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Biotic and abiotic factors affecting ectomycorrhizal diversity in boreal mixed-woods

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Ectomycorrhizal (ECM) diversity was measured in 12 mixed-wood stands in the Abitibi region of north-western Québec. Stands were of similar age and were situated on similar mineral soil deposits, but supported varying proportions of ECM host trees. Host roots were sampled in a manner that enabled their separation into species on the basis of wood anatomy. Shannon diversity indices for the ECM colonizing each host species were determined on the basis of ECM anatomy. The diversity of overstory trees, understory plants and host roots, as well as overstory tree composition, root density and pertinent abiotic factors were measured and used as independent variables in multiple regressions against ECM diversity. We found a positive relationship between overstory tree diversity and ECM diversity, which appears related to fungal host specificity. Although no direct relationship was seen between ECM diversity and soil factors, levels of exchangeable base cations were related to ECM fungal species composition which correlated with ECM diversity at the scale sampled.

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Mycorrhizal fungi are critical for plant growth and survival as they are the main pathway through which plants obtain water and nutrients. Mycorrhizae increase the absorptive capacity of roots while increasing resistance to disease, drought and extreme temperatures (Smith and Read 1997). Recent studies have demonstrated that plant community diversity and productivity increase with increasing diversity of vesicular arbuscular mycorrhizae (VAM, van der Heijden et al. 1998, Klironomos et al. 2000) and that plant productivity increases with increasing ectomycorrhizal (ECM) diversity (Baxter and Dighton 2001, Jonsson et al. 2001). These studies demonstrate the importance of mycorrhizal symbioses in both the structure and functioning of plant communities. Although the relationship between mycorrhizal diversity, plant community diversity and plant productivity has gained recent attention, little is known about the factors which promote mycorrhizal diversity.

Strong relationships have been demonstrated between stand composition and ECM fungal community composition in forests differing both in ECM tree species composition (Billis et al. 1986, Villeneuve et al. 1989, Såstad 1995) and diversity (Jones et al. 1997, Ferris et al. 2000).

Any direct relationships between the plant and ECM fungal communities are most likely to result from the specificity (or preference) of some fungi for particular hosts plants, or vice-versa. However, studies of ECM fungal distributions have also demonstrated strong influences of soil factors on the formation of ECM and sporocarps (Mason et al. 1986, Hansen 1988, Tyler

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1989, Rühling and Tyler 1990). Soils may also have an indirect influence by determining plant community composition, which then influences the ECM fungal community. Thus, mycorrhizal diversity is most likely governed by a combination of vegetation and direct and indirect soil influences (Johnson et al. 1992, Nantel and Newmann 1992, Claridge et al. 2000, Kernaghan and Harper 2001, Burrows and Pfleger 2002).

Other factors that may affect ECM community structure include stand age (Visser 1995, Smith et al. 2002) and climate and topography (Claridge et al. 2000), but the dominant influences on ECM diversity in natural ecosystems have yet to be clearly identified. The objectives of this study were, therefore, to examine the correlations between ECM diversity, plant community attributes and organic soil properties, in a range of boreal mixed-wood plots which vary in overstory diversity and composition. Because of the host specificity (or preference) exhibited by some ECM fungi, we expected ECM diversity to increase with increasing host tree species diversity. However, we also expected ECM diversity to be correlated with organic soil properties, which are related to overstory composition.

Material and methods

Site description and collection

Twelve semi-permanent, 100 m^2 plots were selected from an existing design in the Lake Duparquet Research and Teaching Forest (Paré and Bergeron 1996, Côté et al. 2000, Légaré et al. 2001), located in northwestern Quebec (48°30′N; 79°20′W). The site is in the western *Abies balsamea-Betula papyrifera* bioclimatic domain (Grondin 1996). The average annual temperature is 0.8°C, daily mean temperature is −17.9°C in January and 16.8°C in July, and the average annual precipitation is 856.8 mm (Environment Canada 1993). Plots are located in mature stands (either 79 or 86 years old) which support varying proportions of *Abies balsamea*, *Picea glauca*, *Populus tremuloides*, *P. balsamifera*, *Betula papyrifera* and *Pinus banksiana*. Because plots were originally selected to represent four common overstory types, three were dominated by *Betula*, with small *Abies* and/or *Picea* and/or *Populus* components, 3 were dominated by *Pinus*, with small components of the other 4 host trees, 3 were dominated by *Populus* with small *Abies* and/or *Picea* and/or *Betula* components and 3 were co-dominated by *Abies* and *Picea* with a *Betula* component. Shannon diversity indices for overstory trees ranged from 0.18 to 0.74 (Fig. 1a). The plots are situated on a large glaciolacustrine clay deposit, making mineral soils relatively homogenous (Paré and Bergeron 1996), but post-fire successions have proceeded along various pathways, leading to a number of different stand types of similar age (Bergeron 2000).

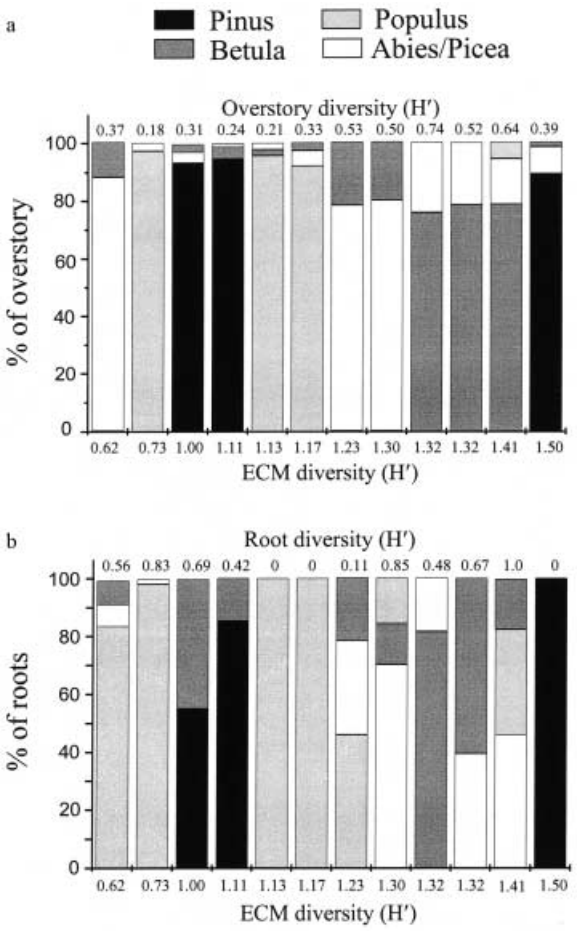

Fig. 1. (a) Stacked histogram of overstory species composition on each of the 12 plots, showing overstory and ECM Shannon diversity indices. Plots are arranged from lowest to highest ECM diversity (H′). (b) Stacked histogram of root species composition on each of the 12 plots, showing root and ECM Shannon diversity indices. Plots are arranged from lowest to highest ECM diversity (H′).

To assess the understory vegetation, herb, shrub and tree species less than 1 m high, or of a diameter at breast height less than 1 cm, were sampled in the summer of 1998. Ten randomly distributed sub-plots (1×1 m) were installed in each 10×10 m plot. The percent cover of each species was estimated in each sub-plot and the mean cover of each species was calculated for each plot. The relative abundance of overstory trees was determined on the basis of relative basal area.

To measure the organic soil properties, four samples were taken from the FH horizon in each plot. The samples were pooled, air dried then ground. The pH was measured in distilled water (McKeague 1978). Exchangeable cations were extracted with 0.1M $BaCl_2$ and determined by atomic absorption (Hendershot et al. 1993). Available phosphorus was extracted with Bray II (McKeague 1978) and analyzed spectrophotometrically. Sub-samples were digested in sulphuric acid and hydro-

gen peroxide (Allen 1989). Concentrations of total N in the digests were determined colorimetrically by Flow Injection Analysis (Tecator Fiastar 5020 Analysis). Mineral N (NH_4 and NO_3) was extracted with 2M KCl and quantified using flow injection analysis (Tecator FIA Star 5020). Organic Carbon was determined by loss on ignition (organic $C = 0.58) \times$ organic matter (Allen 1989).

Available light at the forest floor was assessed using an LAI-2000 plant canopy analyzer (LICOR Inc., Lincoln, NE), which measured photosynthetic photon flux density (PPFD). Climactic factors were considered to be similar across the plots. For more detailed descriptions of the study area and of soil and vegetation sampling methods, see Légaré et al. (2001).

Because forests in the region are unmanaged and naturally regenerate as mixed stands after fire, no single species stands were available on sites with comparable soils and climate. We therefore assessed the ECM species composition and diversity on individual host species as follows. Three 15×15 cm samples of forest floor material were collected from each plot in October 2000. Intact root systems were removed from the soil by wet sieving and coarse roots (> 1 mm $\varnothing$) were separated according to host tree species on the basis of wood anatomy. The characters used included the type of perforation plate, cross field pitting and the presence of resin canals (Core et al. 1979, Agerer 1987–1998). For each species, the length of all coarse roots was measured. Fine roots were then removed from the coarse roots and cut into small (0.5–1 cm) lengths and distributed evenly in water across the surface of a 22×26 cm pan marked with 2×2 cm squares. Fine roots which fell into any one of 30 randomly chosen squares were removed and assessed for ECM until 100 tips had been collected.

ECM diversity on individual hosts

One hundred ECM tips from each host in each soil sample were characterized as follows: using a dissecting microscope, they were first grouped into general morphological categories based on colour, texture and the abundance and type of emanating hyphae. Several ECM representative of each group were then squash-mounted for anatomical characterization using the $100 \times$ oil immersion objective of a Ziess photomicroscope. The choice of mountant for anatomical description was made on the basis of ECM morphology. For example, ECM which exhibited general morphologies characteristic of the Russulaceae were mounted in sulphovanillin (Singer 1986), in order to observe potential reactions with steryl velutinol (Camazine and Lupo 1984, Kernaghan et al. 1997), whilst those with morphologies characteristic of the Thelephoraceae were mounted in KOH, in order to observe possible reactions with Thelephoric acid (Agerer et al. 1995, Kernaghan 2001). Other anatomical characters used to distinguish phenotypicially distinct ECM included; 1) mantle characteristics, such as the cellular pattern and presence of cystidia, laticifers, or other distinctive cells and 2) hyphal characteristics including the presence or absence and type of clamp connections, melanization, ornamentation (e.g. crystals and papillae), hyphal constrictions, septation and formation of hyphal strands. General anatomical characters of ECM are described in detail in Agerer (1987–1998), Ingleby et al. (1990) and Goodman et al. (1996–1997).

Data on the relative proportions of morphologically distinct ECM on each host were used to produce Shannon diversity indices for each individual host occurring in each soil sample. Because *Picea glauca* and *Abies balsamea* have similar growth requirements and co-occur in the study area, data on their above ground abundance have been pooled in previous studies (Paré and Bergeron 1996, Côté et al. 2000, Légaré et al. 2001). Because of this, and the fact that smaller roots of *Picea* and *Abies* could not be reliably separated, data on the abundance of their roots were also pooled. If less than 100 root tips of a given host species were found in a sample, the data for that species were not used for diversity calculations. In order to determine the influence of sample size on ECM diversity, simple linear regressions were also performed on the ECM diversity data against root abundance for each host species.

Relationships among individual ECM fungi and hosts were explored graphically using correspondence analysis. This analysis was performed on a host species-ECM morphotype matrix containing data on the abundance of the 20 most common and distinct ECM types using PCord software (McCune and Mefford 1999).

ECM diversity in soil samples (multiple hosts)

ECM diversity indices for soil samples containing the roots of multiple hosts were then calculated from the data on individual host roots. Data from each host in each plot were pooled and a reduced data set comprising an equal number of root tips (100) from each host was randomly generated. Shannon diversity indices for each soil sample were then calculated from this reduced data set.

The χ^2 distance (Legendre and Legendre 1998), a measure of community dissimilarity, was calculated for the ECM fungi colonizing the hosts found within each soil sample. In other words, the differences between the ECM communities on each host species' root system in each soil sample were quantified. The magnitude of the χ^2 distance for a soil sample is due to the level of host specificity/preference occurring in that sample. χ^2 values were averaged for each host combination across all soil samples (average χ^2 (host)).

Relationships between ECM diversity and environmental factors

In order to correlate ECM diversity with environmental factors measured at the plot level, diversity indices calculated for each soil sample were averaged (n = 3) to obtain a single Shannon index for each plot. Exchangeable base cations (K, Ca and Mg) were summed after transformation to charge unit (cmol/kg). A correlation matrix was then produced which included data on ECM diversity, the measured independent environmental variables and the combined base cation data. This matrix was inspected for colinearity and used to select variables for further statistical analysis.

Two stepwise regression analyses were performed using SPSS v. 10.0.0 (SPSS Inc. 1999) with ECM diversity as the dependent variable. The first regression used the following independent variables: % overstory *Populus*, % overstory *Betula* % overstory *Pinus*, % overstory *Abies*/*Picea*, amount of light reaching the forest floor and Shannon indices for overstory tree diversity, host root diversity and understory plant diversity. The second regression used the following independent organic soil variables: pH, sum of $K_e + Ca_e + Mg_e$, available P, C/N ratio and the depth of organic material. In each case the residuals were plotted to assess deviations from the assumptions required for the multiple regression analysis. Data on the abundance of the two most common mycorrhizal types, *Cenococcum geophilum* and members of the genus *Russula*, were also compared to ECM diversity in simple linear regressions.

χ^2 values were averaged across soil samples from each plot (average χ^2 (plot)). In cases with more than two species of host roots per sample, values for the two most dissimilar communities were used. Average χ^2 (plot) values were also correlated with data on ECM diversity in a simple linear regression.

Results

ECM diversity and composition

Populus was the most common host species, with roots occurring in 19 of the 36 soil samples and on 7 of the 12 plots. *Betula* roots were found in 16 of the soil samples and on 8 of the plots, either *Abies* or *Picea* roots were found in 14 samples and on 7 plots and *Pinus* roots were found in only 7 samples and on 3 plots (Fig. 1b). Simple linear regressions of ECM diversity against the abundance of roots for each host species indicated that there was no significant relationship between root density and the calculated sample ECM diversity for any of the host species. There was also no significant relationship between the species richness of roots and ECM diversity. Analysis of variance also indicated no significant differences in ECM diversity among hosts (F = 0.494, p = 0.688, n = 4, Table 1), or among plots (F = 2.208, p = 0.055, n = 12). However, the average χ^2 distances for each host root combination (*Betula*-*Abies*/*Picea*, *Betula*-*Populus*, *Betula*-*Pinus* and *Populus*-*Abies*/*Picea*) were significantly different among host combinations (ANOVA, F = 9.393, p = < 0.000) and the fungal communities colonizing *Betula* and *Populus* roots were significantly more similar that the fungal communities colonizing other host root combinations (Fig. 2). Correspondence analysis of the host species and the 20 most common and distinctive ECM types ($\lambda_1 = 0.4146$, $\lambda_2 = 0.03225$, Fig. 3) demonstrates the levels of host specificity/preference exhibited by each ECM type. Three ECM types were either specific to (Ascomycete 1, and Thelephoraceae 1), or showed strong preference for (*Russula* 4), *Abies*/*Picea*. *Russula* 1 was specific, and Thelephoraceae 5 showed a strong preference for, *Populus*. *Russula* 2 was only

Table 1. Percentages of dominant ECM types, average richness values (S), and average Shannon diversities (H′) on each host species. For H′, values with the same superscript are not significantly different.

	Host			
	Abies/*Picea*	*Betula*	*Pinus*	*Populus*
Piloderma fallax			13.7	
Cenococcum	23.6	34.8	14.4	54.4
Cortinarius like			14.7	
Lactarius spp.		9.1		
Russula spp.	16.5	15		16
Thelephoraceae				13.5
Ascomycete 1	15.2			
Misc. types	30	26	12	23
Ave. S	5.08	4.8	4.7	4.6
Ave. H′	0.924[a]	1.045[a]	1.02[a]	0.913[a]

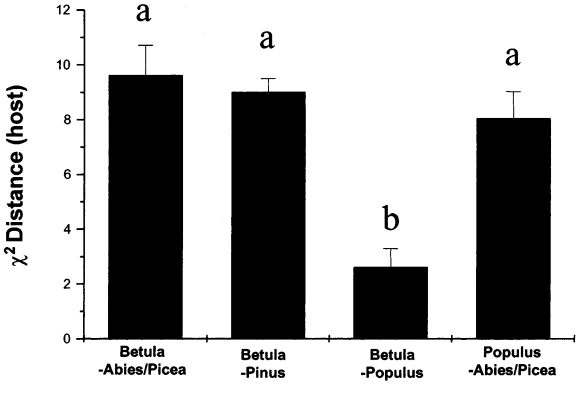

Fig. 2. Histogram of average χ^2 distances (host) calculated for each host root combination found. Different letters on bars denote significant statistical difference.

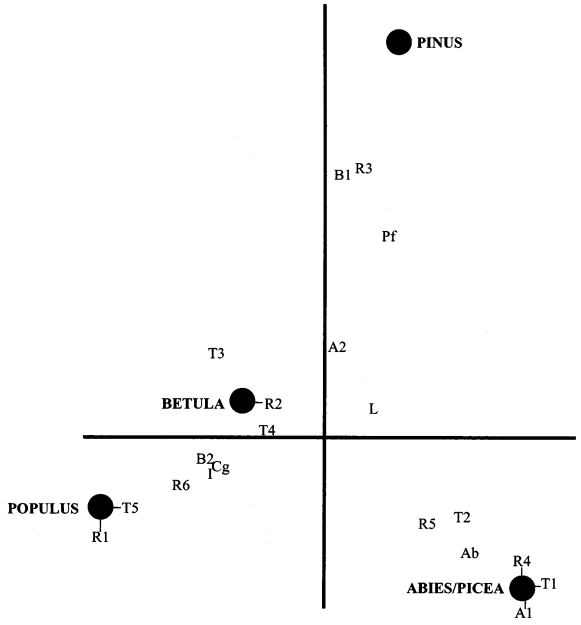

Fig. 3. Correspondence analysis of hosts and ECM fungi. Hosts are represented by large circles and ECM types by letters. Abbreviations of ECM types are: ascomycete 1-2, A1-A2; Ab, *Amphinema byssoides*; unidentified basidiomycete 1-2, B1-B2; Cg, *Cenococcum geophilum*; I, cf. *Inocybe*; L, *Lactarius*; Pf, *Piloderma fallax*; *Russula* 1-6, R1-R6; Thelephoraceae 1-5, T1-5. ECM types found exclusively on a single host are connected to that host symbol by a line.

found on *Betula* roots. None of the dominant ECM types were specific to *Pinus*, although *Russula* 3 and Basidiomycete 1 showed some preference. *Populus* and *Betula* are relatively close together on the diagram, again indicating that they are the most similar with respect to the ECM communities they support. Twelve of the 20 ECM types plotted were found on both *Betula* and *Populus* and form a distinct group on the left of the diagram. Similar relationships among hosts were observed when the ordination was performed using all ECM types encountered.

Relationships between ECM diversity and environmental factors

The average ECM diversity of the twelve plots studied (based on 3 samples per plot) ranged from 0.616 in a plot dominated by *Abies*/*Picea* to 1.504 on a plot dominated by *Pinus* (Fig. 1a, b). The multiple regressions using biotic and abiotic data indicated that overstory tree diversity was the only measured factor that had a significant relationship with ECM diversity (ECM diversity $= 0.730 + 1.002 \times$ overstory tree diversity, $R^2 = 0.379$, $p = 0.044$). Fig. 4a depicts this relationship as a simple linear regression. Although none of the other factors measured exhibited a significant relationship with ECM diversity, the correlation matrix revealed significant relationships among soil factors, vegetation factors and the abundance of the two most common ECM types (Table 2).

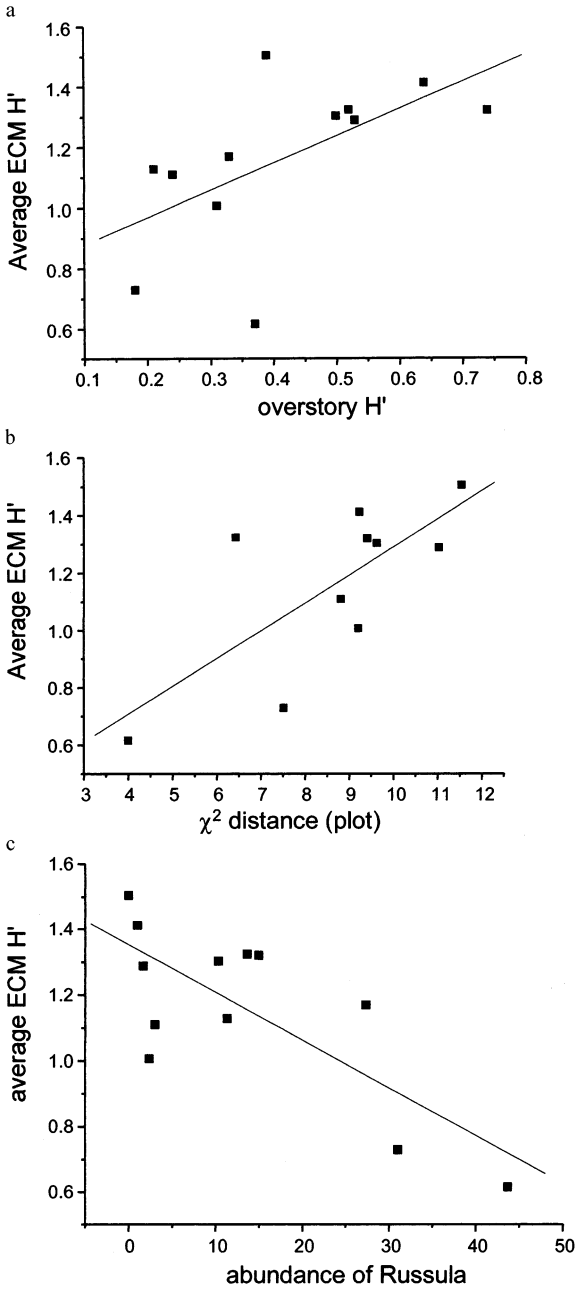

Fig. 4. (a) Linear regression of overstory diversity (H′) against ECM diversity (H′). $r^2 = 0.345$, $p = 0.045$. Each point represents the average ECM diversity from 3 samples per plot. (b) Linear regression of χ^2 distance (plot) against ECM diversity (H′), $r^2 = 0.532$, $p = 0.016$. Each point represents the average ECM diversity from 3 samples per plot. (c) Linear regression of abundance of *Russula* mycorrhizae against ECM diversity (H′), $r^2 = 0.577$, $p = 0.004$. Each point represents the average ECM diversity from 3 samples per plot.

Table 2. Significant Pearson correlations between vegetation factors, edaphic factors and the abundance of the two most common ECM types.

Vegetation factors	Edaphic factors	Slope (r)	Significance (p)
Overstory *Populus*	Summed exchangable cations	0.874	0.000
Overstory *Abies*/*Picea*	pH of organic soil horizon	−0.691	0.018
Overstory *Pinus*	pH of organic soil horizon	0.706	0.015
Diversity of understory plants	Depth of organic material	0.583	0.047
Diversity of understory plants	Summed exchangable cations	−0.788	0.002
Abundance of *Russula* ECM	Summed exchangable cations	0.606	0.037
Abundance of *Cenococcum* ECM	Summed exchangable cations	0.763	0.004
Abundance of *Cenococcum* ECM	Overstory *Populus*	0.674	0.016
Abundance of *Cenococcum* ECM	Overstory *Pinus*	−0.811	0.001
Abundance of *Cenococcum* ECM	Diversity of understory plants	−0.733	0.007

Simple linear regressions showed that the χ^2 distance (plot) and the proportion of *Russula* mycorrhizae had a positive ($r^2 = 0.532$, $p = 0.016$) and a negative ($r^2 = 0.577$, $p = 0.004$) relationship, respectively, with ECM diversity (Fig. 4b and c).

Discussion

We have demonstrated a positive correlation between ECM diversity and overstory host tree diversity. This agrees with the general relationship seen between plant diversity and the diversity of a wide variety of other organisms (Murdoch et al. 1972, Huston 1994). The most probable mechanism for the observed increase in ECM diversity with tree diversity is an increase in resource heterogeneity (Tilman 1987, Rosenzwieg 1997) in combination with specificity/preference of ECM fungi for certain hosts. The influence of host specificity/preference on local ECM diversity is illustrated by the positive relationship between the dissimilarity among the ECM fungi on different host species (estimated by the χ^2 distance) and the ECM diversity on each plot (Fig. 4b).

Molina et al. (1992) reviewed published data pertaining to specificity in ECM fungi and found that although ECM fungi can vary greatly in their host ranges, species associated with particular host genera (narrow range fungi) were common. In a similar review of British ECM fungi, Newton and Haigh (1998) estimated that 40% were specific to individual host plant genera. This trend was also demonstrated empirically by Massicotte et al. (1999), who found host genus specific ECM associations in artificially constructed mixtures of tree seedlings. Although recent studies using PCR based identification of ECM fungi directly from root tips have demonstrated only low levels of host specificity in mixtures of *Pinus* and *Picea* (Cullings et al. 2000) and *Pinus* and *Pseudotsuga* (Horton and Bruns 1998), our results indicate that 30% of the most abundant ECM fungi we encountered exhibited host specificity and another 25% exhibited some level of host preference (Fig. 3). Our data also suggest that ECM host specificity/preference plays a particularly important role in the ECM diversity of mixed stands comprised of both angiosperm and gymnosperm hosts.

The identification of host species on the basis of root anatomy allowed us to separate the influence of overstory composition from the influence of overstory diversity on ECM diversity. Using this approach we determine that the average ECM diversity was similar on each host (Table 1), allowing us to compare ECM diversity across plots with different species compositions. Also, the proportions of each tree species in both the overstory and in the soil (as roots) proved to be non-significant in the multiple regression analysis against ECM diversity.

Our ability to separate the host roots by species also allowed us to determine the differences between the ECM species composition supported by each host (essentially the β diversity) within a soil sample. *Betula* and *Populus* supported more similar ECM communities than the other host combinations (Fig. 2 and 3), even though *Betula* and *Populus* do not commonly co-occur on the same plots. This trend is also evident from the differences in χ^2 distances among the angiosperm-angiosperm and angiosperm–gymnosperm host combinations (Fig. 2). Soil samples containing hosts which support relatively similar ECM communities, such as *Populus*-*Betula* mixtures, also supported lower ECM diversities (average H′ of 0.86) compared to combinations with higher χ^2 distances, such as *Picea*/*Abies*-*Betula* (average H′ of 1.14). This trend is apparent in Fig. 1a, in which 5 of the 6 plots with the highest ECM diversities support significant proportions of both angiosperm and gymnosperm hosts. Examination of the ECM of the individual hosts on these plots reveals that this is not related to any difference in ECM diversity on the individual host species per se, but rather to both higher overstory diversity and perhaps more importantly, greater differences (β diversities) among the ECM communities supported by the hosts. Although the plot with highest ECM diversity (ECM $H' = 1.50$, overstory $H' = 0.39$) supported mainly conifers (*Pinus* and *Picea*/*Abies*, Fig. 1a), these hosts also had very dissimilar ECM communities, based on ordination of the most abundant ECM types (Fig. 3).

Therefore, even though there was no significant difference seen in the ECM diversities supported by individual tree species, host species composition still plays an important role in determining local ECM diversity in mixed stands, through the combination of the different ECM species associated with each host.

We found a correlation between ECM diversity and overstory diversity, but not with root diversity or with root richness. This may be due to the fact that the three *Picea*/*Abies* dominated plots were located within relatively small conifer stands, and there was introgression of surrounding angiosperm roots, leading to poor correlations between above-ground and below-ground measures of host plants on these plots. The relationship between ECM diversity and overstory diversity, rather than root diversity, could also reflect the effects of overstory tree composition beyond that imparted by the roots alone. Higher overstory diversity should lead to increased litter heterogeneity, which has been suggested as a possible determinant of ECM diversity (Bruns 1995).

Although we did not see any direct relationships between soil factors and ECM diversity, there was a positive relationship between the summed exchangeable base cations and the abundance of ECM formed by the two most common ECM types (*Cenococcum* and *Russula*, Table 2). The importance of forest soil chemistry in fungal species distributions has also been reported by Hansen (1988) and Rühling and Tyler (1990). We also noted a strong negative relationship between the abundance of *Russula* ECM and ECM diversity at the scale of our soil samples (Fig. 4c). Although the relationship between *Russula* and ECM diversity is based on pooled data on all *Russula* types encountered, it is most clearly seen with *Russula* 1 and *Russula* 6 (Fig. 2), which tend to dominate soil samples (sometimes completely), excluding other ECM types. A relatively high density of *Russula* ECM has also been noted for *Russula brevipes* in Californian *Pinus* stands (Taylor and Bruns 1999).

In conclusion, we have demonstrated that ECM diversity in a boreal mixed-wood forest is positively related to overstory diversity. This pattern may be explained by the positive relationship between ECM diversity and the dissimilarity among the fungal communities supported by different hosts occupying the same soil sample. These dissimilarities are most likely due to specificities or preferences exhibited in some of the plant-fungal symbioses and appear to be greatest between angiosperm and gymnosperm hosts. Although these conclusions are based on correlative data, the obligately symbiotic nature of many ECM fungi make them difficult to culture (Taylor and Alexander 1989, Köljalg 1992) and therefore not amenable to laboratory experiments.

Our study demonstrates a positive correlation between plant and ectomycorrhizal (ECM) diversities. As van der Heijden et al. (1998) have recently demonstrated a positive influence of endomycorrhizal (VAM) diversity on plant diversity, the possibility then exists that ECM diversity in mixed-wood forests may be maintained by a positive feedback between plant and fungal communities.

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