ECOLOGY OF ECTOMYCORRHIZAL-BASIDIOMYCETE COMMUNITIES ON A LOCAL VEGETATION GRADIENT

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Abstract. To understand the factors that structure ectomycorrhizal-basidiomycete communities at a local scale, we measured the strength of the relations among the fungal communities, the tree communities, and the environment of a series of forest ecosystems in southern Québec. We collected fruit bodies belonging to ectomycorrhizal-basidiomycete families and genera, sampled the woody vegetation, and described soils and landforms at 11 permanent sampling stations. We first calculated similarity matrices among stations, one for each descriptor (fungal species abundance, woody species abundance, and abiotic variables). We then explored the dependence among these matrices using Mantel and partial Mantel tests, path analysis, and comparisons of ordinations and classifications. Similarity among ectomycorrhizal fungus communities was strongly and significantly correlated with tree community similarity, even when controlling for the effect of environmental similarity. When the tests were made with a similarity matrix based on those tree species that are known to be hosts of ectomycorrhizal fungi, abiotic similarity explained a significant portion of the residual variation in the similarity among fungus communities. To explore this complex relationship further, we analyzed species associations. The preference of fungus associations for different sets of abiotic conditions showed that some factors affecting fungal species distribution were different from those affecting the distribution of their tree hosts. Direct and indirect gradient analyses showed that humus characteristics seemed to be important niche dimensions of ectomycorrhizal fungi. The continuum concept was useful to interpret the complex relations among symbiotic species. Trees were the main component of the realized niche of ectomycorrhizal Basidiomycetes, but the fungal symbionts of a particular tree species followed that tree species for only a part of the abiotic gradients over which the host tree was found. This type of distribution predicts that beta diversity of fungi would be generally higher than beta diversity of ectomycorrhizal-forming trees. It also means that the ratio of fungus species richness to woody species richness would be high for most community gradients. Our results and those of previous mycosynecological studies agree with these predictions. The results have implications for the conservation of biodiversity: site selection for conservation based on vegetation classification or mapping, or on distribution of tree species, may miss important fungal species.

Key words: Basidiomycetes; biological associations; canonical correspondence analysis; diversity of ectomycorrhizal fungi; ecological classification; ectomycorrhizae; gradient analysis; macrofungal synecology; Mantel tests; path analysis; tree communities; trees-fungi-environment relationships.

INTRODUCTION

Synecology of macrofungi has been investigated mostly by European mycologists (Cooke 1948, 1953, 1979, Hueck 1953, Apinis 1972, Darimont 1973). Many of these studies were inspired by the "floristic-sociological approach" that had been developed with vascular plants. Results show generally a high fidelity of many fungus species for particular plant associations (e.g., Lisiewska 1974). However, the different ecophysiological groups of fungi (saprotrophes, mycorrhizae, parasites) play quite different roles in an ecosystem and are linked in different ways to the host plant species. Consequently, studies of trees–fungi–environment relationships must aim at one of these groups at a time, as in the work of Bills et al. (1986) on ectomycorrhizal-basidiomycete communities (EBC). Recently, the work of Villeneuve et al. (1989) shows that the diversity of ectomycorrhizal taxa is more clearly related to percentage cover of ectomycorrhizal hosts than to the diversity of vascular plants.

An association between two taxocenes, like EBC and plant communities, poses an obvious problem of interpretation. Indeed, it can imply: (1) that some environmental factors controlling the distribution of symbiont (plant) species are the same as those structuring the distribution of fungal species, (2) that the composition of a plant community affects directly or indirectly the composition of the fungal community that shares the same habitat, or (3) both.

The purpose of this study was to identify the factors...
that affect the composition and structure of EBC at a small ecological scale. Trees-fungi-environment relationships were treated as a problem of multiple correspondence between three matrices (descriptors by sampling station) where the descriptors were: (1) woody species abundance (including the different growth stages of the trees); (2) ectomycorrhizal-basidiomycete species abundance, evaluated using the frequency and biomass of basidiomata (sporophores of Basidiomycetes; “fruit bodies”); and (3) the environmental variables. We measured the relationship between such matrices using a two-step procedure: (1) computation of similarity matrices among stations, one for each type of data, and (2) computation of a series of: (i) correlations between all combinations of two of these similarity matrices, and (ii) partial correlations between the same pairs of matrices, removing the effect of the third one. This last step involved Mantel tests (Mantel 1967) as well as partial Mantel tests as described in Smouse et al. (1986). The reasoning behind this approach is the following: if the composition of EBC depends upon the composition of the tree community, then when a pair of tree communities are similar, the EBC of the same two sample stations should also be similar to the same extent. This approach was needed to provide an objective measure of the strength of the association between taxocenes and an unequivocal way to interpret it. To our knowledge, our work represents the first direct and quantitative approach to this problem.

The results are discussed within the framework of the continuum concept (Whittaker 1967); ecological relations between symbionts are viewed as relations between distribution curves of the associated species of the two taxocenes along an environmental gradient. Most fungal species may follow their tree symbionts for only a part of the abiotic gradients over which the host tree was found or along all of these gradients; this will have different consequences on the beta diversity and on the ratio of fungus species richness to woody species richness in the corresponding community gradient (coenoclone). This, in turn, has important implications for the conservation of biodiversity.

**METHODS**

**Geographic and biogeographic aspects of the sampling site**

The sampling site was located at the “station de biologie de l’Université de Montréal,” which occupies a portion of the lower Laurentides, ≈80 km north of Montréal (74° W; 46° N; altitude: 400 m). The climate is continental-temperate: the mean annual temperature is 2.5°C (maximum: 10°C, minimum: −2.5°C), total annual precipitation is 1000 mm, thermic amplitude is 32°C with a mean number of 110 d without frost (Wilson 1971, Houde 1978). The site, with an undulating and mountainous relief, lies on the southern flank of the Precambrian Shield. Soil parent material is mostly glacial till, but organic soils are common. The dominant soils are ferro-humic podzols (Commission canadienne de pédologie 1978) with a sandy-loam texture. In Grandnert’s classification of Québec forests (1966) the climax vegetation of the site is yellow birch–maple. Today, it is dominated by white birch (Betula papyrifera) stands mixed with sugar maple (Acer saccharum) that occupy mesic sites disturbed in the past by cutting and fire (Gagnon 1975). Pure sugar maple stands mixed with yellow birch (Betula alleghaniensis) and beech (Fagus grandifolia) are mostly found in mesic areas where the till is thick and where the disturbances have been minor. White pine (Pinus strobus) stands and balsam fir (Abies balsamea) stands occupy rapidly drained sites where soil is thin. Organic soils are colonized by boggy vegetation in most places, but Thuja occidentalis stands have developed on organic soils localized at the bases of seepage slopes.

**Vegetation sampling and description of the stations**

With aerial photographs and field experience we selected 11 sampling plots of 20 × 20 m that represented the six different major vegetation types that we perceived. In each plot we recorded the woody vegetation using the methods described in Gagnon and Bouchard (1981), except that we sampled neither the woody vegetation nor the bryophyte strata. This method includes estimates of abundance for all tree species in three different diameter classes (seedlings, saplings, and trees) and of all shrub species. For plot descriptions we recorded the following geomorphological characteristics using the guidelines and terminology of Day and McMenamin (1983): altitude, aspect, slope (percentage, form), position of the station on the slope, superficial deposit type and relative thickness, micro-relief, stoniness, rockiness, and flooding. We also noted signs of past disturbances.

**Soil analyses**

All soil samples were taken within 2 d in the 1st wk of June to reduce variability imposed by the weather. In the field we measured the horizon thickness, including the humus layers (with the definitions found in Day and McMenamin [1983]). The definition of mineral horizons was based on that of the Commission canadienne de pédologie (1978): A = pale horizon where leaching occurs (eluvial horizon); B1 = dark horizon where accumulation of organic matter and iron oxides occurs; B2 = lower horizon (BC) with a yellower hue and a weaker color value. To record the color of mineral horizons, we took fresh samples and used the Munsell code of colors (Munsell Color Company 1969). We measured pH with fresh soils, <24 h after the sampling, using a Metrohm Herisau pH meter and a 0.01 mol/L CaCl2 solution. Soil samples were then dried, allowing us to evaluate their water content—here defined as the mass of water expressed as a percentage of the total mass of the undried sample (percent
water). Dry samples were used for the remaining analyses: (1) granulometric analysis (for particles >4 mm in diameter, using the sieving technique; for particles <2 mm, using the hydrometer method [Bouyoucos 1962] with the pre-treatment found in McKeague [1978: 16-17]); (2) determination of the organic matter content, which corresponds to the percentage of dry sample mass that was lost on ignition (percent organic matter); and (3) measure of major elements, including: (a) exchangeable bases, using the methods of Brown (1943); (b) concentration of individual exchangeable cations Ca$^{+2}$, Mg$^{+2}$, and K$^+$, using a Perkin-Elmer 2380 atomic absorption spectrophotometer, following the extraction procedures and calculation found in McKeague (1978: 84-87); (c) phosphorus soluble in water (as an availability index), using the molybdenum blue technique [Olsen and Dean 1965]; (d) the total nitrogen content, using the Kjeldahl method.

**Sampling of the ectomycorrhizal-basidiomycete communities (EBC)**

For sampling of the ectomycorrhizal Basidiomycetes, we divided each station (plot) in 100 2 x 2 m sub-quadrats to evaluate the spatial frequency of each species according to the principles discussed in Bills et al. (1986). During the summer of 1986, we regularly visited six stations and collected all the basidiomata of ectomycorrhizal species that could be found. Each station was sampled at least eight times between 15 June and 30 August. In 1987 we regularly visited 11 stations and each was sampled 9 or 10 times between 28 May and 8 September. At each visit we recorded the position in the grid of all basidiomata and identified specimens in the laboratory. After dry-mass determination, all specimens were kept dried in a herbarium.

We collected all the Basidiomycetes taxa considered as ectomycorrhizal by Trappe (1962) and Miller (1983). We were also guided in our choice by Godbout and Fortin (1985) and several taxonomic monographs (Hesler and Smith 1963, Largent 1977, Pomerleau 1980, 1984, Singer 1986). For practical reasons we excluded all the "Gasteromycetes" taxa which were, in any case, rarely found in our sampling stations. On the other hand, we included taxa for which the mycorrhizal status had not been proven yet: some Hygrophorus and Entolomaceae species in particular.

**Data analysis**

Before analysis we made the following manipulations and transformations of the raw data. (1) Within each station we calculated the relative dry mass for each species of ectomycorrhizal Basidiomycetes by dividing its dry mass by the total dry mass of all the species of the same plot and multiplying the result by 100. This was done for the biomass of one or two seasons, according to the length of the record for each plot. We also counted the number of sub-quadrats in which each species was found (spatial frequency), for one or two seasons as above, and computed a value of relative spatial frequency by dividing its frequency by the total frequency of all the species of the same plot.

(2) We calculated a relative "importance" value for each species at each plot. For the ectomycorrhizal Basidiomycetes this was done by adding relative dry mass and relative spatial frequency. For members of the canopy layer (mature trees) we added relative dominance (percentage of the total basal area) and relative density. For the shrubs we combined the relative spatial frequency with the relative dominance based on total shrub cover. For the seedlings we added relative frequency, relative cover, and relative density. For the sapling stratum the importance value was simply the relative density. By keeping canopy trees, saplings, and seedlings separate we were able to search for relations between fungal species and life stages of the tree species. Indeed, successions of ectomycorrhizal species during the developmental stages of different tree species are documented by Marks and Foster (1967), Mason et al. (1982), Dighton et al. (1986) and Garbaye et al. (1986).

Finally, (3) we removed from the final matrices: (a) the fungi not completely identified (identification to the genus only) and (b) the fungus and tree species that occurred at one sampling station only. The abundance values of unidentified rare species contributed to the percentage values of the other species in the same plot but were not involved in the other steps of the analysis.

Some soil descriptors were combined to reduce the number of abiotic variables and to ease interpretation. The concentration of all nutrients (Ca$^{+2}$, Mg$^{+2}$, K$^+$, available P, and total N) determined in the organic horizon and in three mineral horizons (Ae, B1, B2) were combined by horizon after standardization to a mean of 0 and a variance of 1. These combinations gave, respectively, an index of richness in mineral nutrients of the organic horizon (humus) and an index of the richness in mineral nutrients of the mineral soil. The total exchangeable H$^+$ was combined with the total exchangeable bases to give an index of the total exchange capacity of the different horizons. The total exchange capacities of the three mineral horizons were summed to give an index of exchange capacity of the mineral soil. Finally, for mineral soil the pH, percentage of clay, silt, and sand, and the percentage of water and organic matter were expressed as the mean of the values for the three mineral horizons.

**Comparison of data matrices.**—The relationships among the vegetation, EBC, and the environment can be expressed as the relations among three matrices. We began by computing three similarity matrices among all pairs of plots, one for each type of data. For the similarity among community sample, we chose the Steinhaus coefficient for two reasons: (1) being an asymmetrical coefficient, it does not consider double zeros as an indication of resemblance; (2) Gower and Legendre (1986) showed its reliability for measuring
high and low similarities with the same fidelity. For the abiotic similarity matrix, we used the Estabrook and Rogers coefficient (Estabrook and Rogers 1966) because it can handle data with different levels of precision. The equations and rationale for these two coefficients can be found in Legendre and Legendre (1983).

**Mantel tests among similarity matrices.**—To measure the relations among the three similarity matrices, we computed a series of three Mantel tests (Mantel 1967) and three partial Mantel tests (Smouse et al. 1986). The Mantel test is a correlation test adapted to similarity or distance matrices (Legendre and Fortin 1989). Using the standardized Mantel statistic as the input, we then performed a path analysis (Sokal and Rohlf 1981). This way, the analysis is not standard because Mantel statistics are used instead of Pearson correlation coefficients. Therefore, significance tests of path coefficients cannot be used for interpretation. In a second series of tests, we took a similarity matrix among tree communities computed with only the tree species that are known to be hosts of ectomycorrhizal fungi, according to Trappe (1962), Malloch and Malloch (1981, 1982), Brundrett and Kendrick (1988), and Berliner and Torrey (1989).

**Ordinations and classifications of community samples.**—The main purpose of this step of the analysis was to allow a finer resolution of the relationships revealed by the Mantel tests. All three similarity matrices were used to compute classifications and ordinations. The latter were done through principal coordinate analyses (PCOA). We chose this technique to project, on an orthogonal system of axes, the similarities among samples that have been described above. For the cluster analyses of community samples, we used hierarchical, agglomerative, proportional-link linkage clustering, with connectedness between 0.50 and 0.60. These values of connectedness were chosen to overcome the chaining phenomenon (Legendre and Legendre 1983). Results of the classifications were superimposed on the minimum spanning tree (MST) of the clusters. MST is defined (in a single linkage clustering) as the chain formed by the first similarity link that put an object in a group or that allows two groups to merge (Gower and Ross 1969, Legendre and Legendre 1983). In his computer program for cluster analysis, Legendre (1985) generalizes this concept to the other agglomerative clustering methods. This superimposition was useful to visually compare the structure of the two related taxocenes. To produce abiotic groups of sampling stations, we used a K-means algorithm (MacQueen 1967) with the three first axes of PCOA extracted from the abiotic similarity matrix as the input variables. To associate each station group with the set of abiotic characteristics that caused it, we computed Kendall's nonparametric correlations between the two first axes of the ordination and the environmental variables. We also computed the average of each abiotic variable within each group.

**Direct gradient analyses.**—To analyze in more detail the effect of soil variables on the structure of the tree communities and on the structure of EBC, we computed two canonical correspondence analyses (CCA) (ter Braak 1986, 1987), one for each species data set, but using the same soil variables. CCA is a technique that selects the linear combination of environmental variables that maximizes the dispersion of species scores. We used it because, unlike PCOA, it is able to detect unimodal relationships between species and external variables (ter Braak 1988). We took as the external variables the ones that describe the mineral horizons of the soil, in order to see the different responses of the two taxocenes to the same gradient. The rest of the abiotic variables were correlated with this edaphic gradient after the extraction of the axes. We also computed partial correlations between abiotic variables and the two first axes of the CCA of fungal communities, removing the effect of the corresponding axes of the tree communities. This allowed us to identify the abiotic variables that might influence the distribution of Basidiomycetes independently from the effect of the composition of their associated tree community.

**Relations between trees, Basidiomycetes, and the environment.**—The objective of this series of analyses was to bring out relationships at the species level rather than at the community level. Grouping of species was used mainly to reduce variability because the number of samples is low compared to the high number of species and abiotic variables. Also, we wanted to analyze the effect of environmental variables when these are considered collectively. Therefore, the analysis of the distribution of clusters of species was made using sets of abiotic variables to characterize their habitat.

**Cluster analyses of species.**—To study the relations between each species of ectomycorrhizal Basidiomycetes and individual tree species, we merged in a single table the importance values of fungi and trees for each sampling station. Following the method used by Bergeron and Bouchard (1983) we then computed an association matrix among species using the chi-square similarity coefficient (Roux and Reyssac 1975). With this matrix, we computed a cluster analysis using the agglomerative, complete-linkage method. Species associations were then defined by clusters established at an arbitrarily fixed similarity value.

**Biological associations and habitat preferences.**—To study the interrelations between sets of abiotic conditions and the abundance of the species that belonged to each biological association, we grouped in a two-way contingency table (1) the stations of the same abiotic group and (2) the species of the same clusters of the complete linkage. In this table each combination of a station group with a species cluster forms a cell. In each cell we computed the relative constancy ($R_c$) of the species cluster in the abiotic group of stations. This value ($R_c$) is a measure of the relative weighted average ubiquity of a cluster of species within the series of groups of stations representing different sets of abiotic...
otic conditions. The weighted average ubiquity \( (U) \) of a cluster of species \( (q) \) is given by the following formula:

\[
U_q = \frac{\sum_{i=1}^{m} \left( \frac{\sum_{j=1}^{n} a_{ij}}{n} \right)}{m},
\]

where \( a_{ij} = \) relative abundance of the \( i \)th species of cluster \( q \) in the \( j \)th station of abiotic group \( k \), \( n = \) number of species in the cluster \( q \), and \( m = \) number of stations in the cluster \( k \).

The relative weighted average ubiquity of a group of species \( \text{"q"} \) is given by the following formula:

\[
R_q = 100 \left( \frac{U_q}{\sum_{k=1}^{q} (U_q)_k} \right),
\]

where \( p = \) number of abiotic groups of stations.

We repeated the computation of \( R_q \) using the total relative abundance of each corresponding tree species cluster in each station group. For this, we kept only those tree species that are known to be ectomycorrhized (see references given above in Mantel tests among similarity matrices). Then we computed a correspondence statistic (Neu et al. 1974) with the relative constancy of tree groups as the expected value of the constancy of basidiomycete clusters (observed value). For each comparison, the null hypothesis is that there is no difference between the expected and the observed value; this would indicate that the “habitat preference” of a cluster of fungi is determined by the habitat preference of its associated cluster of ectomycorrhized trees. The alternative hypothesis would indicate an avoidance or a preference (depending on the sign of the difference) of the fungal species clusters over different sets of abiotic conditions, controlling for the effect of ectomycorrhized trees.

Similarity matrices, principal coordinate analysis, cluster analysis, Kendall’s \( \tau \) and Mantel and partial Mantel tests, were all computed with the “\( R \)” package of Legendre and Vaudor (Legendre 1985). Canonical correspondence analyses were computed with CANOCO (ter Braak 1988). Correspondence statistics were computed using our own program.

**RESULTS**

During the two seasons of sampling (summer of 1986 and of 1987) we collected \( \approx 240 \) species of ectomycorrhizal Basidiomycetes at the 11 sampling stations. We were able to identify half of these species (120); 59 of the species were found in more than 1 plot (Table 1). Unidentified species belong mostly to genera Cortinarius and Russula and to the Entolomaceae family. These groups are poorly known in eastern North America and especially in Québec. At the same 11 sampling stations 33 woody species were sampled: 15 trees and 18 shrubs. Of these, 13 species of trees, present in one growth stage or another (Table 2), and 14 shrub species, were identified in >1 station. The similarity matrix among plant communities that was used in the first series of Mantel tests was computed with data of Table 2 only.

For each sampling station, we measured or observed 70 environmental variables: 28 and 15 of them, respectively, describe the chemical and physical properties of the mineral horizons of the soil, 14 measure the chemical and physical properties of the organic horizon (humus), and 13 result from geomorphological observations. After the combinations mentioned above, 37 variables remained (Table 3). They were used in the computation of the abiotic similarity matrix among stations.

Results of Mantel and partial Mantel tests show that the structures of the tree community and the ectomycorrhizal-basidiomycete community (EBC) are strongly correlated, whether the similarity matrix used was based on all tree species (Table 4) or ectomycorrhized tree species only (Table 5). Moreover, the partial relation between composition of tree communities and composition of EBC, removing the effect of abiotic variables, is strong in both comparisons.

For the comparison based on all tree species, the abiotic similarity matrix (SimABIO) is not significantly correlated with any other similarity matrix (Table 4). For the comparison based on ectomycorrhized tree species, correlation and partial correlation between abiotic similarity and EBC similarity, removing the effect of tree communities, are weak but statistically significant (Table 5). The path diagram in Fig. 1 further summarizes these results. The path coefficients presented could not be tested in the usual manner for statistical significance, because similarity matrices are always non-independent variables; the partial Mantel tests in Table 4 can be used as tests of significance of these path coefficients, however. Fig. 1 shows the linear relationships between similarity matrices, and we can see that, in this context, most of the variance of the two biotic similarity matrices remains unexplained by the abiotic data used in this study. The main point, however, is the strong causal relation in Fig. 1 between SimEBC and SimTREES: it represents a significant causal link, because it corresponds to a significant partial Mantel statistic in Table 4, controlling for the effect of the abiotic data.

The structures of the three data matrices are rather similar (Figs. 2–4). Indeed, many pairs of sampling stations are positioned near each other (e.g., 1 and 3, 10 and 7, 11 and 9) on the three ordination diagrams and cluster in the same way. Ordination of either tree communities or EBC separates clearly those communities dominated by deciduous tree species from those dominated by coniferous trees.

The ordination and classification of stations based on abiotic variables separates three groups of stations (plots), each identified by a distinct symbol (Fig. 4). First, there is a clear distinction between the “group” with a wet organic soil (station 5) and the two groups with mineral soils (the rest of the plots). Thus, the first principal coordinate analysis (PCOA) axis is highly
Table 1. Relative importance values* of ectomycorrhizal-basidiomycete species identified in more than one sampling station. Stations were 20 x 20 m plots; here they are sorted according to the similarity of their tree community.

| Basidiomycete species† | Sampling stations |
|------------------------|-------------------|
|                        | 1     | 3     | 2     | 10    | 8     | 7     |
| Hydrophorus ceraceus (Fr.) Fr. | 39.17 | 64.26 | 0     | 0     | 0     |
| Nolanea lutea Pk.§ | 10.66 | 0     | 17.6  | 0     | 0     |
| Nolanea quadrata B. & C. | 7.227 | 0.859 | 15.74 | 0     | 0     |
| Nolanea strietior (Pk.) Pomerleau | 5.715 | 3.637 | 5.334 | 3.78  | 0.706 | 7.492 |
| Hydrophorus parvulus Pk. | 3.402 | 3.271 | 0     | 0     | 0     |
| Hydrophorus cantharellus (Schw.) Fr. | 2.715 | 1.695 | 6.023 | 0     |
| Hydrophorus marginatus Pk. | 2.091 | 45.55 | 3.984 | 1.193 |
| Laccaria laccata (Fr.) B. & Br. | 1.143 | 0     | 1.269 | 3.779 |
| Amanita muscaria (Fr.) Hooker var. formosa (Fr.) Bertillon | 0     | 26.8  | 0     | 18.1  | 3.256 |
| Clavulinopsis fusiformis (Fr.) Cor. | 0     | 7.674 | 29.04 | 0     | 6.06  |
| Hydrophorus laetus (Fr.) Fr. | 0     | 6.223 | 0     | 2.254 | 0.016 |
| Amanita brunnescens Atk. | 0     | 5.131 | 0     | 1.609 | 9.898 |
| Ramariopsis kunzei (Fr.) Donk | 0     | 5.037 | 6.805 | 0     |
| Hydrophorus pallidus Pk. | 0     | 4.586 | 0     | 0     |
| Russula fragilis (Fr.) Fr. | 0     | 3.132 | 2.163 | 9.851 | 12.56 |
| Amanita citrina Schaeff. ex S.F.G. | 0     | 2.645 | 0     | 13    | 0.758 |
| Amanita porphyria (Fr.) Secr. | 0     | 2.52  | 0     | 0     | 4.61  |
| Hydrophorus pratensis (Fr.) Fr. | 0     | 1.692 | 0     | 0     |
| Lactarius thejogatus (Fr.) Fr. | 0     | 1.509 | 29.33 | 0     | 0.719 |
| Paxillus involutus (Fr.) Fr. | 0     | 1.503 | 0     | 0     |
| Hydrophorus anguineus (Fr.) Fr. | 0     | 1.021 | 0     | 0     |
| Russula cyanoxantha (Schaeff.) Fr. | 0     | 12.96 | 0     | 0.839 |
| Amanita flavoconia Atk. | 0     | 0     | 12.51 | 0     |
| Rozites caperata (Fr.) Karst. | 0     | 0     | 8.106 | 6.228 |
| Amanita vagina (Fr.) Vitt. var. fulva Gill. | 0     | 0     | 5.991 | 3.84  |
| Hydrophorus nitidus Berk. & Curt. | 0     | 0     | 3.898 | 0     | 0.622 |
| Russula silvicola Shaffer | 0     | 0     | 47.89 | 9.714 |
| Boletus piperatus Fr. | 0     | 0     | 11.91 | 0     |
| Russula raoulitii Quel. | 0     | 0     | 3.293 | 0     |
| Cortinarius armillatus (Fr.) Fr. | 0     | 0     | 1.997 | 0     |
| Cantharellus cibarius Fr. | 0     | 0     | 1.509 | 3.986 |
| Hebeloma mesophaeum (Pers.) Quel. | 0     | 0     | 24.16 |
| Russula clavariata Grove | 0     | 0     | 6.827 |
| Russula paludosa Britz. | 0     | 0     | 4.395 |
| Cortinarius flexipes (Fr.) Fr. | 0     | 0     | 4.308 |
| Inocybe umbrina Bres. | 0     | 0     | 3.769 |
| Suillus granulatus (Fr.) Kunt. | 0     | 0     | 3.754 |
| Lactarius glyciosmus (Fr.) Fr. | 0     | 0     | 3.549 |
| Amanita virosa Secr. | 0     | 0     | 1.933 |
| Russula puelatis Fr. (?) | 0     | 0     | 1.422 |
| Lactarius lignonius (Fr.) Fr. | 0     | 0     | 1.016 |
| Lactarius thinos Smith | 0     | 0     | 0.948 |
| Boletinus pectus (Pk.) Pk. | 0     | 0     | 0     | 9.848 |
| Leccinum scabrum (Fr.) S. F. Gray | 0     | 0     | 0     | 3.32 |
| Leccinum insigne Smith. Thiers & Watling | 0     | 0     |
| Russula roxipes (Secr.) Bres. | 0     | 0     | 0     |
| Cortinarius bolari (Fr.) Fr. | 0     | 0     | 0     |
| Cortinarius evennus (Fr.) Fr. | 0     | 0     | 0     |
| Lactarius sordidus Pk. | 0     | 0     | 0     |
| Hebeloma testaceum Fr. (?) | 0     | 0     | 0     |
| Russula peckii Sing. | 0     | 0     | 0     |
| Clavulina crisata (Fr.) Schroet. | 0     | 0     | 0     |
| Leccinum holopus (Rostk.) Watling | 0     | 0     |
| Xerocomus submarmosus (Fr.) Quel. | 0     | 0     |
| Cortinarius vibratilis (Fr.) Fr. | 0     |
| Tylopilus felleus (Fr.) Karst. | 0     |
| Hydrophorus miniatus var. miniatus (Fr.) F | 0     |
| Leptonia formosa (Fr.) Gill. | 0     |

* Relative importance value = [relative dry mass (%)] + [relative spatial frequency (%)]
† Nomenclature follows that of Pomerleau (1980, 1984). Species are sorted according to their relative importance value in all sampling plots.
‡ New species for the Québec province.
§ Based on total abiotic similarity (see Fig. 4).
correlated with moisture, which was mainly determined by the nature and the thickness of surface deposits. From right to left on Fig. 4 the soils are also less acidic and richer in mineral nutrients. In the two groups with a mineral soil, we can distinguish stations 1, 4, and 3 at the left bottom of the plan from the rest of the stations at the upper left. Those three plots were dominated by shade-tolerant trees (Table 2), and no burned or cut stumps were observed in them. In the other group of stations (2, 5, 6, 7, 8, 9, 10, and 11), shade-intolerant trees such as Betula papyrifera and Populus grandidentata, and burned or cut stumps were more abundant. This suggests a disturbance gradient.

When examining the means of different variables for each group of plots defined abiotically (Table 3), the mineral horizons of group 1 (stations 1, 3, 4, and 10) were rather rich in mineral nutrients, had a low percentage of water (weak capacity of water retention), and a low percentage of organic matter (loss on ignition). The humus was thick but had a low percentage of organic matter and of water, and was poor in mineral nutrients. Compared to group 1, group 2 (stations 2, 6, 7, 8, 9, 11) had mineral horizons that were poorer in mineral nutrients, but had a greater exchange capacity and a higher percentage of water and of organic matter. The thin humus had a higher percentage of organic matter and of water, and was richer in mineral nutrients.

Canonical correspondence analysis (CCA) dispersed the community samples on environmental axes, i.e., on axes that were linear combinations of edaphic variables. The contribution of each variable involved in the analysis is shown in the table of canonical coefficients (Table 6). The variables that combine a high canonical coefficient with a high associated t value are those that may have had the most effect on community structure. These values have an exploratory use only, since we cannot test their statistical significance (ter Braak 1988).

For tree communities, the first two axes of CCA explain a greater fraction of the variability (67.2%) than for EBC (42.9%). Also, there are more variables with high canonical coefficients for the first axis of tree communities than for the same axis of EBC. All variables have low coefficients on the first axis of EBC, but some contribute more to the second axis (like the total exchange capacity and the mean richness). These results suggest that the edaphic gradient had more effect on the distribution of tree species than on the distribution of Basidiomycetes. Many external abiotic variables are linked to the edaphic gradient, as shown by their correlations with environmental axes (Table 7). For the tree communities, these variables are the slope and humus characteristics (percentage of water, percentage of organic matter and richness in mineral nutrients). For EBC, these variables are the thickness of the litter, percentage of water in humus, slope, thickness and nature of the surface deposit, and aspect.

| Sampling stations | 6 | 11 | 4 | 9 | 5 |
|-------------------|---|----|---|---|---|
| 0                 | 0 | 0  | 0 | 0 | 0 |
| 0                 | 0 | 0.542 | 1.437 | 0.965 | 0.507 |
| 0                 | 0 | 4.514 | 0  | 2.982 | 0  |
| 1.893             | 1.022 | 2.241 | 0  | 0  | 0  |
| 0                 | 0 | 0  | 1.185 | 7.788 | 0  |
| 0                 | 0 | 1.678 | 1.175 | 0  | 0  |
| 2.426             | 2.815 | 0  | 1.609 | 21.74 | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 1.59 | 0  | 5.503 | 0  |
| 6.24              | 0 | 0  | 0  | 0  | 0  |
| 29.18             | 0 | 4.404 | 0  | 1.014 | 0  |
| 2.972             | 5.039 | 0.567 | 21.83 | 4.192 | 0  |
| 4.381             | 0 | 3.722 | 0  | 0  | 0  |
| 2.027             | 8.144 | 17.23 | 7.947 | 6.231 | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0.481 |
| 0                 | 0 | 2.519 | 0  | 1.456 | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0.346             | 17.77 | 0  | 30.41 | 0  | 0  |
| 0                 | 0 | 5.004 | 0  | 1.873 | 0  |
| 0                 | 8.647 | 0  | 3.203 | 1.64 | 0  |
| 0                 | 0 | 12.67 | 0  | 2.072 | 0  |
| 25.85             | 9.519 | 1.592 | 38.17 | 2.558 | 0  |
| 0                 | 1.462 | 0  | 0  | 0  | 0  |
| 2.479             | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 2.786 | 8.141 | 0.535 | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 2.186 | 0  | 0.493 | 0  |
| 13.32             | 3.219 | 0  | 0  | 0  | 0  |
| 0                 | 4.446 | 0  | 0  | 0  | 0  |
| 0                 | 2.194 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 12.03 | 0  | 0  | 0  | 0  |
| 2.435             | 6.63 | 0.565 | 0  | 0  | 0  |
| 0                 | 1.947 | 0  | 16.63 | 0.55 | 0  |
| 0                 | 0 | 0  | 0  | 1.861 | 0  |
| 7.837             | 0 | 75.94 | 8.748 | 0  | 0  |
| 0                 | 7.166 | 0  | 4.553 | 3.641 | 0  |
| 27.52             | 0 | 0  | 0  | 0  | 0  |
| 8.592             | 3.549 | 0  | 0  | 0  | 0  |
| 2.189             | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 17.58             | 0 | 0  | 0  | 0  | 0  |
| 0                 | 13.26 | 9.102 | 0  | 0  | 0  |
| 0                 | 9.395 | 1.556 | 0  | 0  | 0  |
| 0                 | 7.316 | 0.692 | 0  | 0  | 0  |
| 0                 | 5.912 | 0  | 0  | 1.431 | 0  |
| 0                 | 1.273 | 0  | 7.372 | 0  | 0  |
| 0                 | 1.247 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 0                 | 0 | 0  | 0  | 0  | 0  |
| 2                 | 2 | 1  | 2  | 3  | 0  |
Table 2. Relative importance values* of tree species occurring as mature trees or saplings in more than one sampling station. Stations were 20 x 20 m plots; here they are sorted according to the similarity of their tree community.

| Tree species† | 1  | 3  | 2  | 10 | 8  | 7  |
|---------------|----|----|----|----|----|----|
| Acer saccharum (tree)‡ | 200.00 | 161.75 | 0.00 | 0.00 | 0.00 | 0.00 |
| Acer saccharum (sapling)‡ | 60.00 | 100.00 | 65.00 | 4.84 | 64.90 | 0.00 |
| Acer rubrum (tree)‡ | 0.00 | 30.79 | 72.99 | 0.00 | 4.53 | 12.70 |
| Populus grandidentata (tree) | 0.00 | 7.46 | 14.69 | 111.80 | 38.20 | 93.50 |
| Betula papyrifera (tree) | 0.00 | 0.00 | 96.17 | 64.50 | 91.00 | 19.30 |
| Abies balsamea (sapling) | 0.00 | 0.00 | 7.50 | 9.68 | 18.90 | 15.80 |
| Betula alleghaniensis (sapling) | 0.00 | 0.00 | 5.00 | 0.00 | 0.00 | 0.00 |
| Acer rubrum (sapling)‡ | 0.00 | 0.00 | 2.50 | 75.80 | 16.20 | 0.00 |
| Populus tremuloides (tree) | 0.00 | 0.00 | 0.00 | 19.15 | 0.00 | 0.00 |
| Betula papyrifera (sapling) | 0.00 | 0.00 | 0.00 | 9.68 | 0.00 | 57.90 |
| Abies balsamea (tree) | 0.00 | 0.00 | 0.00 | 4.56 | 49.10 | 0.00 |
| Picea glauca (tree) | 0.00 | 0.00 | 0.00 | 0.00 | 6.19 | 0.00 |
| Picea mariana (tree) | 0.00 | 0.00 | 0.00 | 0.00 | 5.81 | 0.00 |
| Pinus strobus (tree) | 0.00 | 0.00 | 0.00 | 0.00 | 5.15 | 74.70 |
| Pinus strobus (sapling) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 15.80 |
| Populus grandidentata (sapling) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 10.50 |
| Thuja occidentalis (tree)‡ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Thuja occidentalis (sapling)‡ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Abiotic group§ | 1  | 1  | 2  | 1  | 2  | 2  |

* Relative importance value for trees = [relative dominance (%) + relative density (%)]; relative importance value for saplings = [relative density %].
† Nomenclature follows that of Marie-Victorin (1964). Species are sorted according to their relative importance value in all sampling stations.
‡ Endomycorrhized species.
§ Based on total abiotic similarity (see Fig. 4).

Many variables show relatively strong partial correlations with the axes of EBC, taking into account the relation between axes of tree communities and axes of EBC. These partial correlations may be interpreted as a measure of the direct effect of variables with the structure of EBC, removing the indirect effect of tree communities. The variables with rather high partial correlation are mostly humus descriptors (thickness of the litter, percentage of organic matter, exchange capacity), mineral soil richness, and variables associated with drainage (percentage of water in mineral soil, percentage of organic matter, slope).

Species associations (Table 8) may have resulted partly from symbiotic relations with trees and partly from simple co-occurrence due to similar habitat requirements. Some tree-fungus associations revealed by this analysis had been identified as symbiotic by previous investigations (Pinus strobus—Suillus granulatus; Picea spp—Russula paludosa). On the other hand, the clustering failed to bring out some well-known symbiotic relationships (e.g., Pinus strobus—Boletinus picus). Most of the symbiotic associations suggested by Table 8 have not been documented yet, but many must now be suspected as symbiotic.

For clusters of fungi that have been associated with trees that are known to be endomycorrhized (like species of the genus Acer, for example), we included in Table 8 the ectomycorrhized trees that were ecologically associated with these trees. These associations were identified by an independent cluster analysis of tree species only. This caused some tree hosts to appear in more than one set: therefore, tree-fungus sets can be considered as "fuzzy sets."

According to the correspondence statistic (Neu et al. 1974), there are significant departures between relative constancy of basidiomycete clusters (observed value) and constancy of associated tree clusters (expected value) (Table 9). These departures are informative about particular habitat preferences for Basidiomycetes.

Species of cluster 2 (Table 8) avoided hydric humisol, the condition prevailing in the station of group 3 (Fig. 4), and preferred the two other groups of stations. Therefore, they were associated with black spruce (Picea mariana) but mostly on dryer locations. Species of cluster 3 preferred stations of group 1 and avoided those of group 2. They were associated with Populus grandidentata and P. tremuloides on soils that were richer in mineral nutrients, with thick humus that were poor in mineral nutrients. Species of clusters 4, 7, 9, and 13 all preferred humid organic soils. Clusters 4 and 9 also avoided stations of group 1. Species of cluster 10 avoided stations of group 2 and were found almost exclusively on rich mesic stations dominated by sugar maple (Acer saccharum). They were most probably associated with beech (Fagus grandifolia). Species of cluster 11 avoided rich mesic soils and preferred: (1) soils that were poor in mineral nutrients but where the humus had a higher percentage...
of organic matter, and (2) wet organic soils. Every other cluster of Basidiomycetes seems to have followed their tree symbions wherever they grew.

**DISCUSSION**

*Similarity matrices and ordinations*

The partial correlation between composition of tree communities and composition of the ectomycorrhizal-basidiomycete communities (EBC), removing the effect of abiotic variables, is as strong as the simple correlation between the two taxocenes (Table 4). This may be partly caused by the absence of significant correlation between the abiotic similarity and the similarity among tree communities. Tree species showing a bimodal type of distribution along abiotic gradients create conditions where station pairs may share many species without sharing important abiotic conditions. Abundant species in our samples, such as *Thuja occidentalis*, *Abies balsamea*, *Picea mariana*, and *Acer rubrum*, are trees that show this pattern, for example in their response to soil drainage.

The correlation and partial correlation between abiotic similarity and EBC similarity, removing the effect of tree communities, are statistically significant when we used only ectomycorrhized tree species in the analysis. This suggests that abiotic gradients have a more linear effect on EBC structure than on structure of the ectomycorrhized tree community.

We interpret the differentiation of tree communities composition and structure as the effect of a complex gradient of soil thickness (drainage) and richness and of disturbance. For example, stations 1 and 3, at the right of the principal coordinate analysis (PCOA) (Fig. 3), were dominated by sugar maple (*Acer saccharum*) and were characterized by low disturbance and thick mineral soils that were well drained. Stations 7 and 10, at the bottom of the ordination, had in common an abundance of poplar (*Populus grandidentata*) and white birch (*Betula papyrifera*), two shade-intolerant species, and were characterized by well-drained soils.

The relative positions of pairs of stations in the three multidimensional spaces pertain to eight different types. If $A$ is the space defined by basidiomycete data, $B$ the one defined by tree data, and $C$ the one defined by abiotic variables, then pairs can be:

1. close in all three spaces;
2. distant in all three spaces;
3. distant in spaces $A$ and $B$, close in space $C$;
4. distant in spaces $A$ and $C$, close in space $B$;
5. distant in spaces $B$ and $C$, close in space $A$;
6. close in spaces $A$ and $B$, distant in space $C$;
7. close in spaces $A$ and $C$, distant in space $B$;
8. close in spaces $B$ and $C$, distant in space $A$.

Each of these combinations reflects a particular ecological situation. If abiotic conditions strongly influenced both tree community composition and EBC composition (directly or via their effect on tree communities), then the most common situations should have been the first two. With those remarks in mind, the position of some station pairs and some individual stations is worth noticing. Station 2, for example, shared few abiotic conditions and tree species with stations 4 and 5, but the EBC of the three had many species in common. White birch (*Betula papyrifera*) was the main tree species growing at the three stations, and it is possible that the EBC was mostly affected by the presence of this species despite the widely different physical properties of their substrate. This would suggest that many ectomycorrhizal Basidiomycetes associated with white birch were indifferent to some soil properties like texture and water content. It can also mean that in the past (before disturbances) the tree community of station 2 had shared more species with stations 4 and 5 than it did when we sampled it. The ectomycorrhizal Basidiomycetes may then have persisted in the station while their associated trees had disappeared. Indeed, we found that burned stumps belonged to coniferous species in station 2 while there were but a few weak saplings of balsam fir (*Abies balsamea*) growing at the station or around it when we sampled. In his field observations of *Salix repens* communities in the British Isles, Watling (1981) concluded that the species composition of an EBC is influenced not only by the present composition of the tree community but also by its past composition.

In Fig. 4, station 5 is positioned far from all the
Table 3. Abiotic variables used in the computation of the abiotic similarity among stations. Stations are sorted according to the similarity of their physical environment.

| Variables                      | Sampling stations |
|--------------------------------|-------------------|
|                                | 1     | 3     | 4     | 10    | 2     | 6     | 7     |
| Abiotic groups                 |       |       |       |       |       |       |       |
| Humus descriptors              |       |       |       |       |       |       |       |
| Thickness of L horizon (cm)*   | 1.5   | 0.6   | 2     | 0.5   | 0.5   | 0.5   | 2     |
| Thickness of F horizon (cm)*   | 4     | 1.1   | 4.5   | 1.5   | 2     | 1.5   | 2     |
| Thickness of H horizon (cm)*   | 4     | 5.6   | 25    | 2.25  | 2     | 5.5   | 1.5   |
| Total thickness                | 9.5   | 8.3   | 21.5  | 4.25  | 4.5   | 7.5   | 5.5   |
| % water                        | 58.5  | 55.5  | 75    | 58    | 73    | 64.5  | 64    |
| % organic matter               | 48.27 | 47.79 | 95.92 | 72.42 | 90.32 | 84.22 |
| pH                             | 3.5   | 3.1   | 2.6   | 3.9   | 2.9   | 3     | 3.1   |
| Exchange capacity*             | -4.045| 0.378 | -2.589| 4.572 | 2.237 | 1.058 | -1.909|
| Mineal soil descriptors        |       |       |       |       |       |       |       |
| Hue of B1†                     | 2     | 4     | 4     | 3     | 5     | 3     | 2     |
| Hue of B2†                     | 1     | 2     | 2     | 2     | 2     | 2     | 3     |
| Chroma of B1                   | 4     | 6     | 6     | 10    | 4     | 8     | 8     |
| Chroma of B2                   | 4     | 6     | 4     | 10    | 6     | 10    | 8     |
| Value of B1                    | 3     | 4     | 3     | 4     | 2.5   | 4     | 4     |
| Value of B2                    | 4     | 4     | 5     | 5     | 5     | 4     | 4     |
| Exchange capacity*             | 40.9  | 44.2  | 42.1  | 42.4  | 55.4  | 44.2  | 40.7  |
| Average pH*                    | 4     | 3.867 | 3.633 | 4.033 | 3.867 | 3.967 | 3.833 |
| Richness*                      | 3.098 | 4.766 | -7.456| 0.452 | -0.713| -8.599| -2.823|
| % clay                         | 5.25  | 5     | 6.75  | 3.375 | 5     | 4.125 | 4.625 |
| % silt                         | 21    | 22.5  | 20.315| 16    | 20.625| 16.5  | 22.5  |
| % sand                         | 73.75 | 72.5  | 72.81 | 80.625| 74.375| 79.375| 72.875|
| % water*                       | 6.892 | 10.351| 10.321| 9.381 | 20.607| 12.005| 6.501 |
| % of particles >4 mm           | 28.7  | 11.5  | 22.5  | 43.8  | 10.6  | 28.8  | 29.8  |
| General descriptors            |       |       |       |       |       |       |       |
| Altitude (m)                   | 371   | 393   | 348   | 363   | 379   | 379   | 386   |
| Aspect‡                        | 2     | 3     | 1     | 4     | 8     | 8     | 7     |
| Slope (°)                      | 13    | 13    | 20    | 35    | 7.5   | 27    | 21    |
| Microrelief                    | 3     | 3     | 4     | 3     | 3     | 4     | 4     |
| Stoniness*                     | 2     | 3     | 1     | 4     | 3     | 4     | 5     |
| Rockiness*                     | 1     | 1     | 1     | 1     | 1     | 1     | 2     |
| Disturbance*                   | 2     | 2.5   | 1     | 2.5   | 3     | 3     | 3     |
| Superficial deposit§           | 3     | 3     | 2     | 2     | 3     | 2     | 1     |
| Position on slope*             | 3     | 3     | 2     | 3     | 1     | 2     | 3     |
| Slope shape*                   | 2     | 1     | 2     | 1     | 1     | 1     | 1     |
| Flooding§                      | 1     | 1     | 1     | 1     | 1     | 1     | 1     |

* See Methods: Vegetation sampling... and Methods: Soil analyses for details and references on these variables.
† Values are classes of the intensity of the red hue based on Munsell code: I = 2.5 Y; 2 = 10 YR; 3 = 7.5 YR; 4 = 5 YR; 5 = 2.5 YR.
‡ Values are classes of angular distances from the south of the aspect of a station.
§ Values are qualitative descriptors: 1 = very thin till; 2 = thin till; 3 = thick till; 4 = organic deposit.
‖ Presence (2) or absence (1) of the feature on the sampling station.

Table 4. Results of the first series of Mantel tests (above diagonal) and partial Mantel tests (below diagonal) between pairs of similarity matrices. All tree species (Table 2) were used in the computation of community similarity (simTREES).†

| simEBC‡ | simTREES§ | simABIO‖ |
|---------|-----------|----------|
| r       | 0.48600   | 0.049    |
| P       | 0.004*    | 0.123    |
| r       | 0.46431   | 0.16917  |
| P       | 0.005*    | 0.049    |
| r       | 0.20987   | 0.04905  |
| P       | 0.049     | 0.375    |

* Significant at the Bonferroni-corrected probability level of (.05/3 = .0167) for an overall significance level of .05 (Miller 1966).
† P = probability of H0 (= no relationship) after 1000 permutations; r = standardized Mantel statistic.
‡ simEBC = similarity matrix of ectomycorrhizal-basidiomycete communities based on data of Table 1.
§ simTREES = similarity matrix of tree community samples based on data of Table 2.
‖ simABIO = abiotic similarity matrix among stations based on variables of Table 3.
TABLE 3. Continued.

| Sampling stations | 8  | 9  | 11 | 5  |
|-------------------|----|----|----|----|
| 2                 | 2  | 2  | 3  |    |
| 0.9               | 0.6| 1  | 0  |    |
| 1.6               | 1.7| 1.5| 0  | 0  |
| 2                 | 7.5| 5.7| 0  | 0  |
| 4.5               | 9.8| 8.2| 100|    |
| 63                | 66.5| 59| 89 |    |
| 48.22             | 93.58| 66.98| 93.21|    |
| 3.4               | 2.9| 2.7| 4.2|    |
| 37.5              | 36.2| 36.2| 28.15|    |
| −1.304            | 0.95| −1.242| 2.094|    |

|               | 4  | 3 | 4  | 2  |    |
|---------------|----|---|----|----|----|
| 2             | 6  | 8 | 1  |    |    |
| 3             | 6  | 6 | 1  |    |    |
| 4             | 3  | 4 | 2.5|    |    |
| 5             | 4  | 4 | 2.5|    |    |
| 46.75         | 55.4| 60.5| 28.15|    |
| 4             | 3.567| 3.767| 4.2 |    |
| −0.984        | −2.342| 13.08| 2.094|    |
| 4.25          | 5.375| 6.875| 0  |    |
| 33.875        | 17.125| 13.75| 0  |    |
| 61.875        | 77.5| 79.375| 0  |    |
| 41            | 29.333| 38.333| 89 |    |
| 10.938        | 14.119| 17.716| 93.21|    |
| 2.6           | 62.4| 17.9| 0  |    |
| 341           | 341| 341| 348|    |
| 5             | 8  | 7 | 0  |    |
| 18            | 13 | 5 | 0  |    |
| 5             | 4  | 5 | 1  |    |
| 5             | 5  | 5 | 1  |    |
| 1             | 1  | 1 | 1  |    |
| 3             | 3  | 3 | 3  |    |
| 2             | 2  | 2 | 4  |    |
| 4             | 4  | 4 | 5 | 6  |
| 1             | 1  | 1 | 1  | 0  |
| 1             | 1  | 1 | 2  |    |

**TABLE 5.** Results of the second series Mantel tests (above diagonal) and partial Mantel tests (below diagonal) between different pairs of similarity matrices. Ectomycorrhizae-forming tree species (Table 3) were used in the computation of community similarity (simEctoTREES).†

| simEBC‡            | simEctoTREES§ | simABIO¶  |
|--------------------|---------------|-----------|
| simEBC‡            | ...           | ...       | ...       |
| r = 0.47592        | r = 0.26299   | r = 0.049  |
| P = 0.004*         |               | P = 0.049  |
| simEctoTREES§      |               | r = 0.08278 | ...       |
| r = 0.004*         |               | P = 0.03994 |
| P = 0.389          |               | r = −0.10044 | ...       |
| simABIO¶           |               | P = 0.009*  | ...       |
| r = 0.27763        |               | P = 0.370  |
| P = 0.009*         |               | ...       |

* Significant at the Bonferroni-corrected probability level of (.05/3 = .0167) for an overall significance level of .05 (Miller 1966).
† P = probability of H0 (no relationship) after 1000 permutations; r = standardized Mantel statistic.
‡ simEBC = similarity matrix of ectomycorrhizal-basidiomycete communities based on data of Table 1.
§ simEctoTREES = similarity matrix of tree community samples based on abundance data of ectomycorrhizae-forming trees (see Table 2).
¶ simABIO = abiotic similarity matrix among stations based on variables of Table 3.

![Fig. 1. Path diagram of the relationships among similarity matrices. Numbers are “path” coefficients, computed from the Mantel statistics in Table 4.](image)

... others, indicating that it was abiotically very different. This station had two important uncommon characteristics: it was wet—the water table remaining constantly high during the summer—and it had a hydric humisol (Commission canadienne de pédologie 1978). However, the tree community and EBC that it supported makes it more similar to other dryer stations (4 and 9). Stations 4 and 5 shared many tree species (*Thuja occidentalis*, *Abies balsamea*, *Betula papyrifera*) and ectomycorrhizal species (*Lactarius thejogalus*, *Hygrophorus nitidus*, *Rozites caperata*, *Russula paludosa*, etc.), although the abiotic conditions seemed quite different. However, the organic layer of soil was thick on both, and this characteristic may be an important dimension of the ectomycorrhizal species niche. Moreover, while the dominant species of these two communities, *Thuja occidentalis*, is not known as an ectomycorrhizae-forming species, its abundance may have affected indirectly the composition of EBC, by influencing, for example, the chemical and microflora composition of the soil, which affects the ectomycorrhizae formation (Slankis 1974). Some pairs, like stations 1 and 3, shared abiotic conditions, tree community composition, and EBC...
composition. There, the dominant tree (*Acer saccharum*) is generally endomycorrhized (Brundrett and Kendrick 1988, Berliner and Torrey 1989) and many Basidiomycetes gathered in those stations were only hypothetically ectomycorrhizal: *Hygrophorus ceraceus, H. marginatus, Nolanea* spp, *Leptonia* spp, etc. However, the stipes of those species were always deeply buried in the soil and their mycelia were diffuse and rarely visible. This habit is not typical of most litter saprotrophes. Therefore, it is possible that a tree species that forms ectomycorrhizae, present as saplings or seedlings (like *Fagus grandifolia* and *Betula alleghaniensis*) was associated with those Basidiomycetes.

Other pairs of sampling stations supported different tree communities but their EBC were more similar. For example, stations 6 and 7 shared important abiotic characteristics, and two important ectomycorrhizae-forming trees (*Pinus strobus* and *Populus grandidentata*) were present in both, but not in the same proportions. The similarity of EBC was due, here, to the abundance of *Amanita brunnescens* and *Boletinus pictus*, two species possibly associated with *Pinus strobus* (Table 8; Trappe 1962). As in station 2, this suggests that the presence of a particular tree species in a station may have had a stronger influence on EBC composition and structure than others.

**Abiotic gradients**

In Figs. 2 and 3 the configuration of the minimum spanning tree (MST) superimposed onto the plan of principal coordinates suggests the presence of the "horseshoe" effect (Legendre and Legendre 1983). It was then legitimate to rely on another technique of

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**Fig. 2.** Principal coordinates analysis (PCOA) and minimum spanning tree of ectomycorrhizal-basidiomycete community (EBC) samples using the Steinhaus similarity matrix for stations 1 to 11. Stations belonging to the same group formed by proportional-link linkage agglomeration are identified by the same symbol. Lines joining sampling stations represent the minimum spanning tree (MST).

**Fig. 3.** Principal coordinates analysis and minimum spanning tree of plant communities using the Steinhaus similarity matrix for stations 1 to 11, computed with relative importance values of trees and saplings (Table 2). Stations belonging to the same group formed by proportional-link linkage agglomeration are identified by the same symbol. Lines joining sampling stations represent the minimum spanning tree.
axes extraction, such as canonical correspondence analysis (CCA), for detection of abiotic gradients.

The direct gradient analysis pointed out the effect of drainage quality (or moisture) of a station on plant community composition and structure. This effect is well documented (see, for example, Whittaker 1956, 1967, Bouchard and Maycock 1978, Gagnon and Bouchard 1981, Bergeron and Bouchard 1983, Gauvin and Bouchard 1983). However, the EBC composition could have also been affected by drainage since water availability is identified as a limiting factor of ectomycorrhizal development (references in Slankis 1974 and Bowen 1972). Moreover, trees that grow on soils where the mineral soil does not retain water well may depend more on ectomycorrhizae for their water supply (Slankis 1974). In our sample, more rapidly drained stations were also richer in ectomycorrhizae-forming trees. Also, as an indirect effect of plant community composition or not, the humus of those stations had a higher percentage of organic matter (loss on ignition), a characteristic identified as favorable for ectomycorrhizal formation (Slankis 1974). On the other hand, mesic stations were usually dominated by *Acer saccharum*, a non-ectomycorrhized species, and the humus it created had a lower percentage of organic matter.

Since most ectomycorrhizae are found in the humus (see references in Slankis 1974), some variables associated with this soil layer may directly affect the EBC composition. Many properties of this layer may be determined by plant community composition, which is responsible for chemical composition and the physical structure of the litter. Correlations between humus descriptors and edaphic gradients that structure tree communities support this hypothesis. The interpretation of interrelations between abiotic and biotic gradients is summarized in Fig. 5.

These results are similar to those of Favre (1948) and Hering (1966) who compared the macrofungal species composition of forests having similar tree composition but established on different soils. Favre (1948) showed that chemical characteristics of the soils, mostly pH, affect the species composition of mycofloras. Hering (1966) suggested that the nature of the soil parent material is responsible for differences in macrofungal community composition. Also, Garbaye et al. (1986), working on the distribution of ectomycorrhizae types (which may or may not represent different species) on young oaks, showed that soil texture, pH, and organic-matter content are the main factors affecting their distribution. The results of Bills et al. (1986) previously showed how plant communities at two extreme poles of a complex environmental gradient support different ectomycorrhizal communities. However, knowledge of the composition of intermediate communities was needed to bring out a deeper understanding of factors affecting the composition of EBC.

**Table 6.** Canonical coefficients and associated *t* values for internal variables of canonical correspondence analysis (CCA) of tree and basidiomycete communities.

| Edaphic variables       | Tree communities |          |          |          |          |        |          |          |          |          |        |          |          |          |          |
|-------------------------|------------------|----------|----------|----------|----------|--------|----------|----------|----------|----------|--------|----------|----------|----------|----------|
|                         | Canonical coef.  | *t* values |          |          |          |        |          |          |          |          |        |          |          |          |          |
|                         | Axis 1 | Axis 2 |          |          |          |        |          |          |          |          |        |          |          |          |          |
| Total exchange capacity | -0.12  | 2.50   | -0.15    | 2.74    |          |        |          |          |          |          |        |          |          |          |          |
| Mean pH                 | -0.88  | 0.74   | -2.49    | 1.77    |          |        |          |          |          |          |        |          |          |          |          |
| Mean richness           | -0.48  | -0.64  | -1.75    | -1.95   |          |        |          |          |          |          |        |          |          |          |          |
| Mean % of sand          | 1.21   | -4.83  | 0.72     | -2.42   |          |        |          |          |          |          |        |          |          |          |          |
| Mean % of water         | 1.10   | -5.21  | 0.79     | -3.16   |          |        |          |          |          |          |        |          |          |          |          |
| Mean % of organic matter| 1.30   | 1.37   | 1.50     | 1.34    |          |        |          |          |          |          |        |          |          |          |          |
Table 7. Correlations between abiotic variables and axes of canonical correspondence analysis (CCA) for tree communities and ectomycorrhizal-basidiomycete communities (EBC). Axes are linear combinations of internal variables (canonical axes).

| Abiotic variables | Weighted correlations | Partial correlations |
|-------------------|-----------------------|----------------------|
|                   | Tree communities       | Ectomycorrhizal communities | Ectomycorrhizal communities |
|                   | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1* | Axis 2† |
| **External variables (not used in CCA)** | | | | | | |
| Humus descriptors | | | | | | |
| Thickness of L horizon | -0.2339 | -0.1014 | -0.5561 | 0.0281 | -0.537 | 0.024 |
| Thickness of F horizon | -0.1409 | -0.2188 | -0.4763 | -0.1468 | -0.537 | -0.174 |
| Thickness of H horizon | 0.3337 | -0.2836 | -0.2714 | -0.1546 | -0.581 | -0.468 |
| Total thickness | 0.6006 | -0.0618 | 0.3954 | 0.0948 | 0.199 | 0.062 |
| % water | 0.8111 | 0.1527 | 0.3239 | -0.4502 | -0.075 | -0.395 |
| % organic matter | 0.7633 | 0.434 | 0.1175 | -0.7406 | -0.47 | -0.635 |
| pH | -0.1743 | 0.2759 | 0.0071 | 0.2556 | 0.176 | 0.601 |
| Exchange capacity | -0.0815 | -0.1965 | 0.0081 | -0.3986 | -0.052 | -0.516 |
| Richness | 0.1321 | 0.5666 | 0.2641 | 0.2447 | 0.23 | 0.063 |
| **General descriptors** | | | | | | |
| Aspect | -0.05 | 0.2893 | 0.1737 | -0.4784 | 0.155 | -0.412 |
| Slope | -0.5218 | 0.414 | -0.8136 | -0.1553 | -0.718 | 0.108 |
| Mirorelief | -0.3666 | -0.0043 | -0.2041 | -0.1999 | -0.581 | -0.47 |
| Storiness | -0.3467 | 0.2941 | 0.0425 | -0.1511 | 0.067 | -0.0015 |
| Disturbance | 0.0195 | 0.2804 | 0.4633 | -0.1228 | 0.56 | 0.139 |
| Superficial deposit | 0.3017 | -0.3204 | 0.4903 | 0.2689 | 0.413 | 0.308 |
| Position on slope | 0.2347 | -0.1651 | 0.5145 | 0.3626 | 0.537 | -0.308 |
| **Internal variables (used in CCA)** | | | | | | |
| Mineral soil descriptors | | | | | | |
| Exchange capacity | -0.0226 | -0.0827 | 0.4343 | -0.2275 | 0.396 | -0.355 |
| Average pH | -0.2747 | 0.0101 | 0.0338 | 0.3852 | 0.281 | 0.498 |
| Richness | -0.2235 | -0.3837 | 0.5978 | 0.6927 | 0.875 | 0.619 |
| % sand | -0.4853 | 0.0176 | -0.3764 | -0.1093 | -0.251 | 0.103 |
| % water | 0.3857 | -0.1817 | 0.6834 | 0.0787 | 0.564 | -0.064 |
| % organic matter | 0.5997 | -0.0055 | 0.3855 | 0.0481 | 0.436 | 0.042 |

* Partial correlation between the first axis of EBC and variables, removing the effect of the first axis of tree communities.
† Partial correlation between the second axis of EBC and variables, removing the effect of the second axis of tree communities.

**Interpretations of species associations**

Since symbiotic partners were not identified with certainty, we do not maintain that the habitat preferences described in the Results section are independent of the distribution of actual (verified) symbiotic partners.

As was the case in the results of CCA, the preference patterns shown in Table 9 help to identify the abiotic factors affecting fungus species distribution that were different from those affecting the distribution of trees (see Fig. 5). Also, while some abiotic conditions influencing tree community structure were the same as those affecting fungal communities, the responses of fungi seem to have differed from those of their tree symbionts. The effect of drainage is a good example of this. The same phenomenon involving the soil acidity was observed by Kotlaba (1953), who studied macromycetes communities of peat bogs in Czechoslovakia. He stated that some ectomycorrhizal species avoid peat bogs although their tree hosts are present. Others, which he called “acidophilic” species, follow their tree symbionts wherever they grow. Moreover, it is known (Slankis 1974) that ectomycorrhizae formation occurs mainly when nutritional conditions for the tree associate are suboptimal. This may partly explain why many ectomycorrhizal Basidiomycetes seem to have avoided rich mesic stations, a phenomenon observed by other researchers (Ubrizsy 1972).

It must be said finally that the limited size of our sample imposes limits on generalizations, mostly because of lack of replication in some of the abiotic conditions. Concerning the gradient analyses, we cannot tell to what extent lack of pattern is due to limited data. Ideally, future work should include more plots that would be sampled for more than two years. This would mean a lot of basidiomata to identify, a difficult task in the absence of taxonomic monographs on complex genera such as Cortinarius and Russula. However, an ecological investigation can be coupled with taxonomic work if restricted to one family or a few genera. In this perspective, collecting in permanent plots may provide good material for an understanding of morphological variations within species. On the other hand, the ecological investigation requires that all material be identified, including damaged basidiomata. This is necessary because the abundance of an ectomycorrhizal-basidiomycete species is usually evaluated using the
TABLE 8. Species associations defined statistically by complete linkage clustering using the chi-squared similarity coefficient and importance values of species. To define these associations, the minimum similarity value for clusters was arbitrarily fixed at 0.9700. The following associations are not necessarily symbiotic.

| Cluster | Basidiomycete species                      | Tree species*                  |
|---------|-------------------------------------------|--------------------------------|
| 1       | *Amanita brunnescens*                     | *Pinus strobus* (tree)         |
|         | *Suillus granulatus*                      | *Pinus strobus* (sapling)      |
|         |                                           | *Populus grandidentata* (sapling) |
| 2       | *Amanita porphyria*                       |                                |
|         | *Russula paludosa*                        | *Picea mariana* (tree)         |
|         | *Leccinum insigne*                       |                                |
|         | *Russula roseipes*                        |                                |
| 3       | *Amanita citrina*                         |                                |
|         | *Boletus piperatus*                       |                                |
|         | *Russula raonitii*                        |                                |
| 4       | *Amanita virosa*                          |                                |
|         | *Cortinarius evernus*                     |                                |
|         | *Russula peckii*                          |                                |
|         | *Clavulina cristata*                      |                                |
|         | *Hebeloma testaceum*                     |                                |
| 5       | *Amanita flavoconia*                      |                                |
|         | *Leccinum scabrum*                        |                                |
|         | *Russula fragilis*                        |                                |
|         | *Russula puellaris*                       |                                |
| 6       | *Amanita fulva*                           |                                |
|         | *Hebeloma sp.*                            |                                |
|         | *Russula silvicola*                       |                                |
| 7       | *Hyphogorphus laetus*                     |                                |
|         | *Hyphogorphus unguinosus*                 |                                |
|         | *Nolanea strictior*                       |                                |
|         | *Rozites caperata*                        |                                |
| 8       | *Boletinus pictus*                        |                                |
|         | *Cortinarius bolaris*                     |                                |
|         | *Hyphogorphus nitidus*                    |                                |
|         | *Xerocomus subalabominatus*               |                                |
|         | *Lactarius sordidus*                      |                                |
| 9       | *Cortinarius flexipes*                    |                                |
|         | *Cortinarius vibratilis*                  |                                |
|         | *Hyphogorphus miniatius*                  |                                |
|         | *Leptonia formosa*                        |                                |
|         | *Laccaria lacaca*                         |                                |
|         | *Lactarius thyinos*                       |                                |
|         | *Nolanea strictior*                       |                                |
|         | *Rozites caperata*                        |                                |
| 10      | *Amanita muscaria*                        |                                |
|         | *Hyphogorphus marginatus*                 |                                |
|         | *Hyphogorphus pallidus*                   |                                |
|         | *Hyphogorphus ceraceus*                   |                                |
|         | *Hyphogorphus parvis*                     |                                |
|         | *Hyphogorphus pratensis*                  |                                |
|         | *Paxillus involutus*                      |                                |
| 11      | *Lactarius lignonus*                      |                                |
|         | *Leccinum holopus*                        |                                |
|         | *Tylopilus felleus*                       |                                |
| 12      | *Cantharellus cibarius*                   |                                |
|         | *Hebeloma mesophaeum*                     | *Populus grandidentata* (seedling) |
|         | *Lactarius glycosioides*                  |                                |
|         | *Russula claroflava*                      |                                |
|         | *Inocybe umbrina*                         |                                |
|         | *Cortinarius armillatus*                  |                                |
| 13      | *Clavulinopsis fiesiformis*               |                                |
|         | *Hyphogorphus cantharellus*               |                                |
|         | *Nolanea lutea*                           |                                |
|         | *Nolanea quadra*                          |                                |
|         | *Lactarius thejolus*                      |                                |
|         | *Ramariopsis kunzei*                      |                                |
|         | *Russula cyanoxantha*                     |                                |

* Tree species names set in roman type are ectomycorrhizal species that are associated with the non-ectomycorrhized trees according to a second cluster analysis computed with only the importance values of tree species.

† Endomycorrhized tree species.
Table 9. Relative constancy* of species clusters in station groups for ectomycorrhizae fungal and tree species. Numbers in boldface type indicate observed constancies that are significantly \( (P < .05) \) different from their expected one according to the correspondence statistic (Neu et al. 1974), Bonferroni-corrected. Observed constancy (upper row for each station group) is the constancy of fungal species; expected constancy (lower row) is the constancy of the associated tree species (ectomycorrhized only).

| Station group† | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 |
|---------------|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1             | 11.69 | 90.78 | 3.50 | 9.83 | 37.13 | 32.79 | 71.81 | 2.77 | 93.08 | 6.59 | 12.72 | 26.31 |    |
| 2             | 93.62 | 76.90 | 9.22 | 56.17 | 65.54 | 51.49 | 38.74 | 22.54 | 6.74 | 2.45 | 85.62 | 73.87 | 40.75 |
| 3             | 0.00 | 11.40 | 0.00 | 40.34 | 24.63 | 11.39 | 28.47 | 5.65 | 90.49 | 4.48 | 7.79 | 13.42 | 32.94 |
|               |    | 0.00 |    | 75.17 | 0.00 | 0.00 | 37.21 | 8.39 | 0.00 | 0.00 | 54.88 | 0.00 |    |

* Formula is explained in detail in Methods: Data analysis: Biological associations and habitat preferences.
† Based on complete linkage clustering using chi-square similarity coefficient (Table 8).
‡ Based on a cluster that minimizes variance of the first three principal coordinates extracted from the abiotic similarity matrix (Fig. 4).

frequency or biomass of all its basidiomata. An alternative approach would consist of the identification of the two symbionts (fungus and tree) directly for ectomycorrhizae that would be sampled. Such an approach would need a systematic or random excavation of roots and thus be extremely time consuming; further, it will become feasible only when more ectomycorrhizae descriptions like those in Godbout and Fortin (1985), Randall and Grand (1986), Agerer (1988), and Samson and Fortin (1988), are available for associations of North American tree and fungus species.

Conclusions

The distribution of ectomycorrhizal Basidiomycetes resulted mainly from their biotic interactions with tree communities. Partial Mantel tests appeared to be quite powerful in bringing out dependence patterns between linked biological communities (or taxocenes) and their environment. Their results offered a much clearer picture of complex interactions among plant communities, environment, and ectomycorrhizal-basidiomycete communities (EBC) than previous mycosociological studies. We suggest their use in all studies involving such material (like parasite–hyperparasite–environment relationships, etc.). Because the computation of this statistic can handle geographical and chronological distance matrices, it may also be useful where spatial or temporal patterns of associated taxocenes are to be revealed, as in the work of Taylor et al. (1984).

Some results of the analyses also suggested that the composition and structure of EBC were not so dependent on the precise composition and structure of the tree community of the same habitat:

1) The partial Mantel test between EBC similarity and abiotic similarity, removing the effect of the similarity among ectomycorrhized tree communities, showed an independent relationship between EBC and the abiotic features of their habitat.

Fig. 5. Summary of the relationships between abiotic and biotic gradients, revealed by Mantel tests and canonical correspondence analyses.
2) The ecological distribution of basidiomycete species associations showed preference/avoidance patterns regarding environmental conditions that sometimes appeared independent of the ecological distribution of hypothetical tree symbionts.

Environmental variables that seem to have affected more directly the EBC structure were descriptors of the physical and chemical properties of the humus, such as litter thickness and percentage of organic matter. Sometimes the composition and structure of EBC may have been determined mainly by the presence of one or two tree species (as with Pinus strobus and Betula papyrifera) that were strongly associated with a few highly productive Basidiomycetes.

In the framework of the continuum concept (Whittaker 1967), our results can be usefully interpreted and visualized as relations between distribution curves of associated species of two taxocenes. For the fungal partner of ectomycorrhizae, there were three possible types of relations between distribution curves:

1) Its curve followed that of its tree symbionts with high fidelity independent of the environment;

2) It followed that of its tree symbionts only on a part of the gradient;

3) It did not follow any tree distribution curve but had its own independent one and formed ectomycorrhizae with whatever suitable hosts were available in its habitat.

The second type best explains the partial correlation between environmental gradient and EBC composition gradient. This type of distribution implies that beta-diversity of fungi is generally higher than beta-diversity of ectomycorrhizae-forming trees, a fact suggested by the results of previous mycosynecological studies (Cooke 1948, 1953, 1979, Favre 1948, Kotlaba 1953, Ubrizsy 1972, Apinis 1973, Darimont 1973, Lisiewska 1974, Villeneuve et al. 1989). Moreover, in the study we had about 240 species of fungi to 27 species of woody plants. From the perspective of species conservation, these facts may both have consequences in the choice of sites for the establishment of ecological preserves: site selection based on vegetation classification or mapping, or on distribution of tree species, may miss several fungal species. Therefore, the general objective of conservation of biodiversity would be better achieved by the conservation of many replicates of the same forest types.

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