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Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories

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Abstract: Effects of forest management on fungal diversity were investigated by sampling fruit bodies of polyporoid and corticioid fungi in forest stands that have different management histories. Fruit bodies were sampled in 15 northern hardwood stands in northern Wisconsin and the upper peninsula of Michigan. Sampling was conducted in five old-growth stands, five uneven-age stands, three even-age unthinned stands and two even-age thinned stands. Plots 100 m × 60 m were established and 3000 m^2 within each plot was sampled during the summers of 1996 and 1997. A total of 255 polyporoid and corticioid morphological species were identified, 46 (≈18%) of which could not be assigned to a described species. Species accumulation curves for sites and management classes differed from straight lines, although variability from year to year suggests that more than 2 y of sampling are needed to characterize annual variation. Mean species richness and diversity index values did not vary significantly by management class, although mean richness on large diameter wood (≥ 15 cm diam) varied with moderate significance. Richness values on small diameter debris varied significantly by year, indicating that a large part of year-to-year variability in total species richness is due to small diameter debris. Ten species had abundance levels that varied by management class. Two of these species, *Cystostereum murraii* and *Rigidoporus crocatus*, were most abundant in old-growth and might be good indicators of stands with old-growth characteristics. *Oxyporus populinus*, an important pathogen of *Acer* spp., was most abundant in even-age stands. Regression analyses indicated that substrate quality (diameter and species), quantity and management history of the stand were important in predicting the number of occurrences of the five most-abundant species. Changes in the diversity and species composition of the wood-inhabiting fungal community could have significant implications for the diversity, health and productivity of forest ecosystems.

Key words: Aphyllophorales, Basidiomycete, Corticiaceae, fungi, Polyporaceae, polypore, species diversity

INTRODUCTION

Polyporoid and corticioid fungi are some of the most common and important wood-inhabiting fungi in forests. These species can account for the majority of fruit bodies found on woody debris (de Vries 1990), yet they often are overlooked in studies of fungal diversity. When polypores and corticioid fungi are sampled, often only the largest or most conspicuous species are collected (e.g. Bader et al 1995, Ohlson et al 1997). Such sampling procedures ignore a large percentage of the fungal community. In a study conducted in an even-aged *Picea abies* stand in the Netherlands, de Vries (1990) found that 75% of wood-inhabiting species had inconspicuous, tiny, thin or crustose fruit bodies and that such species made up 44% of overall fungal species richness. Unfortunately little is known currently about the ecological roles played by many of these cryptic fungi. For some species with larger fruit bodies, such as *Phellinus weirii*, researchers have demonstrated significant effects on the direction of forest succession, influences on the composition and diversity of understory vegetation and effects on microbial biomass and decomposition rates in forests (Cromack et al 1991, Holah et al 1993, Holah et al 1997, Ingersoll et al 1996). Due to the widespread nature and importance of many polyporoid and corticioid species, it will be difficult to implement ''whole ecosystem'' management (e.g. Pilz and Molina 1996) without first understanding how different forest management techniques influence these fungi.

Although rarely collected, polyporoid and corticioid fruit bodies are ideally suited to large-scale, quantitative studies of fungal diversity. Fruit bodies are often woody or rigid with low water content, making collection and transport easier in areas that are difficult to access. Identification of these fungi rarely depends on fresh characters, allowing large numbers of fruit bodies to be collected, dried and stored during peak fruiting periods. It also has been

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proposed that the woody habit of their fruit bodies makes the occurrence of these fungi more regular on both a seasonal and an annual basis (Renvall et al 1991a, b; Wästerlund and Ingelög 1981) compared to many fungal groups. Researchers who have studied both mycorrhizal and saprophytic fungi have concluded that saprophytic fungi fruit more regularly from year to year (Villeneuve et al 1989). Wood-inhabiting species occupying unitary or discrete resources such as logs and depending solely on spore dispersal to travel from one resource to the next must produce fruit bodies to survive when resources are depleted (Cooke and Rayner 1984). This biological strategy, combined with the persistent nature of many polyporoid and corticioid fruiting structures, suggests these fungi can be characterized with a relatively small number of sampling periods in a given year and that fruit body occurrence should be relatively independent of short-term changes in temperature or moisture availability.

To date little quantitative sampling of polyporoid or corticioid fungi has occurred in North America. In Europe more sampling has taken place and numerous polyporoid and corticioid species are considered sufficiently rare or threatened to warrant being placed on European red lists (Arnolds 1997, Rydin et al 1997, Stokland et al 1997). Work done in northern Europe suggests that the harvesting of trees at various levels of intensity can affect the diversity of wood-inhabiting fungi (Bader et al 1995, Høiland and Bendiksen 1997, Lindblad 1998, Ohlson et al 1997, Wästerlund and Ingelög 1981). In a paper reviewing the distribution of macrofungi in Sweden Rydin et al (1997) concluded that one of the main threats to macrofungi in Sweden was modern forestry and that ''the high proportion of threatened macrofungi in spruce forests of Sweden indicates how strong the impact of forestry and management has been on the Swedish landscape.'' The effect of forest management on fungal diversity also was noted in a paper by Wästerlund (1989), who concluded that although the total production of fungi in Scandinavian coniferous forests was not necessarily decreased there were qualitative changes that usually resulted in a decrease in species diversity. The studies from northern Europe concerning the effects of forest management on the diversity of wood-inhabiting fungi have shown that species diversity of wood-inhabiting fungal fruit bodies correlates with the quality of woody substrates (as measured by a diversity of diameters and decay classes), as well as with total volume of wood at a site (Bader et al 1995, Høiland and Bendiksen 1997, Lindblad 1998, Ohlson et al 1997, Wästerlund and Ingelög 1981).

To the best of our knowledge the only studies in North America that have addressed the question of how forest management relates to the amount of coarse woody debris in a stand, and therefore to the diversity of fungi found in the stand, have been conducted in the Pacific Northwest on hypogeous fungi (Amaranthus et al 1994, Colgan et al 1996). Amaranthus et al (1994) found that mature, naturally established *Pseudotsuga menziesii* forest fragments had a greater percent frequency of occurrence of truffles than plantations and that truffle number and dry weight also were greater in mature forests. They also noted that coarse woody debris had a significant effect on the numbers and biomass of truffles and concluded that forest management practices ''that emphasize the retention of mature trees and coarse woody debris promote the abundance and diversity of truffles.''

In the Midwestern United States old-growth forests are rare. The majority of northern hardwood forests in the upper Midwest were intensely clear-cut and swept by fires in the early 1900s. This period produced many even-age, second-growth forests. The trees in even-age stands are usually in the same size and age classes, and such stands tend to lack trees or woody debris greater than 60 cm diam (Goodburn and Lorimer 1998). These forests are characterized by the conspicuous absence of many of the structural attributes of old-growth forests, including tree-fall mounds, snags, cavity trees, large diameter logs in many stages of decay and a large volume of both standing and down coarse woody debris (Goodburn and Lorimer 1998). Even-age, unthinned stands therefore represent the lower extreme in terms of the quantities and diversities of woody substrates available for fungal colonization, while old-growth forests represent the upper extreme. In addition to old-growth and even-age forests, some northern hardwood stands have been selectively harvested throughout their entire management history, producing stands comprised of trees in many age classes. Selectively managed, uneven-age forests fall somewhere between unmanaged even-age forests and old-growth forests in availability of woody substrates.

Two important questions regarding the management of northern hardwood forests in the upper Midwest are whether certain forest management techniques influence species diversity and whether such techniques produce forests capable of supporting ''old-growth dependent'' species. To help answer these questions with regard to fungi, we tested the null hypothesis that there is no difference in the species richness or diversity of wood-inhabiting polyporoid and corticioid fruit bodies among northern hardwood forest stands that have experienced different management regimes. Due to obvious constraints the individual forest stands were not

randomized to treatment (i.e. history of forest management). Thus this study does not directly investigate whether forest management causes differences in the diversity of fungal fruit bodies but rather whether there are correlations between fungal diversity and a stand's management history.

MATERIALS AND METHODS

Site selection and sampling procedures.—Fifteen sites were located in mesic northern hardwood stands in northern Wisconsin and the adjacent upper peninsula of Michigan (TABLE I). These stands are a subset of those studied by Goodburn and Lorimer (1998), who describe the area's soils, climate and landscape classification. Although dominated by *Acer saccharum* (sugar maple), stands also often contained *Betula alleghaniensis* (yellow birch), *Tilia americana* (basswood), *Carya ovata* (ironwood) and *Tsuga canadensis* (eastern hemlock). All stands were classified as the *Acer-Tsuga-Dryopteris* (ATD) habitat type (Coffman et al 1983, Kotar et al 1988), although a few were transitional between ATD and *Acer-Viola-Osmorhiza* (AViO) or *Acer-Tsuga-Maianthemum* (ATM) (Goodburn and Lorimer 1998).

Old-growth stands were greater than 20 ha and were located in the Sylvania Wilderness Area, Ottawa National Forest, Michigan, which contains more than 6000 ha of old-growth forest (USDA. 1964). Only localized cutting has been done for personal use in Sylvania, and tree ages range up to approximately 350 y (Goodburn and Lorimer 1998). To qualify as old-growth, a stand had at least 34% of its basal area (ba) in large trees with a diameter at breast height (dbh) > 46 cm, and at least 67% of its total ba in mature and large trees > 26 cm dbh. Uneven-age, selectively managed sites were chosen based on ''previous management by the selection system on a cutting cycle of 8–15 y, a minimum residual ba of 16.1 m^2/ha (70 ft^2/ha), and a maximum residual tree diameter > 45 cm dbh'' (Goodburn and Lorimer 1998). All uneven-age stands have been actively managed to fulfill forestry objectives but have not been cut within the previous 4 y. Such stands generally do not contain trees greater than 200 y of age (Cole and Lorimer 1994). Even-age sites were located in second-growth stands that had naturally regenerated from clear-cutting. These stands were dominated by sugar maples 65–75 y of age (Goodburn and Lorimer 1998). Even-age unthinned stands experienced no active management after the initial clear-cutting, while even-age thinned stands were thinned 9–14 y before sampling.

Plots 100 × 60 m were established at randomly located plot centers within each site in spring 1996 (FIG. 1). Each plot ran east to west and was composed of three contiguous subplots 20 × 100 m. Each subplot in turn was composed of two transects, each 10 × 100 m, and the entire plot was divided into 5 × 5 m quadrats. Because sampling is destructive (specimens must be collected and all logs and debris must be turned and examined), a design was employed whereby no area was resampled. All large diameter wood (≥15 cm diam) was sampled in 3000 m^2 of

TABLE I. Site description and location information for northern hardwood stands with different management histories

Stand	Stand structure	Max. tree age (y)	Management history	Stand location	
				Latitude	Longitude
#1	Old-growth	≈350	None	46° 13′ 18.829″ N	89° 17′ 59.561″ W
#2	Old-growth	≈350	None	46° 12′ 27.630″ N	89° 15′ 50.683″ W
#3	Old-growth	≈350	None	46° 12′ 05.427″ N	89° 16′ 56.467″ W
#4	Old-growth	≈350	None	46° 11′ 36.970″ N	89° 15′ 38.317″ W
#5	Old-growth	≈350	None	46° 11′ 11.269″ N	89° 15′ 53.979″ W
#6	Uneven-aged	≈200	Selective cutting	45° 54′ 07.603″ N	89° 01′ 29.847″ W
#7	Uneven-aged	≈200	Selective cutting	46° 11′ 30.977″ N	89° 05′ 49.117″ W
#8	Uneven-aged	≈200	Selective cutting	46° 14′ 02.415″ N	89° 00′ 31.279″ W
#9	Uneven-aged	≈200	Selective cutting	46° 18′ 15.682″ N	89° 14′ 11.308″ W
#10	Uneven-aged	≈200	Selective cutting	46° 15′ 40.606″ N	89° 02′ 23.705″ W
#11	Even-aged	65–70	Clear-cutting with natural regeneration	46° 11′ 26.693″ N	89° 04′ 36.045″ W
#12	Even-aged	65–70	Clear-cutting with natural regeneration	46° 12′ 00.225″ N	88° 59′ 55.413″ W
#13[a]	Even-aged	65–70	Clear-cutting with natural regeneration	46° 19′ 17.400″ N	89° 13′ 43.680″ W
#14	Even-aged	65–70	Clear-cutting with natural regeneration followed by thinning	45° 57′ 28.195″ N	88° 57′ 14.604″ W
#15	Even-aged	65–70	Clear-cutting with natural regeneration followed by thinning	46° 15′ 40.720″ N	89° 03′ 29.874″ W

[a] Location data for Stand #13 are approximate.

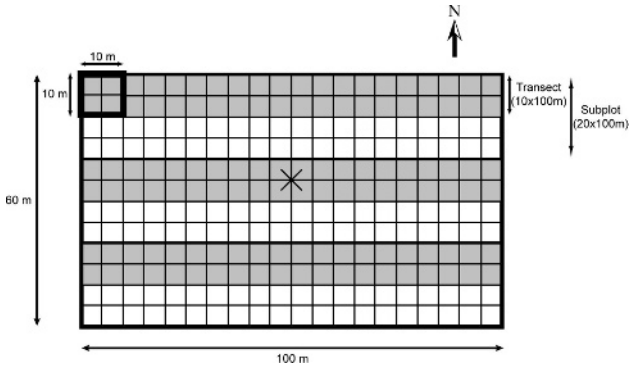

FIG. 1. Plot design for the sampling of polyporoid and corticioid fruit bodies. Each 100 × 60 m plot had its long axis running east to west. The ''X'' designates the point where GPS data were taken. Each plot was divided into 5 × 5 m quadrats, although most data analyses used 10 × 10 m quadrats (outlined in upper left). During 1996 large diameter wood (≥15 cm) was sampled in 3000 m^2 of the plot and a replicate plot contiguous to the initial plot was sampled in 1997 in a similar fashion. The area sampled for large diameter wood was determined by randomly selecting either the northern or southern transect within each subplot. Small diameter wood (≥1 cm but <15 cm diam) was sampled in 1500 m^2 of the plot by randomly sampling either the northern or southern 5 × 100 m strip of quadrats within each transect sampled for large diameter debris.

the plot during summer 1996. (The authors sampled all 6000 m^2 of the plot during 1996, but the data obtained from the first 3000 m^2 were uninformative because sampling occurred in spring before most fruit bodies were fertile; therefore, only summer data were analyzed.) A replicate plot was established and sampled contiguous to the initial plot in 1997. Within each plot, the area sampled for large diameter wood was determined by randomly selecting either the northern or southern transect within each subplot. Small diameter wood (≥1 cm but <15 cm diam) was sampled in 1500 m^2 of the plot by randomly choosing to sample either the northern or southern 5 × 100 m strip of quadrats within each transect sampled for large woody debris. All sampling was done from ground level to a height of 2.5 m. Within each 5 × 5 m quadrat, all polyporoid and corticioid species that could be identified by sight were recorded, while all unknown species were collected. At least one voucher specimen was collected for each species each year.

Substrate data were recorded for each piece of large diameter woody substrate in each 5 × 5 m quadrat. Information taken for large woody substrates (≥15 cm) included substrate species, diameter at midpoint within each 5 × 5 m quadrat, length within each 5 × 5 m quadrat, height off the ground (data taken only in 1997), form (e.g. log, tree, snag, stump, suspended log) and decay class. Decay classification was based on the procedures employed by Goodburn and Lorimer (1998). For small diameter debris (≥1 cm but <15 cm), the diameter of each piece bearing a fruitbody was estimated as being either <15 cm but >10 cm, ≤10 cm but >5 cm, or ≤5 cm but ≥1 cm. During 1997 the amount of small, woody debris was estimated on a scale of 1–5 within each 5 × 5 m quadrat, with 1 representing the smallest amount of debris (often a skid trail) and 5 representing the largest amount (often a treetop).

Sampling began 5 Aug 1996 and 9 Aug 1997, and once sampling was initiated one stand was sampled ca each day for 15 consecutive days. For every three sites consecutively sampled (hereafter referred to as a group of sites), sampling included one old-growth stand, one uneven-age stand and one even-age stand (either thinned or unthinned). Groups were sampled in random order, and the order of sites within each group was randomized. Even-age sites and uneven-age sites were paired based on geographic location, and then each pair was randomly grouped with an old-growth site. Groups therefore were based on a combination of geographic proximity and time of sampling. In 1997 new plots contiguous to the 1996 plots were sampled as described above, again employing the same grouping scheme.

Species identification.—The families Polyporaceae s.l. and Corticiaceae s.l. are phylogenetically diverse (Gilbertson and Ryvarden 1986, Gilbertson and Ryvarden 1987, Ginns and Lefebvre 1993, Hibbett and Donoghue 1995, Hibbett et al 1997) and contain species that produce fruit bodies with either a more or less poroid hymenophore (see Gilbertson and Ryvarden 1986, 1987) or fruit bodies with a flat to toothed (rarely poroid) hymenophore (see Ginns and Lefebvre 1993, Parmasto 1997). These fungi will be referred to here simply as ''polyporoid and corticioid fungi.''

Fruit bodies were dried within 24 h after collection and identified to species with morphological characters. Microscopic observations were made with an Olympus BH-2 compound microscope at 400× and under oil immersion at 1000×. When specimens could not be matched to known species descriptions, they were assigned to a genus and given a species number (e.g. *Hyphodontia* sp. No. 1). Voucher specimens were deposited in the herbarium of the Center for Forest Mycology Research (CFMR) at the USDA Forest Service Forest Products Laboratory (Madison, Wisconsin).

Incomplete sampling dictated the exclusion of one corticioid species, *Aleurodiscus oakesii*, from final analyses. Also excluded from final analyses were coralloid species (e.g. *Clavicorona pyxidata*, *Ramaria stricta*) and larger ''jelly fungi'' in the Tremellales, Auriculariales, Dacrymycetales, etc. (with the exception of one species, *Pseudohydnum gelatinosum*, for which complete data were available). Fruit bodies macroscopically undistinguishable from corticioid or polyporoid fungi (e.g. *Aporpium caryae, Heterochaetella dubia, Helicogloea farinacea, Basidiodendron* spp. and *Tulasnella* spp.) were included in analyses. All ecological guilds of wood-inhabiting fungi were analyzed, including mycorrhizal species that consistently produce fruit bodies on woody substrates (e.g. *Tomentella* spp.).

Due to a lack of recent taxonomic work, some species concepts were necessarily broad. This was true for *Hymenochaete fuliginosa*, *Hyphoderma sambuci*, *Hyphodontia*

rimosissima and some *Botryobasidium* species. Nomenclature for corticioid fungi generally followed Ginns and Lefebvre (1993), with the exception that *Botryobasidium botryosum* was considered a synonym of *Botryobasidium vagum* and *B. botryoideum* is considered distinct from *B. pruinatum*. For corticioid species not found in Ginns and Lefebvre (1993) nomenclature followed Parmasto (1997). Polypore nomenclature followed Gilbertson and Ryvarden (1986, 1987).

Data analysis.—The smallest sampling unit analyzed within our sites was the 5 × 5 m quadrat (FIG. 1). However only half of the 5 × 5 m quadrats were examined for both large and small diameter debris. Therefore the most basic unit that experienced a uniform sampling effort for large and small diameter debris was a block 5 (east-west) × 10 m (north-south) within each transect. Such a unit had all wood ≥ 15 cm diam examined for fruit bodies, while all wood ≥ 1 cm but < 15 cm diam has been examined in half the area (either the northern or southern 5 × 5 m quadrat). For analysis purposes species occurrence could be based on presence or absence within these 5 × 10 m units or could be based on larger groupings of these units. A preliminary analysis based on different grouping sizes demonstrated that the size of the sampling unit did not appreciably affect analyses. For example species accumulation curves generated with any of four different quadrat sizes (25, 50, 100 or 500 m^2) were almost indistinguishable (see Czederpiltz 2001). Accumulation curve shapes were essentially independent of quadrat size, with the variation between sites being much greater than the variation caused by the size of the sampling unit. A 10 × 10 m quadrat therefore was chosen as the basic unit used to quantify species abundance, primarily because this size yields a reasonable number of quadrats per site and is regular in shape.

Species accumulation curves were calculated with Sanders' (1968) rarefaction equations as modified by Hurlbert (1971). These equations allow for the exact calculation of the mean species accumulation curve over all possible permutations of sampling order. The equation used to construct an exact mean species accumulation curve is given by Smith et al (1979) as:

$$\hat{s}(m) = \sum_{i=1}^{K} \left[1 - \binom{M - L_i}{m} \Big/ \binom{M}{m} \right] \qquad (1)$$

Where:

$\hat{s}(m)$ = the expected number of species encountered after sampling m units

m = the number of "observed" sampling units, from 0 to M

M = the total number of sampling units

L_i = the number of sampling units in which species i is present

K = the total number of species

Equation 1 was used to calculate species accumulation curves for each site (FIG. 2), as well as for each management class (FIGS. 3, 4). All L_i values (abundance data) were calculated with a quadrat size of 10 × 10 m (100 m^2), thus giving a total of 30 quadrats per site ($M = 30$). Values for L_i were calculated for each treatment by summing abundance data (the number of quadrats in which a species occurred) for each species across sites within a treatment (FIG. 3). Average species accumulation curves for each treatment were calculated by averaging $\hat{s}(m)$ values for each value of m for all sites of a given treatment (FIG. 4).

Richness, diversity and evenness measures also were calculated for each site (TABLE III). Multiple diversity indices were calculated because there is no generally agreed upon method of characterizing diversity (Magurran 1988). Richness was calculated as the total number of species observed after 1 y of sampling at a site. In terms of species density, this is the number of species observed per 3000 m^2 given our sampling effort, which included sampling only half the area for small diameter debris. For the calculation of diversity indices, species abundance was measured as the number of 10 × 10 m quadrats in which a species occurred (frequency). The equations for diversity measures were adapted from Magurran (1988).

An analysis of variance (ANOVA) was conducted on all species richness and diversity calculations with the statistical software SAS 8.0 (©1999 SAS Institute Inc., Cary, North Carolina). Because this was an exploratory study and our replication number was relatively low, liberal α-levels were employed. *P*-values of 0.05–0.10 were considered "moderately significant," while *P*-values less than 0.05 were considered "significant." The ANOVA analyses for species richness and diversity took into account our grouping scheme, management history of the stands and the year of sampling (1996 or 1997). The *P*-values associated with management history, year of sampling and the management history by year interaction are shown (TABLE III). Species richness was calculated separately for large diameter (≥15 cm) wood and small diameter (≥1 cm but <15 cm) wood, and an ANOVA was run on these data in a similar fashion (TABLE IV). Trends in species abundance were analyzed by calculating the number of 10 × 10 m quadrats in which each species was observed at a site (TABLE V). Mean abundance for each species was compared among management classes with the same ANOVA used for the species richness analysis. An ANOVA for differences in abundance was run only for species that occurred at five or more sites and that occupied more than 10 quadrats overall (73 of the 255 species fit these criteria).

The occurrence of woody substrates (including substrates without fruit bodies) also was characterized at each site (see Czederpiltz 2001). Living trees, snags and stumps ≥15 cm diam were counted in the 3000 m^2 area that was sampled for fruit bodies. A stump was defined as being less than 1.5 m high, while snags were greater than 1.5 m high. Log volume was calculated by diameter class as well as by decay class. Within each 5 × 5 m quadrat the circumference or diameter of each log was taken at its midpoint, and the length of the log within the quadrat was measured. Volume occupied within a quadrat was calculated for each log by multiplying the radial area (πr^2) by the length of the log within the quadrat. Log volumes were summed within each quadrat and then across all quadrats at a site. Similar calculations also were performed on suspended logs, defined as logs that maintained a distance of at least 5 cm

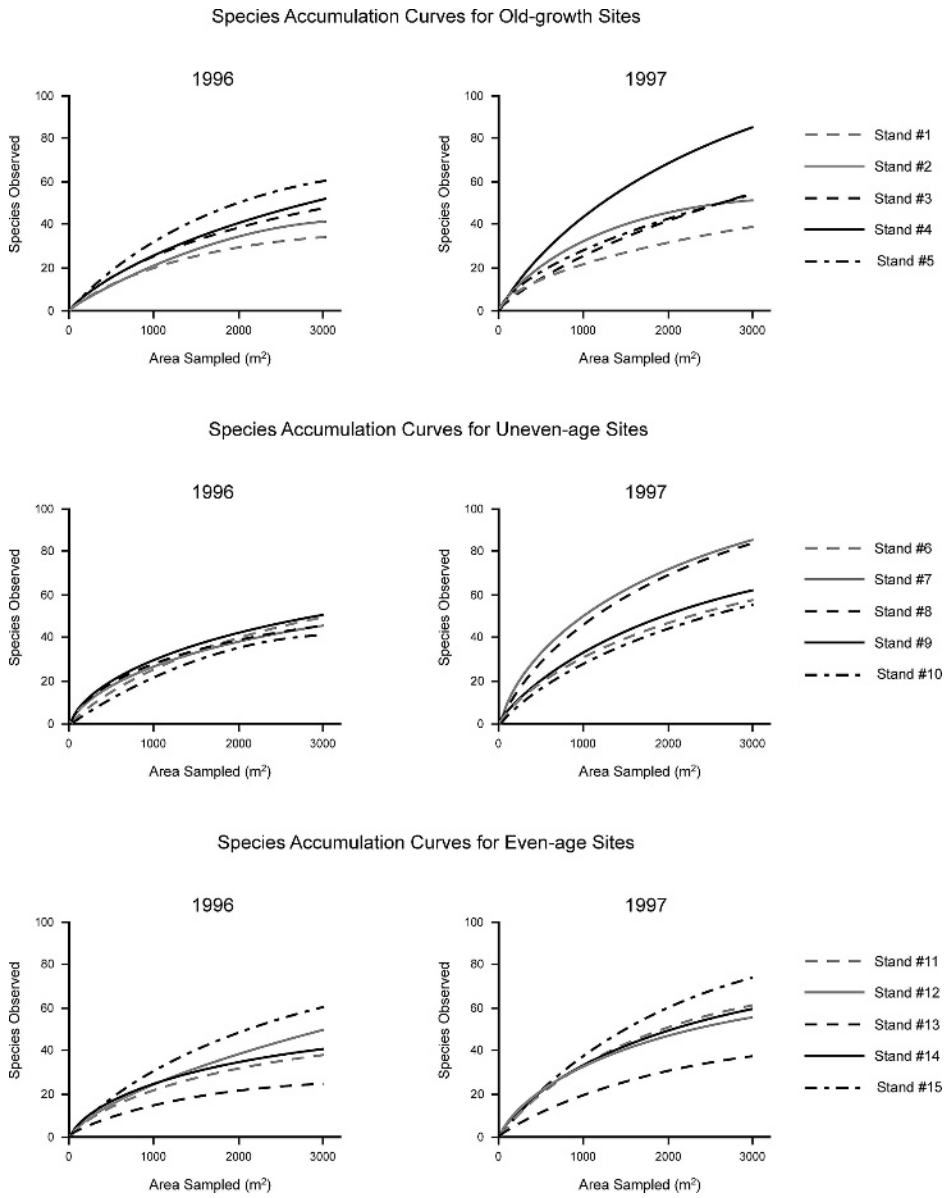

FIG. 2. Species accumulation curves for polyporoid and corticioid fungi for individual northern hardwood stands. Curves were calculated with rarefaction equations, thus permitting calculation of exact mean values over all possible permutations of quadrat sampling order. Calculations were based on 30 10 × 10 m quadrats. Even-age thinned and unthinned stands are presented on the same graph.

from the ground inside the boundaries of the 5 × 5 m quadrat. Small, woody debris (≥1 cm but <15 cm diam) was quantified in 60 5 × 5 m quadrats per site with a scale of 1–5, where 1 represented the smallest amount of woody debris (e.g. a skid trail) and 5 represented the largest (e.g. a fallen treetop). The mean of these values was calculated for each site and an ANOVA was performed on all woody debris values, taking into account our grouping scheme and the management history of the stands (data not shown).

An analysis was performed to determine whether there was a relationship between fruitbody occurrence of selected fungal species and the diameter classes and species of the substrates on which they were found (see Czederpiltz 2001). For these analyses each observation of a species on a distinct piece of substrate within a 5 × 5 m quadrat was treated as a separate observation. The diameter and species preference analyses were limited to wood ≥ 15 cm diam. A linear regression was performed on species occurrence and diameter class data, as well as on species occurrence and substrate species data. The response variable (y) represented the number of fungal occurrences of a species at a site. For the substrate diameter analysis, fungal occurrences were recorded by diameter class. Four diameter classes were recognized: 15–30 cm, 31–45 cm, 46–60 cm and > 60 cm. Log volume data for each diameter class also were calculated and were taken from the 1997 dataset; calculations of log volume included all logs of a given diameter class, including logs not colonized by fungi. The number of

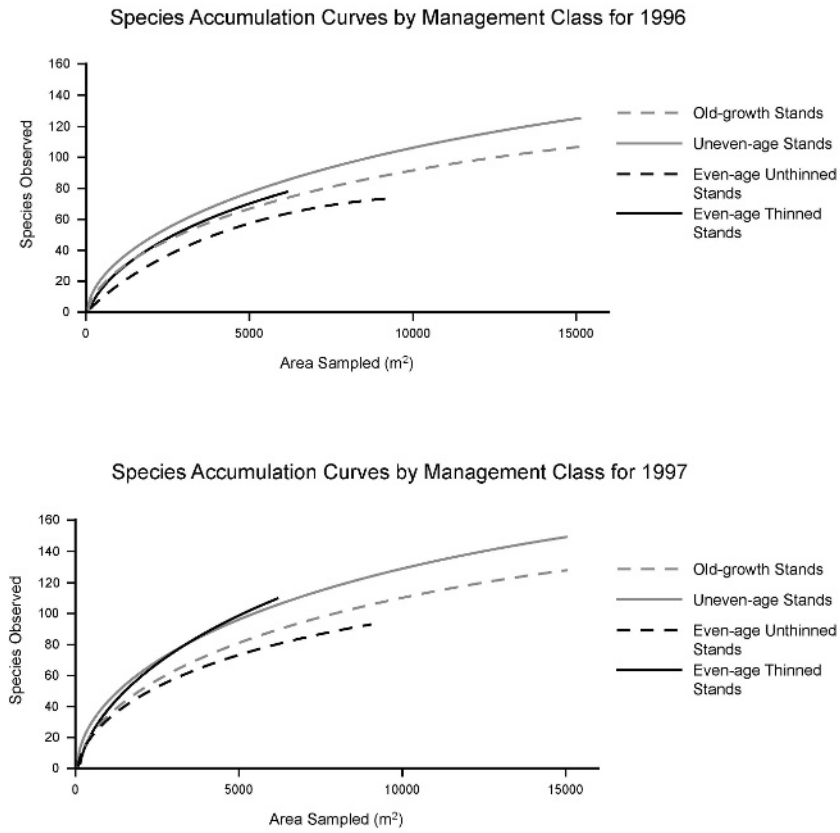

FIG. 3. Species accumulation curves of polyporoid and corticioid fungi for each management class of northern hardwood stands. Curves were calculated with rarefaction equations, and data were pooled for all stands of a given management class. Calculations were based on 30 10 × 10 m quadrats per stand. Five old-growth stands, five uneven-age stands, three even-age unthinned stands, and two even-age thinned stands were sampled.

fungal occurrences and log volume data were calculated on a per diameter class per site basis. The regression on fungal occurrence and substrate species was performed in a similar way. Six classes of substrate species were recognized: sugar maple (*Acer saccharum*), basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), other hardwoods (all other hardwood species pooled), hemlock (*Tsuga canadensis*) and other conifers (all other conifer species pooled). Log volume data again were calculated, this time for each substrate species (data were taken from the 1997 dataset); calculation of log volumes included logs not colonized with fungi. The number of fungal occurrences and log volume data were calculated on a per substrate species per site basis. Based on an analysis of residuals all occurrence data were transformed with the equation: $y = \log_{10}$ (occurrences + 1). These analyses were limited to the five species that occurred at least 70 times: *Fomes fomentarius*, *Ganoderma applanatum*, *Oxyporus populinus*, *Stereum hirsutum* and *Trametes versicolor*.

In all cases the full regression model was considered first and included the management class of the site, the diameter class or species class of the substrate, the volume of logs in that diameter or species class, all two-way interactions and the three-way interaction. Thereafter terms were eliminated from the model with hierarchical backward elimination with an α-value of 0.1. Effective R^2 values then were calculated for each model. This was done by first calculating the model with all significant fixed effects and the random effects (the full model). An intermediate model then was calculated with only random effects (the random model) and a reduced model then was calculated without either fixed or random effects (the reduced model). Effective R^2 values were calculated for the full and random models with:

$$\text{effective } R^2_{\text{full}} = 1 - (\text{SSErr}_{\text{full}}/\text{SSErr}_{\text{reduced}}) \quad (2)$$

$$\text{effective } R^2_{\text{random}} = 1 - (\text{SSErr}_{\text{random}}/\text{SSErr}_{\text{reduced}}) \quad (3)$$

Where:

$\text{SSErr}_{\text{full}}$ = estimate of the sum of squares error for the full model

$\text{SSErr}_{\text{random}}$ = estimate of the sum of squares error for the random model

$\text{SSErr}_{\text{reduced}}$ = estimate of the sum of squares error for the reduced model

RESULTS

Over the course of this study 255 polyporoid and corticioid species were identified (TABLE II) and

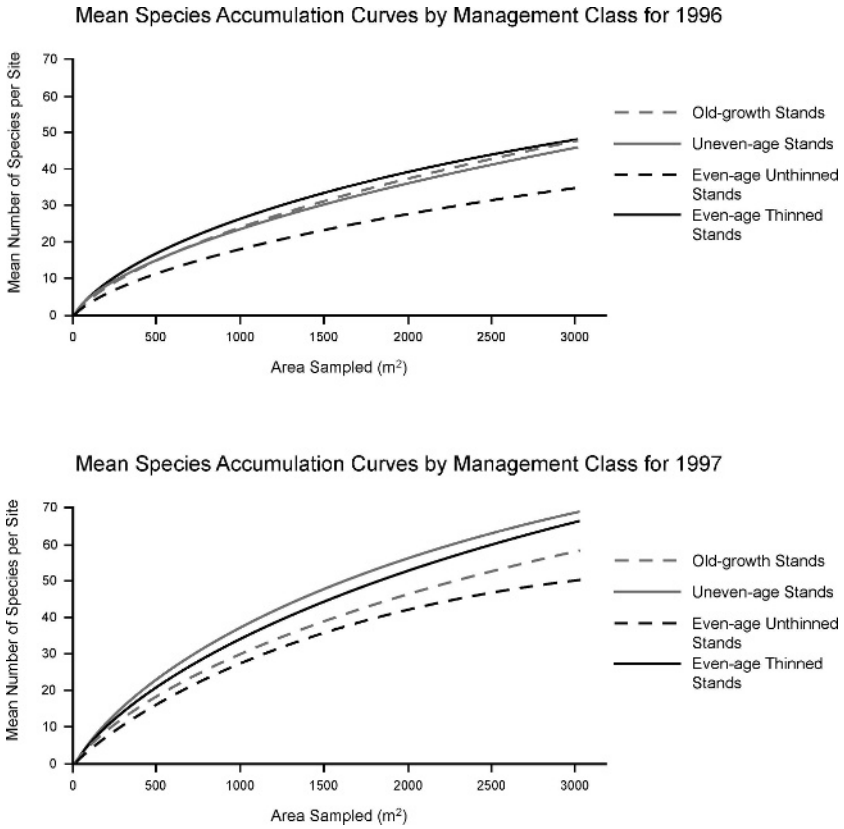

FIG. 4. Mean species accumulation curves of polyporoid and corticioid fungi for each management class. Mean curves were constructed by first calculating stand-level accumulation curves (as in FIG. 2) and then averaging the values at each accumulation step across all stands of a given treatment. The old-growth and uneven-age curves are the average of five stand-level curves, the even-age unthinned curve is the average of three stand-level curves and the even-age thinned curve is the average of two stand-level curves. Stand-level curves were calculated with rarefaction equations, and calculations were based on 30 10 × 10 m quadrats.

approximately 3000 specimens were collected. Fifteen species (≈6%) varied sufficiently from their descriptions that the abbreviation cf. (''compare'') was placed between the genus and species name. In addition, appropriate descriptions could not be found for 46 species (≈18%), so these species were assigned to the genus they most resembled and given a species number.

Many little-known and seldom-reported species were collected, including: *Boidinia furfuracea*, *Clavulicium macounii*, *Cristinia helvetica*, *Cristinia mucida**, *Heterochaetella dubia*, *Hyphodontia juniperi*, *Hypochnicium detriticum*, *Lindtneria chordulata*, *Phlebia canadensis**, *Scytinostromella humifaciens*, *Sistotrema oblongispora**, *Sistotrema sernanderi** and *Trechispora stellulata**. Species with an asterisk have not been reported previously from the United States (TABLE II).

All species accumulation curves differed from straight lines on visual inspection (FIGS. 2, 3), which indicates that sampling was at least moderately complete at both the site and treatment level (Magurran 1988). The slope of a line tangent to the tail end of a species accumulation curve is a good indication of how completely a community has been sampled. A strongly increasing slope indicates that more sampling almost certainly would add new species, while a slope approaching zero indicates that few new species would be encountered with additional sampling (Colwell and Coddington 1994, Magurran 1988).

Species accumulation curves had higher end points in 1997, indicating higher species richness during the second year of sampling (FIGS. 2–4). Of interest, the average number of species observed in 3000 m^2 increased only by nine species for old growth in 1996–1997, while it increased by an average of 17 species for all other management classes (FIG. 4).

In both 1996 and 1997 the even-age unthinned management class displayed the lowest expected number of species per unit area (FIGS. 3, 4). Measurements of mean species richness, diversity and evenness were not significantly different ($P >$ 0.10) among management classes (TABLE III). Mean

TABLE II. Fungal occurrence data by species of substrate for all fungal observations on wood ≥15 cm in diameter

Species of fungi	Fungal occurrence data by substrate species[a]														
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	Total
Acanthophysium cerussatum (Bres.) Boidin[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0[b]
Amylocorticium cebennense (Bourdot) Pouzar[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Anomoporia myceliosa (Peck) Pouzar	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Antrodia heteromorpha (Fr.) Donk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Antrodia malicola (Berk. & M.A. Curtis) Donk.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Antrodiella americana Ryv. & Gilb.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Antrodiella romellii (Donk) Niemala[e,f]	4	—	1	—	—	—	1	—	—	—	—	—	—	1	7
Antrodiella semisupina (Berk. & M.A. Curtis) Ryvarden[f]	—	—	—	2	—	—	—	—	—	—	—	—	—	—	2
Antrodiella sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Aporpium caryae (Schwein.) Teixeira & D.P. Rogers	2	1	—	—	—	—	—	4	—	—	—	—	—	—	7
Asterostroma andinum Pat.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Athelia cf. *salicum* Pers.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Athelia epiphylla Pers.[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Athelia sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Basidiodendron cf. *cinerea* (Bres.) Luck-Allen	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
Basidiodendron cf. *eyrei* (Wakef.) Luck-Allen	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Basidioradulum radula (Fr.) Nobles	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Bjerkandera adusta (Willd.) P. Karst.	9	1	1	—	2	—	—	1	—	—	—	—	—	—	14
Boidinia furfuracea (Bres.) Stalpers & Hjortstam[e]	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Botryobasidium botryoideum (Overh.) Parmasto	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Botryobasidium pruinatum (Bres.) J. Erikss.[f]	3	—	3	—	—	—	—	—	—	—	—	—	—	—	6
Botryobasidium sp. #1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Botryobasidium subcoronatum (Höhn & Litsch.) Donk	1	—	1	—	—	—	—	—	1	—	—	—	—	1	4
Botryobasidium vagum (Berk. & M.A. Curtis) D.P. Rogers	—	—	3	—	4	—	—	—	1	1	—	—	—	4	13
Botryohypochnus isabellinus (Fr.) J. Erikss.	9	3	3	—	—	—	—	1	—	—	—	—	—	1	17
Brevicellicium olivascens (Bres.) K.H. Larss. & Hjortstam[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceraceomyces americana Nakasone, C.R. Bergman & Burds.[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceraceomyces sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceraceomyces subleavis (Bres.) Jülich[e,f]	1	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Ceriporia cf. alachuana (Murrill) Hallenb.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Ceriporia reticulata (Hoffm.) Domanski	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceriporia tarda (Berk.) Ginns[e]	2	1	—	—	—	—	—	—	—	—	—	—	—	—	3
Ceriporia viridans (Berk. & Broome) Donk[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceriporiopsis mucida (Pers.) Glib. & Ryvarden[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ceriporiopsis pannocincta (Romell) Gilb. & Ryvarden[f]	12	1	7	2	—	—	—	3	—	—	—	—	—	1	26
Cerrena unicolor (Bull.) Murrill	51	—	7	2	—	—	—	—	—	—	—	—	—	—	60
Chondrostereum purpureum (Pers.) Pouzar	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Clavulicium macounii (Burt) J. Erikss. & Boidin[e]	—	—	—	—	—	—	—	—	3	—	—	—	1	—	4
Coniophora olivacea (Fr.) P. Karst.[e]	—	—	—	—	—	—	—	2	—	—	—	—	—	—	2

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	Total
Coniophora puteana (Schumach.) P. Karst.	2	—	1	—	—	—	—	5	—	—	—	—	—	1	9
Conohypha terricola (Burt) Jülich[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Coronicium alboglaucum (Bourdot & Galzin) Jülich	1	—	—	—	—	—	—	1	—	—	—	—	—	—	2
Cristinia helvetica (Pers.) Parmasto[e]	2	2	4	—	—	—	—	2	3	—	—	—	—	—	13
Cristinia mucida (Bourdot & Galzin) J. Erikss. & Ryvarden[g]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Cylindrobasidium laeve (Pers.) Chamuris	8	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Cystostereum murraii (Berk. & M.A. Curtis) Pouzar	—	—	49	—	—	—	—	—	—	—	—	—	—	—	49
Cystostereum pini-canadense (Schwein.) Parmasto.	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2
Cystostereum sp. #1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Dacryobolus sudans (Alb. & Schwein.) Fr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Daedaleopsis confragosa (Bolton) J. Schröt.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Datronia mollis (Sommerf.) Donk.	5	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Dentipellis leptodon (Mont.) Maas Geest.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Dentocorticium sulphurellum (Peck) M.J. Larsen & Gilb.[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Diplomitoporus sp. #1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Fibulomyces mutabilis (Bres.) Jülich	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Fomes fomentarius (L.) Kickx.	165	2	236	2	22	—	—	12	—	—	—	—	—	2	441
Fomitopsis cajanderi (P. Karst.) Kotl. & Pouzar	—	—	—	—	—	—	—	—	—	—	1	—	—	1	2
Fomitopsis pinicola (Sw.) P. Karst.	—	—	—	—	1	—	—	—	1	—	—	—	—	—	2
Ganoderma applanatum (Pers.) Pat.	355	12	45	1	6	—	—	9	—	—	—	—	—	—	428
Ganoderma tsugae Murrill	—	—	—	—	—	—	—	—	4	—	—	—	—	—	4
Gloeocystidiellum clavuligerum (Höhn. & Litsch.) Nakasone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Gloeocystidiellum ochraceum (Fr.) Donk[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Gloeocystidiellum porosum (Berk. & M.A. Curtis) Donk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Gloeophyllum sepiarium (Wulfen) P. Karst.	—	—	—	—	—	—	—	—	1	—	—	—	—	2	3
Gloeoporus dichrus (Fr.) Bres.	3	—	—	—	2	—	—	4	—	—	—	—	—	—	9
Gloiothele citrina (Pers.) Ginns & G.W. Freeman	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Granulocystis flabelliradiata (J. Erikss. & Hjortstam) Hjortstam[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hapalopilus nidulans (Fr.) P. Karst.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hapilopilus sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Helicogloea farinacea (Höhn.) D.P. Rogers[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Henningsomyces candidus (Pers.) Kuntze[f]	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2
Hericium coralloides (Scop.) Pers.	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Heterochaetella dubia (Bourdot & Galzin) Bourdot & Galzin[e,f]	7	—	—	—	1	—	—	—	—	—	—	—	—	—	8
Hymenochaete fuliginosa (Pers.) Lév. sensu Burt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hymenochaete tabacina (Sowerby) Lév.[f]	15	—	—	—	—	—	4	2	1	—	—	—	—	—	22
Hyphoderma argillaceum (Bres.) Donk	—	—	—	—	1	—	—	—	1	—	—	—	—	—	2

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														Total
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	
Hyphoderma litschaurii (Burt) J. Erikss. & A Strid[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphoderma medioburiense (Burt) Donk[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphoderma mutatum (Peck) Donk	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma praetermissum (P. Karst.) J. Erikss. & A Strid	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma puberum (Fr.) Wallr.	4	—	—	1	—	—	—	1	—	—	—	—	—	2	8
Hyphoderma sambuci (Pers.) Jülich[f]	5	1	1	—	—	—	—	3	—	—	—	—	—	—	10
Hyphoderma setigerum (Fr.) Donk	1	—	—	—	—	—	—	1	—	—	—	—	—	—	2
Hyphoderma sp. #1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	3
Hyphoderma sp. #2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma sp. #3	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Hyphoderma sp. #4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphoderma sp. #5	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma sp. #6	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Hyphoderma sp. #7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma sp. #8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphoderma sp. #9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia abieticola (Bourdot & Galzin) J. Erikss.[e]	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Hyphodontia alutacea (Fr.) J. Erikss.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Hyphodontia alutaria (Burt) J. Erikss.[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia arguta (Fr.) J. Erikss.	5	—	—	—	—	—	1	1	1	—	—	—	—	—	8
Hyphodontia cf. *alienata* (S. Lundell) J. Erikss.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hyphodontia cf. *rimosissima* (Peck) Gilb.	2	—	—	1	—	—	1	1	—	—	—	—	—	—	5
Hyphodontia crustosa (Pers.) J. Erikss.	—	—	—	—	—	—	—	1	—	—	—	—	—	2	3
Hyphodontia juniperi (Bourdot & Galzin) J. Erikss. & Hjortstam[e]	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Hyphodontia pallidula (Bres.) J. Erikss.	—	—	—	—	—	—	—	1	3	2	—	—	—	—	6
Hyphodontia sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #5	—	—	—	—	—	—	—	1	—	—	—	—	—	1	2
Hyphodontia sp. #6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia sp. #10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hyphodontia spathulata (Schrad.) Parmasto	23	2	6	1	2	—	1	5	3	1	—	—	—	3	47
Hyphodontia subalutacea (P. Karst.) J. Erikss.	—	—	1	—	1	—	—	—	—	—	—	—	—	—	2
Hypochnicium analogum (Bourdot & Galzin) J. Erikss.[e]	1	—	—	—	—	—	—	1	—	—	—	—	—	—	2

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	Total
Hypochnicium detriticum (Bourdot & Galzin) J. Erikss. & Ryvarden[e,f]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hypochnicium polonense (Bres.) Å Strid[f]	8	—	1	1	1	—	—	2	—	—	—	—	—	—	13
Hypochnicium punctulatum (Cooke) J. Erikss.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Hypochnicium vellereum (Ellis & Cragin) Parmasto	1	—	—	—	—	—	—	2	—	—	—	—	—	1	4
Inonotus dryadeus (Pers.) Murrill[e]	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Inonotus glomeratus (Peck) Murrill	4	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Inonotus obliquus (Ach. ex Pers.) Pilát	—	—	6	—	—	—	—	—	—	—	—	—	—	—	6
Irpex lacteus (Fr.) Fr.	2	—	1	—	—	—	—	—	—	—	—	—	—	—	3
Ischnoderma resinosum (Schrad.) P. Karst.	5	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Junghuhnia nitida (Pers.) Ryvarden	1	1	—	—	—	—	—	—	1	—	—	—	—	—	3
Junghuhnia separabilima (Pouzar) Ryvarden[e]	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2
Kavinia alboviridis (Morgan) Gilb. & Budington	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Kavinia himantia (Schwein.) J. Erikss.[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Laxitextum cf. *bicolor* (Pers.) Lentz	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Lenzites betulina (L.) Fr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Leptosporomyces fuscostratus (Burt) Hjortstam	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Leptosporomyces cf. *mundus* (H.S. Jacks. & Dearden) Jülich	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Leptosporomyces sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Leptosporomyces sp. #2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Leptosporomyces sp. #3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Lindtneria chordulata (D.P. Rogers) Hjortstam[e,f]	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Lopharia cinerascens (Schwein.) G. Cunn.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Merulopsis corium (Pers.) Ginns[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mucronella calva (Alb. & Schwein.)Fr.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mycoacia aurea (Fr.) J. Erikss. & Ryvarden[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mycoacia fuscoatra (Fr.) Donk	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Oligoporus caesius (Schrad.) Gilb. & Ryvarden	—	—	—	—	—	—	1	1	—	—	—	—	1	—	3
Oligoporus tephroleucus (Fr.) Gilb. & Ryvarden [e]	2	—	—	—	—	—	—	2	—	—	—	—	—	—	4
Oligoporus undosus (Peck) Gilb. & Ryvarden [e,f]	2	—	—	—	—	—	—	1	—	—	—	—	—	1	4
Oxyporus corticola (Fr.) Ryvarden [e,f]	1	—	—	—	2	—	—	—	—	—	—	—	—	—	3
Oxyporus populinus (Schumach.) Donk	64	—	—	6	—	—	—	1	—	—	—	—	—	—	71
Oxyporus sp. #1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Peniophora cf. *incarnata* (Pers.) P. Karst.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Peniophora cf. *lilacea* Bourdot & Galzin	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Peniophora cinerea (Pers.) Cooke	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														Total
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	
Peniophora rufa (Pers.) Boidin	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Peniophora sp. #1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Peniophora sp. #2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Peniphora violaceolivida (Sommerf.) Massee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Perenniporia medulla-panis (Jacq.) Donk	5	—	3	—	4	—	—	3	1	—	—	—	—	1	17
Perenniporia tepeitensis (Murrill) Ryvarden[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phanerochaete affanis (Burt) Parmasto	—	—	—	—	—	—	1	1	—	—	—	—	—	1	3
Phanerochaete calotricha (P. Karst.) J. Erikss. & Ryvarden	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phanerochaete carnosa (Burt) Parmasto	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Phanerochaete filamentosa (Berk. & M.A. Curtis) Burds.	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Phanerochaete sordida (P. Karst.) J. Erikss. & Ryvarden	6	—	—	—	—	—	—	1	—	—	—	—	—	1	8
Phanerochaete vetulina (DC.) Parmasto	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phellinus cf. *melleoporus* (Murrill) Ryvarden	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phellinus cf. *robustus* (P. Karst.) Bourdot & Galzin	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Phellinus chrysoloma (Fr.) Donk	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
Phellinus ferreus (Pers.) Bourdot & Galzin[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phellinus ferruginosus (Schrad.) Pat.[e,f]	6	—	1	2	—	—	1	—	—	—	—	—	—	—	10
Phellinus gilvus (Schwein.) Pat.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Phellinus ignarius (L.) Quél.	—	—	16	—	—	—	1	—	—	—	—	—	—	—	17
Phellinus punctatus (Fr.) Pilát	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2
Phellinus tremulae (Bondartsev) Bondartsev & Borissov	—	—	—	—	7	—	—	—	—	—	—	—	—	—	7
Phlebia acerina Peck[c]	6	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Phlebia cf. *incarnata* (Schwein.) Nakasone & Burds.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Phlebia centrifuga P. Karst.	—	—	2	—	—	—	—	—	—	—	—	—	—	1	3
Phlebia coccineofulva Schwein.	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2
Phlebia radiata Fr.	4	—	1	—	—	—	—	—	—	—	—	—	—	—	5
Phlebia canadensis W.B. Cooke[d,g]	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Phlebia tremulosus (Schrad.) Nakasone & Burds.	2	—	1	—	2	—	—	—	—	—	—	—	—	—	5
Phlebiella sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Phlebiella sp. #2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Phlebiella sulphurea (Pers.) Ginns & M.N.L. Lefebvre	13	—	—	—	1	—	—	1	1	—	—	—	—	1	17
Physolacria inflata (Schwein. ex Fr.) Peck	10	—	—	—	—	—	—	—	—	—	—	—	—	—	10
Piptoporus betulinus (Bull.) P. Karst.	—	—	8	—	—	—	—	—	—	—	—	—	—	—	8
Platygloea peniopharae Bourdot & Galzin[e]	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Plicatura crispa (Pers.) Rea	—	—	8	2	—	—	—	1	—	—	—	—	—	—	11
Polyporus alveolaris (DC.) Bondartsev & Singer	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Polyporus badius (Pers.) Schwein.	6	1	1	—	—	—	—	2	—	—	—	—	—	1	11
Polyporus brumalis (Pers.) Fr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	Total
Polyporus elegans Bull.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Porotheleum fimbriatum (Pers.) Fr.	17	—	7	—	1	—	1	7	—	—	—	—	—	4	37
Pseudohydnum gelatinosum (Scop.) P. Karst.	—	—	—	—	—	—	—	—	2	—	—	—	—	—	2
Radulomyces confluens (Fr.) M.P. Christ.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Ramaricium albo-ochraceum (Bres.) Jülich[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Resinicium bicolor (Alb. & Schwein.) Parmasto	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Resinicium furfuraceum (Bres.) Parmasto	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Resinicium sp. #1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Rigidoporus crocatus (Pat.) Ryvarden[e]	8	2	6	—	—	—	—	—	—	1	—	—	—	1	18
Schizophyllum commune Fr. [f]	5	—	—	1	—	—	—	1	—	—	—	—	—	1	8
Schizopora paradoxa (Schrad.) Donk[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Scopuloides rimosa (Cooke) Jülich	1	—	—	—	1	—	—	—	—	—	—	—	—	—	2
Scytinostroma galactinium (Fr.) Donk	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Scytinostroma protrusum ssp. *septentrionale* Nakasone	6	—	2	—	8	—	—	12	4	1	—	4	2	1	40
Scytinostromella humifaciens (Burt) Freeman & R.H. Petersen[e,f]	1	—	—	—	1	—	—	—	2	—	—	—	—	—	4
Sebacina sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Sebacina sp. #2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Sistotrema biggsiae Hallenb.[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sistotrema brinkmannii (Bres.) J. Erikss.[f]	3	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Sistotrema oblongispora M.P. Christ. & Hauerslev[g]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Sistotrema raduloides (P. Karst.) Donk	—	—	—	2	—	—	—	—	—	—	—	—	—	—	2
Sistotrema sernanderi (Litsch.) Donk[g]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Sistotremastrum niveocremeum (Höhn & Litsch.) J. Erikss.[e]	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sistotremastrum suecicum Litsch. ex J. Erikss.[e]	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Skeletocutis amorpha (Fr.) Kotl. & Pouzar[e]	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Skeletocutis nivea (Jungh.) Jean Keller	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Steccherinum ciliolatum (Berk. & M.A. Curtis) Gilb. & Budington[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Steccherinum fimbriatum (Pers.) J. Erikss.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Steccherinum ochraceum (Pers.) Gray	20	5	1	—	1	—	3	3	—	—	—	—	—	—	33
Steccherinum oreophilum Lindsey & Gilb.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Steccherinum subcrinale (Peck) Ryvarden[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Stereum hirsutum (Willd.) Pers.	147	3	9	4	—	—	3	13	—	—	—	—	1	1	181
Subulicystidium longisporum (Pat.) Parmasto[f]	4	1	—	—	1	—	—	—	—	—	—	—	—	—	6
Subulicystidium sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella bryophila (Pers.) M.J. Larsen	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]														Total
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	
Tomentella crinalis (Fr.) M.J. Larsen[e,f]	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Tomentella epigaea (Burt) M.J. Larsen[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella ferruginea (Pers.) Pat.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella sp. #2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Tomentella sp. #3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella sp. #4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella sp. #5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentella sp. #6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentellastrum badium (Link) M.J. Larsen[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tomentellopsis cf. *pusilla* Hjortstam	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Trametes hirsuta (Wulfen) Pilát	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Trametes pubescens (Schumach.) Pilát	7	—	1	—	—	—	—	2	—	—	—	—	—	—	10
Trametes sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Trametes versicolor (L.) Lloyd	131	—	11	3	2	—	—	8	—	—	—	—	—	1	156
Trechispora alnicola (Bourdot & Galzin) Liberta[e]	1	—	—	—	—	—	—	2	—	—	—	—	—	2	5
Trechispora cohaerens (Schwein.) Jülich & Stalpers	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Trechispora farinacea (Pers.) Liberta	2	—	—	—	—	—	—	1	—	—	—	—	—	—	3
Trechispora mollusca (Pers.) Liberta[e,f]	1	—	1	—	—	—	—	1	1	2	—	—	1	—	7
Trechispora stellulata (Bourdot & Galzin) Liberta[g]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Trichaptum abietinum (Dicks.) Ryvarden	—	—	—	—	—	—	—	—	9	1	1	—	1	—	12
Trichaptum biforme (Fr.) Ryvarden	10	—	22	5	—	—	—	—	—	—	—	—	—	—	37
Tubulicrinis gracillimus (D.P. Rogers & H.S. Jacks.) G. Cunn.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tubulicrinis sp. #1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tubulicrinis subulatus (Bourdot & Galzin) Donk[e,f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tulasnella bifrons Bourdot & Galzin[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tulasnella pinicola Bres.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Tyromyces cf. *subgiganteus* (Berk. & M.A. Curtis) Ryvarden	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Tyromyces chioneus (Fr.) P. Karst.	3	—	2	—	1	—	—	4	—	—	—	—	—	1	11
Uthatobasidium fusisporum (J. Schröt.) Donk[e,f]	4	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Uthatobasidium ochraceum (Massee) Donk	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Vararia investiens (Schwein.) P. Karst.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Xenasma praeteritum (H.S. Jacks.) Donk[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0

TABLE II. Continued

Species of fungi	Fungal occurrence data by substrate species[a]													
	SM	BS	YB	RM	QA	BC	IW	UH	HM	FR	SP	WC	UC	UN	Total
Total:	1255	41	498	38	78	1	21	141	49	10	3	7	8	45	2195

[a] Occurrence data are pooled from 1996 and 1997. A fungal occurrence is defined as an observation of a species on a unit of substrate within a 5 m by 5 m quadrat. Substrate abbreviations: SM = sugar maple (*Acer saccharum*), BS = basswood (*Tilia americana*), YB = yellow birch (*Betula alleghaniensis*), RM = red maple (*Acer rubrum*), QA = quaking aspen (*Populus tremuloides* and *P. grandidentata*), BC = black cherry (*Prunus serotina*), IW = ironwood (*Carya ovata*), UH = unknown hardwood, HM = hemlock (*Tsuga canadensis*), FR = balsam (*Abies balsamea*), SP = spruce (*Picea* sp.), WC = white cedar (*Thuja occidentalis*), UC = unknown conifer, UN = unknown.

[b] Species with zero total occurrences were only observed on small woody debris (<15 cm diameter).

[c] Ginns and Lefebvre (1993) consider *Phlebia acerina* to be a synonym of *Phlebia rufa*. Careful study by Nakasone and Sytsma (1993), however, revealed that *P. acerina* and *P. rufa* are intersterile and differ in terms of fruiting body characteristics, cultural traits, and DNA sequences.

[d] *Phlebia canadensis* W.B. Cooke is listed as a synonym of *P. albida* by Ginns and Lefebvre (1993). After studying type material, K. Nakasone considered *P. canadensis* to be distinct from *P. albida*.

[e] Not reported from Michigan, USA by Ginns and Lefebvre (1993) or Gilbertson and Ryvarden (1986, 1987).

[f] Not reported from Wisconsin, USA by Ginns and Lefebvre (1993) or Gilbertson and Ryvarden (1986, 1987).

[g] Not reported from the USA by Ginns and Lefebvre (1993) or Gilbertson and Ryvarden (1986, 1987).

values did differ significantly ($P < 0.05$) by year, with the exception of measurements from the Brillouin index (TABLE III). The management history by year interaction was not significant ($P > 0.10$).

When richness was calculated by diameter class of substrate, a moderately significant difference ($P = 0.0839$) was seen for mean species richness on large diameter woody substrates (TABLE IV). This difference was not apparent for richness on small diameter woody substrates ($P = 0.5359$). However mean richness values did differ significantly ($P = 0.0071$) by year for small diameter wood, while they did not differ significantly by year ($P = 0.8623$) for large diameter wood (TABLE IV). Ten species had mean abundance levels that differed ($P < 0.10$) by management class or by management class and year (TABLE V).

Woody debris volume and species composition also varied by management class (see Czederpiltz 2001). The average number of trees per site differed significantly among management classes ($P < 0.05$), and this difference was most pronounced for large trees (>60 cm) or relatively small trees (15–30 cm). Small diameter snags (15–30 cm) were found to differ by management class and were most common in even-age unthinned stands; in contrast large diameter snags (>60 cm) were most common in old-growth stands. The average number of stumps per site was found to differ significantly ($P < 0.01$) by management class, which was true for all four diameter classes. Even-age thinned stands had the greatest number of stumps, followed by uneven-age stands, even-age unthinned stands and then old growth. Total log volume was highly significantly different ($P < 0.0001$) among management classes, as was the volume of suspended logs. For both total log volume and suspended log volume, old growth had the largest values, followed by uneven-age stands, even-age thinned stands and then even-age unthinned stands. The volume of logs by decay class also was found to differ among management classes, with old-growth sites having larger volumes of all decay classes. Even-age unthinned and old-growth sites had the largest amounts of smaller diameter (≥1 cm but <15 cm) debris, although this difference was not found to be significant ($P > 0.10$). The volume of sugar maple and yellow birch logs was found to differ significantly ($P < 0.05$) among management classes, as was the combined volume of all hardwood species. Log volume for sugar maple, yellow birch and the combined volume of all hardwood species was greatest in old growth.

For all five fungal species that occurred at least 70 times diameter class of substrate and the management history of the stand were important in predicting the

TABLE III. Richness and diversity values for polyporoid and corticioid fungi in northern hardwood stands with different management histories

	Species richness		Shannon index (H')		Simpson index ($1/D$)		Brillouin index (HB)		Shannon evenness	
Old-growth	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997
Stand 1	34	38	3.04	3.19	14.13	15.96	116.0	076.1	0.86	0.88
Stand 2	40	50	3.18	3.46	15.41	21.15	132.2	197.6	0.86	0.89
Stand 3	47	53	3.36	3.57	18.74	23.96	126.3	081.4	0.87	0.90
Stand 4	52	86	3.44	4.00	19.90	34.73	142.3	214.6	0.87	0.90
Stand 5	61	52	3.53	3.45	19.48	20.81	162.7	154.0	0.86	0.87
Old-growth mean:	46.8	55.8	3.31	3.53	17.53	23.32	135.9	144.7	0.86	0.89
Uneven-aged										
Stand 6	49	54	3.38	3.55	19.18	23.57	141.2	144.9	0.87	0.89
Stand 7	44	82	3.10	3.88	14.14	32.05	256.0	359.9	0.82	0.88
Stand 8	44	81	3.31	3.91	19.02	31.59	181.2	246.9	0.88	0.89
Stand 9	50	60	3.51	3.73	24.27	28.24	112.5	123.4	0.90	0.91
Stand 10	41	55	3.35	3.60	19.50	24.41	066.1	120.6	0.90	0.90
Uneven-aged mean:	45.6	66.4	3.33	3.73	19.22	27.97	151.4	199.1	0.87	0.89
Even-aged Unthinned										
Stand 11	36	58	3.10	3.63	15.46	26.04	145.5	173.0	0.86	0.90
Stand 12	46	52	3.30	3.60	16.98	26.52	107.3	162.1	0.86	0.91
Stand 13	23	36	2.66	3.39	08.92	24.23	066.8	038.5	0.85	0.95
Even-aged unthin. mean:	35.0	48.7	3.02	3.54	13.79	25.60	106.5	124.6	0.86	0.92
Even-aged Thinned										
Stand 14	37	56	3.09	3.61	13.93	25.99	195.3	160.0	0.85	0.90
Stand 15	58	72	3.67	3.88	27.01	32.64	114.2	137.6	0.91	0.91
Even-aged thin. mean:	47.5	64.0	3.38	3.75	20.47	29.32	154.7	148.8	0.88	0.91
P-values										
Management History:	0.3399		0.2647		0.3152		0.5962		0.5832	
Year:	0.0169		0.0077		0.0074		0.3055		0.0118	
Management History * Year:	0.6204		0.447		0.2182		0.4809		0.2075	

number of fungal occurrences at a site (see Czederpiltz 2001). The volume of logs within each diameter class did not help predict the occurrence of *Fomes fomentarius* or *Oxyporus populinus* but was important for *Ganoderma applanatum*, *Stereum hirsutum* and *Trametes versicolor*. The effective R^2 values indicate that the full regression models for these fungi account for 78–91% of the variability associated with species occurrence, while 19–62% of the variability can be explained by random effects alone. For the second regression analysis, the species of substrate, the management history of the stand and the volume of logs by substrate species all were found to be important in predicting the number of fungal occurrences at a site. The effective R^2 values indicate that the full regression models for these fungi account for 69–94% of the variability associated with species occurrence, while approximately 12% of the variability can be explained by random effects alone (Czederpiltz 2001).

DISCUSSION

Contrary to European findings (e.g. Bader et al 1995, Høiland and Bendiksen 1997, Lindblad 1998), species richness values (i.e. the total number of species observed per site per year) and measures of community diversity did not differ significantly ($P > 0.10$) among management classes (see TABLE III). A possible explanation for this difference is that European researchers have tended to examine only large diameter woody debris (Bader et al 1995, Lindblad 1998) or have restricted sampling to logs of a certain length (Høiland and Bendiksen 1997). If our dataset is restricted to the species found on large diameter wood (≥15 cm), differences in species richness are moderately significant ($P < 0.10$) among management classes (see TABLE IV), and this effect did not vary significantly ($P > 0.10$) by year. In addition to focusing on large diameter debris, most previous research has been conducted in boreal forests

TABLE IV. Species richness values by substrate diameter class for polyporoid and corticioid species in northern hardwood stands with different management histories

	Richness on large diameter wood[a]		Richness on small diameter wood[b]	
Old-growth	1996	1997	1996	1997
Stand 1	24	20	20	26
Stand 2	24	20	28	40
Stand 3	30	23	30	40
Stand 4	30	33	37	69
Stand 5	32	25	43	36
Old-growth mean:	28.0	24.2	31.6	42.2
Uneven-aged				
Stand 6	25	18	35	45
Stand 7	26	32	33	66
Stand 8	29	27	28	67
Stand 9	36	29	29	45
Stand 10	16	15	29	47
Uneven-aged mean:	26.4	24.2	30.8	54.0
Even-aged Unthinned				
Stand 11	16	22	27	45
Stand 12	16	13	36	48
Stand 13	09	16	17	29
Even-aged unthin. mean:	13.7	17.0	26.7	40.7
Even-aged Thinned				
Stand 14	15	24	29	43
Stand 15	32	26	38	57
Even-aged thin. mean:	23.5	25.0	33.5	50.0
P-values				
Management History:	0.0839		0.5359	
Year:	0.8623		0.0071	
Management History * Year:	0.3812		0.421	

[a] Large diameter wood was defined as ≥15 cm in diameter.
[b] Small diameter wood was defined as ≥1 cm but <15 cm in diameter.

dominated by conifers (e.g. Bader et al 1995, Høiland and Bendiksen 1997, Lindblad 1998, Ohlson et al 1997, Wästerlund and Ingelög 1981), while this study was conducted in the northern hardwood forests of the Midwest. These dissimilar forest types may respond to disturbance in different ways.

Regardless of forest type it is likely that some forest management practices, including thinning and selective harvesting, increase the amount of small diameter debris at a site. This is significant for the many fungal species that preferentially colonize smaller substrate classes. An increase in species richness on small diameter debris may offset a decrease in species richness due to a loss of large diameter debris. Thus forest management may not change the overall number of wood-inhabiting species at a site, as reported in previous research. Rather forest management may favor species capable of colonizing small diameter debris.

Measuring the fungal community found on small diameter debris is difficult, however, because these species may be more variable in occurrence compared to species on large debris. In the present study the number of species found on small diameter wood varied greatly in 1996–1997 ($P < 0.01$) and this might have masked differences among management classes. In addition it can be difficult in the field to carefully examine the numerous pieces of fine woody debris that can be found in even a small area. In future studies researchers could choose to exclude a great deal of variability in species richness by sampling only large diameter debris, although this will limit the conclusions that can be drawn with regard to overall species richness.

While particular fungi that inhabit large diameter debris obviously will be affected by forest management practices that reduce the quantity and quality of large diameter logs (Bader et al 1995, Lindblad 1998,

TABLE V. Abundance values for selected polyporoid and corticioid species in northern hardwood stands with different management histories

Species name	Year	Abundance values (number of quadrats occupied per site[a])															*P*-values		
		Old-growth stands					Uneven-aged stands					Even-aged unthinned			Even-aged thinned				
		#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13	#14	#15	Management	Year	Mngt. by Year
Cystostereum	1996	1	3	1	3	1	0	0	3	1	0	0	0	0	0	0	0.0189	0.8359	0.9757
murraii	1997	3	1	5	1	1	0	2	0	2	0	0	0	0	0	0			
Ganoderma	1996	16	12	14	10	21	7	20	7	3	1	0	2	0	12	3	0.0607	0.8842	0.1065
applanatum	1997	12	12	9	10	8	17	18	11	5	2	4	2	1	14	2			
Hyphoderma	1996	1	1	1	0	0	3	2	0	1	3	1	1	1	0	1	0.0801	0.0360	0.6564
setigerum	1997	0	2	4	5	1	2	9	6	5	3	7	8	2	1	3			
Oxyporus	1996	2	3	1	1	5	1	3	0	1	4	3	6	5	3	4	0.0052	0.2560	0.0338
populinus	1997	2	0	0	1	1	2	4	1	2	2	4	6	4	5	9			
Phanerochaete	1996	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0.0378	0.0534	0.1045
sordida	1997	1	1	0	1	0	5	3	3	0	2	1	2	0	1	0			
Rigidoporus	1996	1	2	0	1	2	0	1	0	1	0	0	0	0	0	0	0.0059	0.6726	0.9495
crocatus	1997	0	1	1	3	1	0	1	1	1	0	0	0	1	0	0			
Scytinostroma	1996	0	0	2	1	0	0	0	0	5	2	0	0	3	2	7	0.0851	0.9624	0.3061
protrusum	1997	1	3	0	3	0	2	1	2	2	1	4	1	2	4	0			
Trechispora	1996	0	0	0	0	2	2	0	0	0	0	1	0	2	0	0	0.0613	0.0526	0.0321
farinacea	1997	0	1	1	0	0	0	0	1	1	0	1	1	1	3	3			
Trametes	1996	6	6	5	5	2	13	20	14	7	1	4	1	2	15	5	0.0707	0.0541	0.8782
versicolor	1997	3	2	1	5	1	7	19	12	4	2	2	0	0	9	5			
Vararia	1996	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0.0307	0.4642	0.4893
investiens	1997	0	0	0	0	0	2	1	1	3	0	0	1	0	0	1			

[a] Quadrat size was 10 m by 10 m for this analysis, with 30 quadrats per site.

Ohlson 1997), some forest management practices may increase the overall species richness of polyporoid and corticioid fungi at a site. Our uneven-age and even-age thinned stands averaged approximately equal or greater species richness on small diameter debris than old-growth stands. In addition overall richness in uneven-age and even-age thinned stands was approximately equal to or greater than that of old-growth stands, with this effect being most prominent in the 1997 data. This effect might be due to management practices that increase the amount of small diameter debris in stands and therefore the diversity of fungi found on this diameter class. Because small diameter substrates are common at the landscape level, it is likely that an increase in fungal diversity due to an increase in small diameter debris will mean a site is occupied by many ''common'' species. Therefore increases in species diversity on small diameter debris may not be useful for the conservation of rare species. However, in stands with a large volume of small diameter debris, changes in fungal diversity on smaller diameter classes could greatly affect overall decay rates.

In Europe it has become widely accepted that some ''indicator'' and ''red-listed'' fungi are endangered because they are associated with particular habitats or forest management categories (Arnolds 1997, Rydin et al 1997, Stokland et al 1997). In this study a species was identified as being associated with a particular management class using an α-level of 0.10 to judge significance (P-values < 0.10). A liberal α-level was employed because this was an exploratory study (i.e. a similar study of this nature had not been previously performed) and only modest levels of site-level replication were possible. By considering P-values < 0.10 but > 0.05 as ''moderately significant,'' it is possible to identify species that may show significant trends if more sites had been sampled. Although this strategy increases the risk of Type I statistical error, it makes it possible to identify species that should be surveyed at a larger number of sites in future studies.

In our study 10 species tended to be associated with particular management classes, displaying abundance levels that differed ($P < 0.10$) among management classes (TABLE V). Some of these fungi, such as *Cystostereum murraii* and *Rigidoporus crocatus*, were most abundant in old-growth stands and therefore might be useful indicators of stand with ''old-growth characteristics.'' Other species, in contrast, might be useful indicators of managed stands; *Oxyporus populinus* and *Vararia investiens* were collected most frequently in managed forests and therefore may be useful indicators of disturbance. Further experimental work is needed to determine if even-age management promotes the occurrence of *Oxyporus populinus* and whether this could negatively affect stand health and productivity.

A problem with a study of this scope is that a certain number of species may vary significantly in abundance among management classes simply due to random chance. In our analysis 73 of the 255 species occurred frequently enough to warrant testing with ANOVA. Using an α-level of 0.1 to judge statistical significance, one would expect 7.3 species to vary significantly due to chance alone. In our analysis 10 species had P-values < 0.10, suggesting that 2–3 species may have varied for reasons other than chance alone; for the other species there was not enough statistical power to indicate whether differences were due to chance. If a Bonferroni correction is applied to account for multiple comparisons, none of the species examined had abundance levels that varied significantly. However it is likely that a full Bonferroni correction is too conservative and that the relatively small number of species with significant P-values is due to the small number of sites sampled, which limits statistical power, rather than due to a true lack of species that vary by management class. If all 73 species are considered, the distribution of P-values associated with abundance levels is significantly nonrandom ($P = 0.015$), with 55% of the values being ≤ 0.39. This suggests that further sampling would increase the number of species with abundance levels that varied significantly. In the future directed sampling should be applied to the species (identified in TABLE V) to confirm that they are associated with forest stands of a particular management category.

It is likely that some species vary in abundance among management classes because substrate quantity and quality (species of substrate, diameter class, decay class, height off the ground, etc.) affect the abundance of particular species. For the five species examined in depth in this study, substrate diameter and substrate species were found to be important in predicting fungal abundance (see Czederpiltz 2001). Substrate quantity (log volume) at a site was found to be important in all five cases, with the exception of *Fomes fomentarius* and *Oxyporus populinus*. Both of these fungi tend to occur on standing woody debris, which could explain why log volume is not predictive of fungal occurrence. For all of the other species tested, substrate quality, quantity and management history of the stand were important in predicting the number of fungal occurrences at a site. Our models, although relatively simple, explained a large portion of the error associated with species occurrence. Effective R^2 values for our models with fixed and random effects had a range of 0.78–0.94, while models with random effects alone had R^2 values that ranged from 0.12 to 0.62.

Analysis of species accumulation curves suggests that using larger quadrat sizes would not have significantly affected our analyses (Czederpiltz 2001). Future researchers might find setting up a small number of larger quadrats less time consuming than installing a large number of smaller quadrats, as was done in this study. Large sampling units however can over represent the abundance of ''small'' species (Magurran 1988) or species that occur in small patches. There is therefore a trade-off between time needed to set up a field design and accuracy of abundance measurements. In our case species accumulation curves would not have been appreciably affected had we used sampling units as large as 50 × 10 m. However the accumulation curves produced with 50 × 10 m quadrats are shifted slightly ''downward.'' This indicates that positive (clumping) autocorrelation is present within the data for certain species (Czederpiltz 2001). Further analyses are needed to confirm the magnitude of this autocorrelation and to determine which species contributed to this effect.

Sampling 3000 m^2/y/site worked well, producing site-level species accumulation curves that differ significantly from straight lines, yet do not flatten off to the point where a great deal of effort was spent resampling common species. From a practical standpoint sampling larger areas within a stand might be difficult and might not lead to flatter species accumulation curves. We found it difficult to locate homogenous northern hardwood stands able to accommodate more than two 100 × 60 m plots. Sampling larger plots would necessitate the inclusion of more ''nontarget'' habitats (e.g. marshy areas, small ponds, hemlock stands, etc.), thus leading to continuously increasing species accumulation curves. It would be preferable to sample more sites within each management class to offset the large intersite variability observed within management classes (see TABLE III and FIG. 2) and to represent the range of stands within each management class more fully.

Sampling stands for more than 2 y also would be desirable. Our species accumulation curves show considerable variation in the fungal community in 1999–1997. With the sole exception of old-growth stand No. 5, the 1997 site-level species accumulation curves had higher end-points than the 1996 species accumulation curves. Although species accumulation curves were larger in 1997, it is interesting to note that old-growth sites did not show an average increase as large as other management classes. For old-growth sites, the average number of species observed in 3000 m^2 increased only by nine species in 1996–1997, while it increased by an average of approximately 17 species for all other management classes. Two years of data are too few to tell whether this disparity was due to chance or some biological factor intrinsic to old-growth stands. One possible biological explanation is that the old-growth fungal community is more consistent from year to year because a significant amount of wood at such sites is in large diameter classes. Such pieces of substrate might provide a relatively stable habitat in terms of moisture and temperature conditions (Cooke 1948). On average the old-growth sites we sampled had more than 40% of their total log volume in logs ≥45 cm diam, while the other management classes had from ≈2–17% of their log volume in logs of this size. If such an explanation is correct it would indicate that old-growth sites typically exhibit a large percentage of their potential diversity at all times, while other stands display a large percentage of their potential diversity only during particularly favorable years.

Our sampling procedures were designed primarily to measure diversity of wood-inhabiting fungi in stands and thus were unlikely to detect species that are rare in landscapes. Although changes in community diversity might be of primary concern to researchers interested in ecosystem processes, future investigations also need to address the issue of how to sample for individual species that occur infrequently in landscapes. Local extinction of some rare fungal species endemic to upper Midwest forests might have occurred before their presence could be documented by mycologists. For example, Neuman (1914) reported that ''various collectors'' had noted *Fomitopsis officinalis* (= *Fomes officinalis*) occurring on larch in northern Wisconsin. Although a few reports of this fungus have been confirmed from the Great Lakes region (Gilbertson and Ryvarden 1986), *F. officinalis* no longer is considered to occur in the Midwest. To the best of our knowledge H.H. Burdsall Jr. made the most recent Midwest collection from an old-growth stand of hemlock in the Huron Mountains of Michigan's Upper Peninsula in 1974. Further work is needed to determine whether this fungus still occurs in upper Midwest landscapes. Future work also could document whether other rare wood-inhabiting species, such as the old-growth hemlock inhabiting species *Laetiporus huroniensis* (Burdsall and Banik 2001), have disappeared from significant portions of their former ranges.

Forest management, an important source of disturbance in upper Midwest hardwood forests, appears to have significant effects on wood-inhabiting fungi. Because modern forest management practices can radically alter the amounts and types of debris in forests, wood-inhabiting species might be of special interest for conservation efforts. Most polyporoid and corticioid fungi are obligately dependent on woody debris for growth and reproduction, and such species

will be directly affected by management regimes that affect the quantities and qualities of woody debris available for colonization. Fungi that rely on large diameter woody substrates might be at particular risk, as well as fungi that are specifically associated with tree species that decline in frequency after management, including basswood, hemlock and yellow birch. A reduction in overall species richness of wood-inhabiting fungi could have significant implications for nutrient cycling and health in many forest ecosystems.

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