating that the groups reached maximum abundance on different subplots, while coexisting on others.

## FOREST FLOOR COMMUNITY VS. TREE SEEDLINGS

Ordinal logistic regression using tree seedling cover as a predictor of the occurrence of the three plant groups

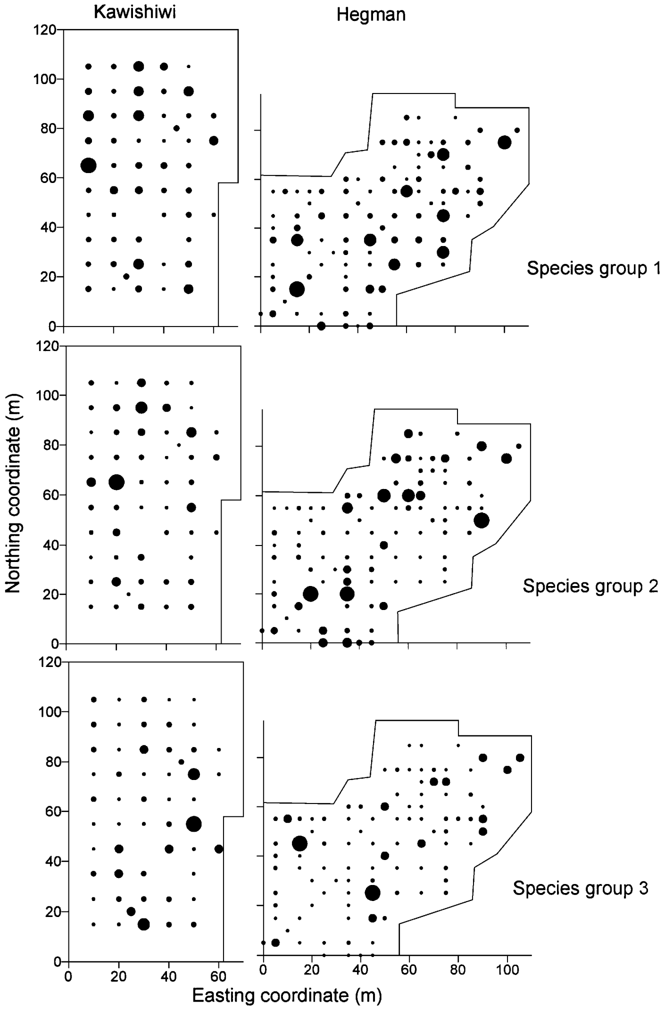

**Fig. 4** Spatial distribution of species groups for the Hegman and Kawishiwi macroplots. For each subplot, dot diameter reflects percentage cover, with the smallest and largest dot sizes representing the minimum and maximum values found for a given species group among the 147 subplots.

indicated that tree seedlings were independent of the herb and shrub community and did not influence its structure ($P = 0.948$, 0.524 and 0.599 for plant groups 1, 2, and 3, respectively).

### FOREST FLOOR COMMUNITY VS. MOSS COVER

Moss cover did not predict the presence of plant groups 1 and 2 ($P = 0.594$ and 0.661, respectively), but was negatively associated with cover of group 3 ($P = 0.011$). These results were expected because the moss community is heavily concentrated in mats on rock outcrops that cannot support significant levels of vascular plant cover, whereas *Aster macrophyllus* is found primarily on deep soil areas (see below). Overall, there is no indication that the moss community has a systematic influence on the structure of this vascular plant community, with the only correlation probably explained by soil depth.

### FOREST CANOPY VS. THE FOREST FLOOR PLANT COMMUNITY, LIGHT AND N

Overall, there was little association between the forest-floor plant community and the local occurrence of seven major tree species or the tall shrub *Corylus* (i.e. within 5 m of the subplot centres). Abundance of species group 1 was however negatively associated with *Acer* and *Corylus* ($P = 0.037$ and 0.035, respectively, for the two macroplots pooled). Species group 2 showed no significant response to any forest canopy attribute. Group 3 was positively associated with mature *Pinus strobus* and *Betula* ($P = 0.006$ and 0.044, respectively) and, like group 1, negatively with *Acer* and *Corylus* ($P = 0.018$ and 0.012, respectively).

Where there was a significant relationship with the understorey communities, tree and shrub species data were converted to quartiles which were used as ordered categories in an ordinal logistic regression against light and N. There were no significant relationships between N and presence of any tree or tall shrub species within a 5 m of the centres of the subplots (*P-value*s from 0.372 to 0.879), but *Corylus* and *Pinus* did have significant negative relationships with light ($P < 0.001$ and 0.002, respectively).

### NITROGEN MINERALIZATION

Species groups 1 and 2 attained maximum abundance on subplots whose median rates of N mineralization were not significantly different from the rest of the subplots, for macroplots analysed separately or pooled (Table 1). *Aster macrophyllus* (group 3) reached maximum abundance on subplots where median N mineralization rates were significantly lower than on the rest of the subplots on the Hegman macroplot and for both sites pooled, but there was no significant effect on the Kawishiwi macroplot.

The ordinal logistic regression analyses for the pooled macroplots, were consistent with these findings. *P*-values for the N parameter for groups 1 and 2 were well above 0.05, indicating no sensitivity to N availability, whereas for group 3, the *P*-value was 0.018, and the odds ratio was also well above 1.0, indicating a preference for low-N environments (Table 1).

**Table 1** N mineralization rates (μg $g^{-1}$ soil $day^{-1}$) vs. forest understorey plant groups

| | Plant species group | | |
|---|---|---|---|
| Macroplot/analysis | 1 | 2 | 3 |
| Hegman: | | | |
| Median N high abundance subplots | 0.930 | 1.185 | 0.455 |
| Median N other subplots | 0.767 | 0.951 | 1.06 |
| Kruskal–Wallis *P*-value | 0.508 | 0.596 | 0.002 |
| Kawishiwi: | | | |
| Median N high abundance subplots | 0.505 | 0.497 | 0.424 |
| Median N other subplots | 0.497 | 0.479 | 0.503 |
| Kruskal–Wallis *P*-value | 0.766 | 0.983 | 0.142 |
| Hegman + Kawishiwi: | | | |
| Median N high abundance subplots | 0.453 | 0.623 | 0.424 |
| Median N other subplots | 0.574 | 0.537 | 0.591 |
| Kruskal–Wallis *P*-value | 0.424 | 0.464 | 0.017 |
| Ordinal logistic regression *P*-value | 0.127 | 0.480 | 0.018 |

The subplots with high N availability (as well as high canopy openness) were those with shallow soils on the Hegman macroplot on the domes of bedrock, which were covered with mosses, but were largely unoccupied by the herbs and small shrubs studied.

### UNDERSTOREY LIGHT

Canopy openness just above the herb/seedling layer (at 1.0 m above ground) was significantly higher, and was also more variable on the Hegman macroplot. The brightest areas had canopy openness up to 35%. Analyses of subplots with maximum abundance indicates that, for both macroplots, groups 1 and 3 showed no response to light, whereas group 2 reached maximum abundance in areas with significantly higher canopy openness. The ordinal logistic regression confirmed this trend, with a significant *P*-value only for group 2 (Table 2).

### SOIL DEPTHS

Soil depths were similar on the Hegman and Kawishiwi macroplots (Table 3). Analyses of subplots with maximum abundance showed that, for both macroplots when pooled, none of three species groups had a significant preference (Table 3). However, species group 3, *Aster macrophyllus*, showed a significant preference for relatively deep soil on the Hegman macroplot, which probably reflects the avoidance of bedrock knobs on that plot. Ordinal logistic regression results were generally consistent with this trend, with no significant *P-value*s for the soil parameter for any species group.

**Table 2** Canopy openness (%) at a height of 1 m vs. forest understorey plant groups

| | Plant species group | | |
|---|---|---|---|
| Macroplot/analysis | 1 | 2 | 3 |
| Hegman: | | | |
| Median openness high abundance subplots | 9.11 | 18.0 | 9.38 |
| Median openness other subplots | 9.72 | 9.21 | 9.72 |
| Kruskal–Wallis *P*-value | 0.576 | 0.021 | 0.434 |
| Kawishiwi: | | | |
| Median openness high abundance subplots | 7.46 | 9.08 | 8.05 |
| Median openness other subplots | 6.34 | 6.04 | 6.04 |
| Kruskal–Wallis *P*-value | 0.766 | 0.023 | 0.102 |
| Hegman + Kawishiwi: | | | |
| Median openness high abundance subplots | 7.25 | 11.4 | 8.03 |
| Median openness other subplots | 6.66 | 6.13 | 6.44 |
| Kruskal–Wallis *P*-value | 0.836 | 0.002 | 0.509 |
| Ordinal logistic regression *P*-value | 0.176 | 0.008 | 0.094 |

**Table 3** Soil depths (cm) vs. forest understorey plant groups

| | Plant species group | | |
|---|---|---|---|
| Macroplot/analysis | 1 | 2 | 3 |
| Hegman: | | | |
| Median depth high abundance subplots | 26.0 | 21.3 | 32.6 |
| Median depth other subplots | 23.6 | 24.0 | 22.2 |
| Kruskal–Wallis *P*-value | 0.509 | 0.754 | 0.001 |
| Kawishiwi: | | | |
| Median depth high abundance subplots | 19.2 | 19.4 | 23.4 |
| Median depth other subplots | 23.4 | 23.5 | 21.4 |
| Kruskal–Wallis *P*-value | 0.177 | 0.303 | 0.953 |
| Hegman + Kawishiwi: | | | |
| Median depth high abundance subplots | 17.4 | 26.3 | 24.8 |
| Median depth other subplots | 23.7 | 23.4 | 23.5 |
| Kruskal–Wallis *P*-value | 0.207 | 0.437 | 0.486 |
| Ordinal logistic regression *P*-value | 0.862 | 0.188 | 0.913 |

## Discussion and conclusions

### SPECIES GROUPS

Individual species abundances corresponded poorly to environmental gradients. As is typical of biological abundance data, relationships had a triangular shape, with the upper edge of the triangle indicating the potential abundance for each species. Most subplots have abundances falling far below the potential maximum because of interactions with other environmental variables (known and unknown), and because of sharing abundance with other species. In a system with 29 important species few, if any, species can approach the maximum potential abundance allowed by the environment at a given spot on the forest floor.

However, we did find evidence that the forest floor is occupied by three species groups, which could potentially form a mosaic of communities. These groups were verified by: (i) separation in the cluster analysis (Fig. 2); (ii) separation of subplots with the highest level of dominance by each of the three species groups in an nMDS ordination (Fig. 3); and (iii) the fact that niches occupied by the three species groups are consistent, and consistently distinct, across two different macroplots (Tables 1, 2 and 3, Figs 3 and 4).

### THE ROLE OF CANOPY, NITROGEN AND LIGHT IN COMMUNITY STRUCTURE

The main objective of this paper was to test whether N and light are major forces in structuring the understorey community within a stand. A sub-hypothesis is that the canopy type above a given spot on the forest floor may influence the light and N environment, in turn influencing the understorey communities. The results show that there was a detectable, statistically significant yet modest effect of within-stand variability of N and light on community structure.

Clearly, variation in N is not providing the degree of control over community structure within these two stands that it exerts at the landscape scale. We found a negative relationship between N mineralization and species richness, which would seem to agree with the results of Turkington *et al.* (2002) who found reduced understorey herb diversity after 10 years of fertilization in a boreal forest in north-western Canada. However, reduced diversity at high N in our study is not due to competitive exclusion, but rather to the interaction of soil depth with N, whereby high N occurs on mats of moss on rock outcrops that support few vascular plants.

The locations with maximum abundance of each group had a characteristic environment. For group 1, the combination of no significant difference in N and light levels between those subplots where it reaches maximum abundance and other subplots, and the lack of significance in ordinal logistic regression, indicate that it was insensitive to within-stand variation of N and light levels (Tables 1 and 2). However, there was a negative effect of the presence of *Acer* or *Corylus* in the midstorey (Fig. 5).

Species group 2 was insensitive to within-stand variation in N levels, and was found at moderate light levels, but only reached high abundance at what are high light levels for this forest (Table 2, Fig. 5). The group did not exhibit the negative association with *Acer* and *Corylus* shared by groups 1 and 3, nor the preference for neighbourhoods with *Pinus strobus* and *Betula* shown by group 3. High light environments often occur in this forest where gaps in the upper canopy are filled with *Acer* saplings or clusters of *Corylus*, which have only a limited effect on light penetration. Areas with a layer of *Acer* or *Corylus* in addition to the upper tree canopy were nearly devoid of forest floor plants. Group 2 contains all six species of small shrubs, the only growth form shown to be positively related to light, which is consistent with the overall response of the group to light, and with its role as a gap community.

Species group 3, *Aster macrophyllus*, occupied areas with less than average and average N availability on the Hegman and Kawishiwi macroplots, respectively (Table 1, Fig. 5). The average N mineralization rate was higher on the Hegman macroplot than on Kawishiwi, and inspection of the data in Table 1 shows that the median N mineralization rate for those subplots where *Aster macrophyllus* attains maximum abundance at Hegman was similar to the mean for all subplots at Kawishiwi (0.455 and 0.503 $\mu g\ g^{-1}$ soil $day^{-1}$, respectively). It therefore seems likely that *Aster macrophyllus* was selecting environments with low N availability, regardless of whether that level is average or below average within a given forest. This species also had a significant positive association with canopy *Pinus strobus* and *Betula*, and a negative relationship with the tall shrub *Corylus* and the midstorey tree *Acer*. Ordinal logistic regression of the effects of these four canopy and midstorey species showed no significant relationship with N, so that N availability and neighbourhood abundance of these species were independent. Therefore, the ideal niche for *Aster macrophyllus* is where crowns of canopy *Pinus strobus* and *Betula* occur over soils with low N availability, and there is no *Corylus* and/or *Acer* midstorey. Legare *et al.* (2002) found, however, that forest canopy type did not influence *Aster macrophyllus* abundance, although differences in scale and forest type make it difficult to compare the two sets of results. *Aster macrophyllus* abundance did not show sensitivity to light levels in this study, in agreement with Schulz & Adams (1995), who pointed out the broad range of light tolerance for this species.

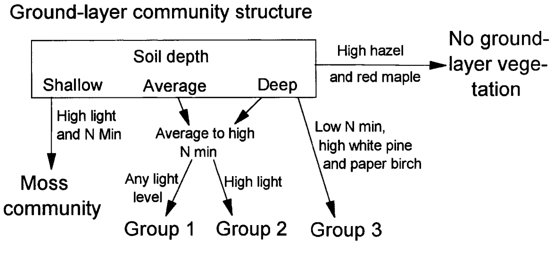

**Fig. 5** Conceptual summary diagram of understorey plant community organization.

Canopy type within a 5-m radius around the centre of subplots explained surprisingly little of the variation in forest-floor community structure. *Pinus strobus* is apparently independent of N supply in this forest and its positive effect on species group 3, which favours a low-N environment, must have an alternative explanation. One possibility is that a high density of *Pinus strobus* may provide just enough shade to exclude the mid-tolerant *Corylus* and *Acer*, which in turn disfavour species group 3, as well as group 1. Because *Acer* abundance was shown to have no relationship with light and N, its mechanism for excluding groups 1 and 3 is unknown, but may be related to smothering of herbs by litter fall. *Acer* species in general are known to have this effect on forest herbs and seedlings (Beatty & Sholes 1988).

These environmental patterns leave much of the spatial distribution of species groups unexplained. Forest understorey species do respond to N and light gradients in the white and red pine forests of our study sites, and there is a modest but significant degree of separation into communities. However, the species groups coexist on some subplots. One possible explanation is that a larger difference in environment than is found within these two forests is required to cause more than minor differentiation of separate plant communities. Our three species groups could then be called ‘potential plant communities’, which do not differentiate fully because of the great amount of overlap in the local environment. Second, there might be more community separation than we can detect. Some subplots (which at 1.77 $m^2$ are relatively large compared to some published studies of forest-floor herbs) may overlap the boundaries between two communities, thus blurring community distinctness.

Neighbourhood effects, as well as historical factors, probably also contribute to the spatial patterns found in these two forests. Previous analyses (Machado 1999) indicate spatial autocorrelation on the Hegman macroplot of 30–80 m for N, 10–30 m for light, and 20–50 m for soil depth. Similar values for the Kawishiwi were 3–12 m for N, 50–60 m for light and 10–30 m for soil (Machado 1999). The grain of the species groups, however, is smaller than our subplot spacing (< 5 m). This mismatch in the grain of the environmental and community mosaics is an indicator that other types of patch dynamics than merely matching up with the appropriate environment are taking place. Clonal reproduction or very short seed dispersal distances are common among our plant species and may provide an alternative explanation for patch formation. These types of neighbourhood effects are known to cause spatial structure in other herbaceous communities (Belsky 1986). Forest tree communities in the Great Lakes region of the USA have also been shown to be partly structured by neighbourhood effects as well as by environmental differences between stands (Frelich *et al*. 1993, 1998; Frelich & Reich 1995, 1999).

Historical factors, such as where plants were established after the last major disturbance (1822 and 1854 on our study areas), could also interact with the clonal nature of the plant species. Forest understorey plants can establish after major disturbance and then maintain themselves through periods of poor environment and, as stand development proceeds, they may be able to respond to gap formation and other stand development processes that allow an increase in abundance by vegetative growth (Ahlgren 1960; McKenzie *et al*. 2000; Lezberg *et al*. 2001; Rankin & Tramer 2002). We propose to look at the hypothesis that the overstorey and understorey communities in this forest have independent neighbourhood-effect patch dynamic systems that contribute to community structure. It would be logical to pursue detailed mapping of individual plants on a section of forest floor, giving us more spatial resolution than we had in this study, as a next step to test more fully the relative importance of N, light, soil and neighbourhood effects in structuring forest floor plant communities in near-boreal white and red pine forests.

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