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Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and associated nitrogen status of boreal forests

J. M. Kranabetter · J. Friesen · S. Gamiet · P. Kroeger

Abstract Soil fertility and associated nitrogen (N) status is a key ecosystem attribute, and surveys of ectomycorrhizal fungal (EMF) communities via epigeous fruiting bodies could provide an effective biotic indicator of forest soil productivity. We explored the utility of aboveground EMF communities in this regard by surveying sporocarps over a 3-year period from contrasting plant associations of southern old-growth boreal forests of British Columbia (Canada). Cumulative richness ranged from 39 to 89 EMF species per plot (0.15 ha) and followed a skewed parabolic correlation with foliar N concentrations and soil N availability. EMF species composition was consistently distinct in ordinations and strongly correlated to the increasing rates of N mineralization aligned with soil productivity. Approximately 40 EMF species were specialists, as they collectively indicated oligotrophic, meso-trophic, and eutrophic nutrient regimes, while the remaining species were categorized as broadly tolerant (distributed over 100% of the N gradient), partially intolerant (approximately 70%), or satellites (rare). The functional organization of EMF communities reflected by distribution classes could help define the ecological integrity of forests, which was charac-terized in this boreal landscape by an average allotment of 20 broadly tolerant, 25 partially intolerant, 15 specialist, and 10 satellite species per plot. Epigeous fruiting bodies provided a disparate yet complementary view to the belowground assessment of EMF communities that was valuable in identifying indicators for ecosystem monitoring.

Keywords Ectomycorrhizal fungi · Mushrooms · Ecosystem monitoring · Indicator species · Nitrogen mineralization · Ecological integrity

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Introduction

Indicator species of migratory songbirds, raptors, small mammals, soil arthropods, epiphytic lichens, and wood-decay fungi have been touted as useful fine-filter tools in ecosystem monitoring, especially in evaluating the retention of old-growth forest conditions and maintenance of biodiver-sity (Nilsson et al. 2001; Kremsater et al. 2003). Some of the criteria to consider in selecting indicator species are that they be readily quantifiable, that they represent key habitat features or processes, and that they be sensitive to ecosystem manipulation (Ferris and Humphrey 1999). Many soil biota, with the exception of select arthropods, have yet to be thoroughly assessed for suitability as indicators (Thompson 2006). Ectomycorrhizal fungi (EMF) deserve further study in this regard given the typically high species diversity of this guild and key roles these symbiotic fungi have in ecosystem function (Read et al. 2004). With taxonomic training, epigeous EMF fruiting bodies can be assessed efficiently over large areas and have proven useful in evaluating, for example,

partial-cutting effectiveness (Luoma et al. 2004) and late-seral dependent EMF species (Kranabetter et al. 2005).

Besides monitoring old-growth forest habitat, indicator species of soil quality and productivity, especially as related to nitrogen (N), could be valuable in a number of applications (Knoepp et al. 2000). The sensitivity of EMF fruiting bodies to edaphic conditions is apparent from surveys of modified sites (e.g., Rűhling and Tyler 1990) and consequently, the response of macrofungi to elevated N availability has received much attention. Evidence from primarily short-term experimental research with N fertilizer applications suggest immediate declines in EMF fruiting body production and species richness with increased N availability, but with some positive responses in abundance for a subset of nitrophilic species (Brandrud 1995; Jonsson et al. 2000; Peter et al. 2001a; Avis et al. 2003; Edwards et al. 2004). Parallel studies from undisturbed forests with naturally contrasting levels of N availability are rare; Trudell and Edmonds (2004) reported lower sporocarp biomass in more productive forests, but more significant differences in species composition rather than richness with soil fertility. Natural and experimental N gradients are not entirely analogous, however, since N availability in pristine forests is not an independent variable, but rather a property of the underlying soil moisture and geochemical drivers (Giesler et al. 1998). Conclusions on N effects should therefore be considered in an ecological context, and studies of undisturbed forest ecosystems would be helpful in fully exploring soil abiotic–biotic relationships (Erland and Taylor 2002). While there has been considerable effort in linking EMF macrofungi composition with site conditions (see review in Trudell and Edmonds 2004), confounding changes in host tree species or macroclimate with different forest types has made edaphic effects difficult to isolate.

In this study, we report on the epigeous EMF macrofungi associated with replicated productivity gradients of upland southern boreal forests in British Columbia (Canada). The plot proximity and uniform elevation, with old-growth stands of *Pinus contorta* (Dougl. ex Loud), *Abies lasiocarpa* ([Hook.] Nutt.), and *Picea glauca* x *englemanni* ([Moench] Voss) at almost every site, created an ideal study design to minimize the effects of climate (O'Dell et al. 1999), stand age (Kranabetter et al. 2005), and host specificity (Durall et al. 2006) on relationships between soil fertility and EMF species distribution. A previous belowground EMF assessment with *A. lasiocarpa* saplings documented strong associations of EMF species with soil conditions, in particular the quantity and types of N (organic N, NH_4^+, and NO_3^-) and an asymptotic correlation of species diversity with foliar N concentrations (Kranabetter et al. 2009). Some of the most prevalent EMF species on root tips from these sites (e.g., *Cenococcum geophilum*, *Piloderma* spp., *Amphinema byssoides*, *Tomentella* spp.) would not be represented aboveground, but macrofungi could provide more comprehensive distribution data for the many infrequent EMF species of these forests (Taylor 2002). Ideally, epigeous fruiting bodies would provide an effective indicator of ecosystem status, based on a subset of readily quantifiable EMF species (albeit over several years of monitoring), in addition to a more complete portrayal of the EMF community (Richard et al. 2005; Smith et al. 2007).

The objectives in the second phase of this productivity gradient analysis were to (1) examine how closely EMF macrofungi assemblages and richness align with the plant associations and corresponding soil properties, (2) document the extent of widely distributed (multisite) species versus more narrowly distributed specialist species which could indicate N status of forest soils, and (3) provide EMF macrofungi community data from these largely pristine old-growth forest ecosystems to help define benchmarks for ecological integrity (species composition, diversity, and functional organization) in future managed landscapes.

Materials and methods

Site descriptions and study design

Study sites described previously (Kranabetter et al. 2009) were used for the macrofungal surveys, but with four replicates of each plant association (rather than five) for a total of 16 plots. The four replicates of each plant association over five blocks represent a balanced incomplete block design that met the requirement for connectedness (Mead 1988). Briefly, the plots were located at approximately 900-m elevation in the moist cold subzone of the Sub-Boreal Spruce zone near Smithers, British Columbia, Canada. Four plant associations (poor-Cladonia, medium-Huckleberry, rich-Oak fern, and very rich-Devil's club) from five blocks located within a 25-km area (54°40′ to 47′ N and 127°16′ to 36′ W) were sampled to provide a wide range in upland edaphic conditions. Each plot was 50×30 m (0.15 ha) in size.

Almost all plots had mixed old-growth coniferous forests (~180 years), but with differences in relative canopy composition of *P. contorta*, *A. lasiocarpa*, and *P. glauca* x *englemanni* across the gradient (Table 1). In addition to the codominant canopy, a very minor amount of *Tsuga heterophylla* (Raf. Sarg.) was found regenerating in the understory of four plots. Possible EMF hosts among shrub species included *Alnus viridis* ([Chaix.] D.C.), *Arctostaphylos uva-ursi* ([L.] Spreng.), *Amelanchier alnifolia* ([Nutt.] Nutt.), and *Shepherdia canadensis* ([L.] Nutt) (Hagerman et al. 2001). A contribution of sporocarps by understory western hemlock and shrub species is perhaps possible but we expect this is to be a very minor influence compared to the dominant conifer species of the forest canopy.

Foliar N concentrations ($N_{\%}$) of the regenerating *A. lasiocarpa* understory and selected soil properties (kilo-

Table 1 Selected stand and soil properties of the plots surveyed for epigeous EMF fruiting bodies

Plant association	Age (years)	Stand height (m)	*Pinus* (%)	*Abies* (%)	*Picea* (%)	Moisture (kg ha^{-1})	DON (kg ha^{-1})	NH$_4^+$ (kg ha^{-1})	NO$_3^-$ (kg ha^{-1})	DIN/DON ratio
P-Cladonia	180	20.2	80	20	0	16	26	0.3	0	1
P-Cladonia	190	16.8	83	17	0	13	18	1.5	0	8
P-Cladonia	115	23.1	79	11	11	11	14	0.9	0	6
P-Cladonia	165	24.9	88	3	9	17	15	1.3	0	9
M-Huckleberry	185	27.3	57	34	9	17	28	1.8	0	6
M-Huckleberry	180	26.5	36	62	2	14	22	1.9	0	9
M-Huckleberry	173	27.3	51	41	8	21	32	4.3	0	14
M-Huckleberry	205	29.1	32	58	10	27	25	6.5	0	26
R-Oak fern	180	31.4	25	67	8	23	28	5.6	0	20
R-Oak fern	179	32.1	5	90	5	21	36	5.9	0	17
R-Oak fern	188	31.5	26	36	38	40	34	11.2	0.3	34
R-Oak fern	177	30.5	7	79	14	33	35	7.1	0.1	21
VR-Devil's Club	174	35.3	23	64	13	28	34	4.5	0	13
VR-Devil's Club	185	34.6	22	62	16	25	28	8.1	15.1	83
VR-Devil's Club	178	37.8	19	64	17	32	26	11.2	3.8	59
VR-Devil's Club	206	35.9	12	77	12	26	40	13.1	3.1	40

Canopy composition % cover estimated visually and includes codominant and subdominant canopies

P poor, *M* medium, *R* rich, *VR* very rich, *DIN* dissolved inorganic N, *DON* dissolved organic N, *Pinus* lodgepole pine, *Abies* subalpine fir, and *Picea* hybrid white spruce

grams per hectare, upper mineral soil and forest floor combined, with the exception of pH) were tested against EMF macrofungi communities, including a 5-week in situ incubation of dissolved inorganic N (DIN) and organic N (DON), average gravimetric moisture from May to September, organic P, total S, exchangeable cations (Ca, Mg, and K), and pH of mineral soil and forest floor (N indices and soil moisture listed in Table 1). Methodologies for quantifying these properties, along with further descriptions of stand, soil, and vegetation characteristics of the study plots, are listed in Kranabetter et al. (2007).

Fruiting body surveys

Data on epigeous EMF macrofungi species were collected over a 3-year period, from 2006 to 2008. The plots were checked twice each fall during the expected peak in fruiting (August 20–23 and September 11–14) for a total of six sample periods. A species list was generated by searching the entire plot (0.15 ha) during each of the sample periods. Total species richness per site was determined from the cumulative species list collected over the 3 years. Species abundance was quantified by five 15-m transect lines, measuring 1 m in width, randomly located perpendicular to the central axis of the plot. A species found on two of the five transects within a plot, for example, would have an abundance value of 40%. A species found within the plot, but not on any transects, was given an abundance value of 5%. The locations of the transects were randomly reassigned (without replacement) for each of the six sample periods. The values from the six sample periods (including 0 if absent) were used to determine an average abundance for the comparison of EMF communities. Species frequency was calculated as the percent of replicates by plant association where that species had been found.

Taxonomic identification followed Thiers (1982), Moser (1983), Breitenbach and Kranzlin (2000), Bessette et al. (2000), Brandrud et al. (1990), and Tylutki (1987). In addition to the identified species, there were a few *Cortinarius* taxa, especially small brown *Telamonia* (e.g., section *Armeniaci*), which were too difficult to consistently identify to species and were consequently underrepresented in these survey results. Taxa with numerous subspecies, such as *Cortinarius brunneus* and *Cortinarius flexipes*, were not separated further in our surveys and identified collectively as a species group. We did not sample hypogeous fungi because of the soil disturbance required to find these fruiting bodies. Representative voucher specimens were dried and deposited at the University of British Columbia herbarium. A subset of species underwent internal transcribed spacer (ITS) rDNA analysis using the methodology described in Kranabetter et al. (2009) for accession into GenBank (Appendix). Voucher photographs of 40 *Cortinarius* species were also taken to support our taxonomic identification and will be available through MatchMaker (British Columbia Ectomycorrhizal Research 2007).

Statistics

Mean species richness by plant association was determined under Proc Mixed using the Estimate function (SAS Institute Inc 2004), with significant differences in species richness tested in pairwise comparisons. The general linear model procedure in SAS using type 1 sums of squares was used to test linear and curvilinear (polynomial, exponential, logarithmic, and power) correlations between plot means of dependent (total species richness, species per genera, species per distribution class) and independent variables (soil N availability, foliar N$_\%$; $n=16$). Goodness of fit was evaluated using r^2 and step-wise elimination of variables. No significant effect of block or block × treatment interactions was found in any of the correlations.

A comparison of EMF macrofungal communities among plots was undertaken by nonmetric multidimensional scaling (NMS), using the Sorenson (Bray–Curtis) distance measure for species presence/absence and relative Sorenson for species abundance. Computations were undertaken with PC-ORD 5.0 software, using the random starting configurations (McCune and Grace 2002). The ordination of axes was tested against plot soil and stand measures using Pearson and Kendall correlations.

Distribution classes based on the extent of fruiting body frequency and abundance along the productivity gradient were proposed to illustrate the relative extent of habitat occupied by each species and to explore the functional organization of the EMF communities. Species fruiting over the entire productivity gradient were characterized as "broadly tolerant" as defined by a minimum 50% frequency in fruiting for each of the four plant associations. Species narrower in distribution, found over approximately 70% of the soil gradient, were designated "partially intolerant", which included intolerance of the richest soils, the poorest soils, or the soil extremes. Partially intolerant species of poorer or richer soils were defined by a minimum 50% frequency in three of the four plant associations, or three of the four plant associations where sporocarp abundance was <2%; partially intolerant species of soil extremes had at least 50% frequency in the medium and rich plant associations, with less frequent or <1% sporocarp abundance in both poor and very rich plant associations. The most constricted distribution of species was termed the "specialists", each of which occupied approximately 40% of the productivity gradient. Specialist species were defined by a 75% frequency in no more than two plant associations (a maximum of 25% frequency in a third plant association distinguishes specialists from partially intolerant species), or 50% in either plant association where abundance >1%. Any species found on two plots or less, or otherwise not meeting any of the above criteria for classification, were termed "satellites" (Gibson et al. 1999).

Results

We identified 176 epigeous EMF species (or species complexes) from 19 genera over the 3-year survey period. The most species-rich genus was *Cortinarius* (73 species), followed by *Russula* (25), *Tricholoma* (15), *Hygrophorus* (13), *Lactarius* (ten), *Inocybe* (eight), *Suillus* (four), and three or fewer species for the remaining genera (Appendix). Fruiting varied almost twofold between sample years, peaking in 2007 with a total of 168 species across all plots, followed by 2008 (137 species) and 2006 (85 species).

Cumulative species richness for the 3-year period ranged from 39 to 89 species per plot (0.15 ha) and was consistently lowest on poor-Cladonia sites ($p<0.001$), averaging 48 species, compared to 75 for medium-Huckleberry, 80.5 for rich-Oak fern, and 70.5 for very rich-Devil's club sites (the difference in species richness between the latter two plant associations was also significant [$p=0.048$]). Likewise, species richness followed a skewed parabolic correlation with soil productivity, as expressed either by foliar N concentration of *A. lasiocarpa* or N availability of the soil profile (Fig. 1). Positive linear correlations in species richness by genera were found for *Inocybe*, *Russula*, and *Lactarius* along the N gradient, while *Cortinarius*, *Tricholoma*, and *Hygrophorus* had curvilinear correlations in species richness with foliar N$_\%$ (Fig. 2).

The community NMS analysis of macrofungi (Fig. 3a, b) showed a progressive separation by plant association that closely followed the productivity rankings for both EMF species presence/absence ($r^2=0.904$, final stress of 11.2 after 29 iterations) and EMF species abundance ($r^2=0.910$, final stress of 10.8 after 25 iterations). The only exception was the first replicate of the very rich-Devil's club sites (Table 1), which was more closely aligned to the rich-Oak fern plots in both ordinations. Only one axis was generated by the NMS analysis because all of the ordinated distances between plots closely matched the rank order of the original distance matrix. Pearson and Kendall correlations for EMF species
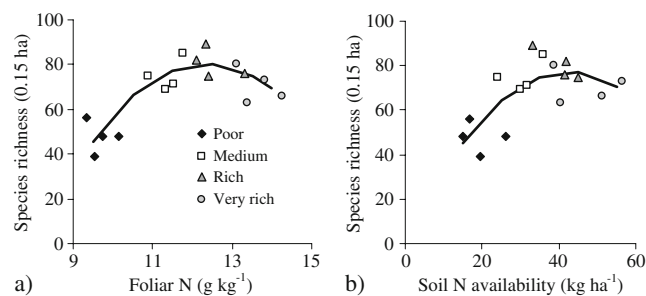
Fig. 1 EMF species richness in correlation with **a** *A. lasiocarpa* foliar N concentrations (g kg^{-1}) and **b** soil N availability (DIN + DON mass; kg ha^{-1}). Species richness (0.15 ha)=−540+99.9 (N$_\%$)−4.0 (N$_\%$)^2; $p<0.001$; $r^2=0.73$. Species richness (0.15 ha)=−0.1+3.7 (soil N)−0.04 (soil N)^2; $p=0.007$; $r^2=0.53$
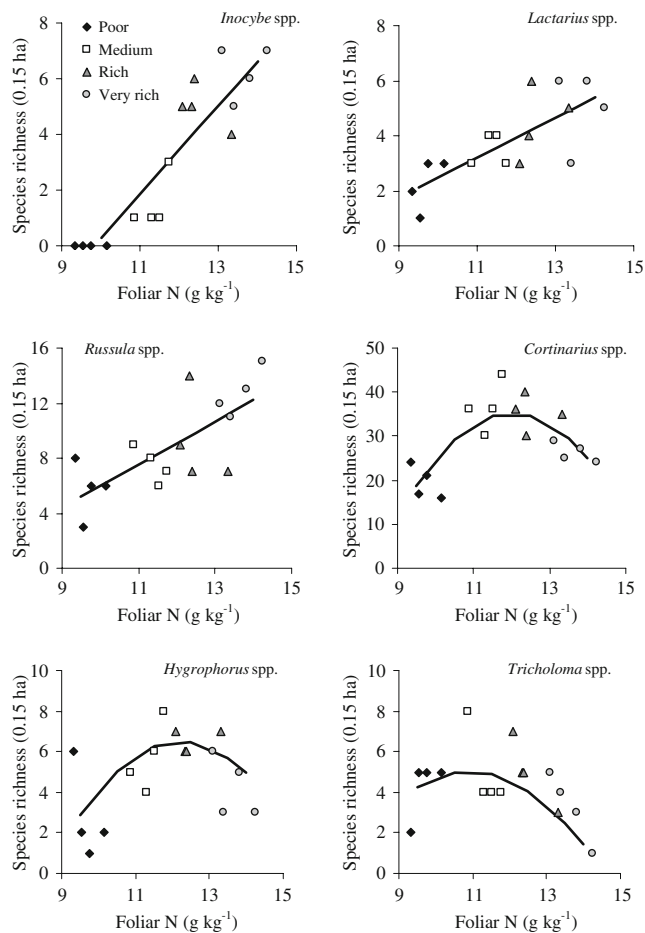
Fig. 2 Species richness per plot (0.15 ha) by genera in correlation with foliar N concentrations (g kg^{-1}) of *A. lasiocarpa*. *Inocybe* spp.$=-15.5+1.6$ (N$_%$); $p<0.001$; $r^2=0.83$. *Lactarius* spp.$=-4.7+0.7$ (N$_%$); $p=0.001$; $r^2=0.58$. *Russula* spp.$=-9.5+1.6$ (N$_%$); $p=0.001$; $r^2=0.53$. *Cortinarius* spp.$=-347+63.7$ (N$_%$)-2.6 (N$_%$)^2; $p=0.002$; $r^2=0.60$. *Hygrophorus* spp.$=-67+12.0$ (N$_%$)-0.5(N$_%$)^2; $p=0.055$; $r^2=0.36$. *Tricholoma* spp.$=-40+8.3$ (N$_%$)-0.4(N$_%$)^2; $p=0.013$; $r^2=0.51$

abundance were the highest between axis 1 and soil N indices, including DIN + DON mass ($r^2=0.800$), inorganic N mass alone ($r^2=0.798$), and DIN/DON ratio ($r^2=0.709$). Other soil properties correlated to axis 1 included soil moisture ($r^2=0.581$), organic P ($r^2=0.635$), organic S ($r^2=0.679$), pH of the forest floor ($r^2=0.650$), exchangeable Ca ($r^2=0.469$), exchangeable Mg ($r^2=0.519$), and exchangeable K ($r^2=0.222$). Correlations between axis 1 and tree species basal area were the highest for *A. lasiocarpa* ($r^2=0.507$), followed by *P. glauca* ($r^2=0.349$) and *P. contorta* ($r^2=0.115$).

The total number of broadly tolerant, partially intolerant, and specialist species was 110, comprising the core of the EMF community, with the remaining 66 as satellite species (Table 2; see "Appendix" for a complete species list by distribution class). Specialist species ranged from nine to 18 per plot and were slightly more numerous on the richest soils (Fig. 4). These species were narrow enough in distribution along the productivity gradient, despite a degree of overlap, to collec-

tively indicate oligotrophic, mesotrophic, and eutrophic soil nutrient regimes (Fig. 5). An average of 20 broadly tolerant fungal species were found in each plot, with no significant trend in frequency ($p=0.347$) along the productivity gradient (Fig. 4). The three partially intolerant groups of fungi peaked along the mesotrophic portion of the productivity gradient, combining for an average of 32 species per plot, which declined to 15 and 19 species per plot at the poor and very rich extremes, respectively (Fig. 4). Lastly were the satellite species, which were typically the least frequent member of the EMF community and positively correlated with soil productivity (Fig. 4). The functional organization of EMF fungal communities would vary with soil productivity to some degree, but, as a general appraisal, these upland late-seral boreal forests were characterized by an average allotment of 20 broadly tolerant, 25 partially intolerant, 15 specialist, and ten satellite species per plot.

Discussion

Ectomycorrhizal macrofungal communities were remarkably consistent between replicates and strongly aligned with plant associations, in support of the belowground EMF assessment, and the results demonstrate again a very high degree of EMF community specialization in relation to soil
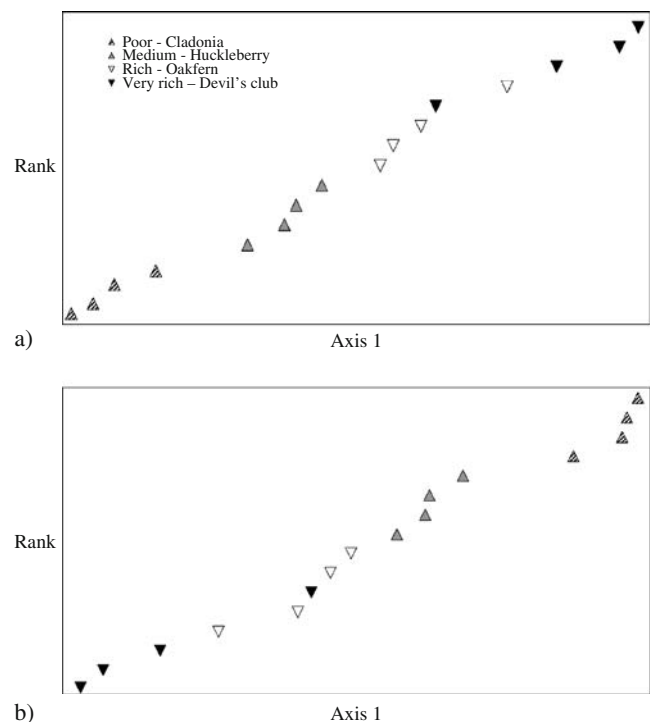
Fig. 3 Nonmetric multidimensional scaling ordination of EMF sporocarp communities (176 species) among plant associations (poor-Cladonia, medium-huckleberry, rich-Oak fern, and very rich-Devil's club) based on **a** species presence/absence and **b** species abundance ($n=16$)

Table 2 Distribution classes for core EMF species along fertility gradients, as expressed by *A. lasiocarpa* foliar N concentration and soil N availability

Foliar N (g kg^{-1})				
9.5	10.8	12.0	13.3	14.5
DIN + DON (kg ha^{-1})				
10	22.5	35	47.5	60

<--- Broadly tolerant (24) -------------------------------------->

Cortinarius cinnamomeus

Laccaria laccata

Lactarius rufus

Intolerant of richest soils (12)   --->

Cortinarius gentilis

Cortinarius semisanguineus

Leccinum aurantiacum

<--- Intolerant of poorest soils (24)

Cortinarius hemictricus

Cortinarius sodagnitus

Russula bicolor

<-------------------- Intolerant of soil extremes (9) ------------------>

Cortinarius renidens

Lactarius kaufmanii

Rozites caperata

<------ Oligotrophic (13) ---->   <----- Mesotrophic (10) ----->   <-------- Eutrophic (18) ----->

Boletopsis subsquamosa   *Cortinarius alboviolaceus*   *Cortinarius elegantior*

Cortinarius pinophilous   *Hygrophorus saxatilis*   *Inocybe geophylla*

Tricholoma magnivelare   *Russula occidentalis*   *Russula cessans*

Three EMF species are given as examples under each category, with the total number of species per distribution class in brackets and the extent of the distribution along the productivity gradient indicated by the dashed lines

properties within climax forests (Gehring et al. 1998; Toljander et al. 2006; Robertson et al. 2006). As expected, only a handful of macrofungal species from the surveys mirrored their belowground abundance to any degree (e.g., *Laccaria laccata*, *Cortinarius semisanguineus*, *Cortinarius hemictrichus*, *Russula decolorans*, *Russula bicolor*; Kranabetter et al. 2009), and the fruiting body data provided a disparate yet complementary view of EMF community composition and structure along the soil fertility gradient. We used the N status of soils and foliage to define oligotrophic, mesotrophic, and eutrophic site conditions, but recognize that these N indices covary with a number of properties in these natural systems (Giesler et al. 1998;

Kranabetter et al. 2007). Possible influences on EMF species distribution beyond N regime could include, for example, tolerance to soil droughtiness or adaptations for P uptake. Nevertheless, the strong correlations between species assemblages and DIN + DON availability or DIN/DON ratios certainly support a fundamental link between EMF species distribution with organic N, NH_4^+, and NO_3^- dynamics (Lilleskov et al. 2001; Avis et al. 2003; Trudell and Edmonds 2004).

It was not possible to locate sites with an equal distribution of host tree species, and the lower host abundance (notably *Picea*) on some poor-Cladonia sites may have exaggerated the reduction in EMF species
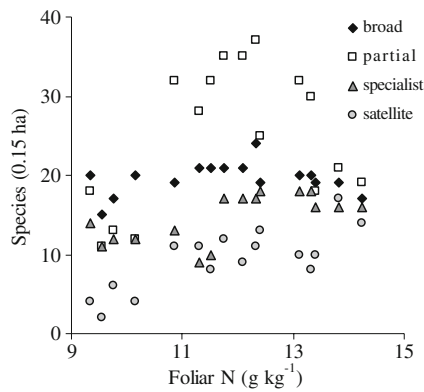
Fig. 4 Number of species per plot (0.15 ha) within the distribution classes of broadly tolerant, partially intolerant (poor, rich, and extremes combined), specialist (oligotrophic, mesotrophic, and eutrophic combined), and satellites in relation to *A. lasiocarpa* foliar N concentrations (g kg^{-1}). Partially intolerant spp. (0.15 ha)$=-414+74.0$ (N$_\%$)-3.1 (N$_\%$)^2; $p<0.001$; $r^2=0.68$. Specialist spp. (0.15 ha)$=-0.5+$ 1.3 (N$_\%$); $p=0.006$; $r^2=0.43$. Satellite spp. (0.15 ha)$=-14.2+2.0$ (N$_\%$); $p=0.001$; $r^2=0.61$

richness on these most stressful sites as compared to the decline measured belowground (40% reduction versus 25%, respectively; Kranabetter et al. 2009). Otherwise, the differences in EMF species richness among sites were relatively small (five to ten species or a 6% to 12% decline for medium-Huckleberry and very rich-Devil's club, respectively, compared to rich-Oak fern sites), and the shifts in EMF species composition along the N gradient were much more indicative of soil conditions than diversity measures. It was interesting to note in this regard that the very rich-Devil's club outlier from both ordinations was actually consistent with N regime because nitrification was not detected in this replicate (Table 1), which suggests the presence of some mesotrophic species in this plot was not entirely unusual.

The curvilinear trend in species richness did not match the decline in EMF species richness generally reported for artificial N gradients (Jonsson et al. 2000; Peter et al. 2001a; Avis et al. 2003), and this discrepancy may reflect in part the inordinately high concentrations of inorganic N created under experimental fertilizer treatments (Toljander et al. 2006). With emigration and immigration of EMF species over time, it might be possible for an altered community with more nitrophilic species to develop in response to the enhanced soil N status of a forest, but this would also depend upon the sensitivity of these EMF species to the other soil properties defining eutrophic habitat.

Trends by genera also indicated broad patterns in community response to N that might be useful in examining related forest landscapes (Lilleskov et al. 2001; Avis et al. 2003; Trudell and Edmonds 2004). Many *Inocybe*, *Lactarius*, and *Russula* species favored richer soils with elevated concentrations of inorganic N, whereas *Cortinarius*, *Tricholoma*, and *Hygrophorus* species richness peaked on

mesotrophic sites with predominantly organic N cycles. Nevertheless, many species within genera occupied all manner of site types (Table 2), so detailed information on core species autecology would perhaps be more useful than simple comparisons among genera in understanding modified ecosystems. Macrofungi biomass was not measured in this study, but we noted how many species of oligotrophic soils produce large sporocarps (e.g., *Russula decolorans*, *Russula cascadensis*, *Tricholoma magnivelare*) in frequent shiros that would be consistent with the peak in biomass production reported elsewhere (Peter et al. 2001a; Trudell and Edmonds 2004). It should be emphasized that 3 years of surveys is likely to be the minimum required for these interpretations to accommodate the natural variation in macrofungal production (Krebs et al. 2008).

A diverse mix of both overlapping and exclusive species distributions along environmental gradients is challenging to synthesize (Whittaker 1975), and in the belowground assessment, a simple distinction was drawn only between multisite and narrowly distributed fungi. This concept was subjectively expanded upon using the more comprehensive frequency data of macrofungi, while recognizing that abundance was not necessarily uniform among species within each distribution category. In this way, the diverse mix of habitats for the core EMF species could be well described by seven possible distribution classes; *Russula xerampelina* was the only species to portray a possible "U" shaped response to N availability, but this may be as likely due to chance in plot selection rather than a particularly unique distribution. An alternative to this intermediate focus would be individual response curves to the N gradient based on sporocarp abundance, but the interpretations would be debatable (especially for host-specific EMF species) given the variable proportions in tree species cover. At the very least, these distribution categories provide possible hypotheses for evaluating niches and specialized functions of core EMF species (Nygren et al. 2007; Cajsa et al. 2008).
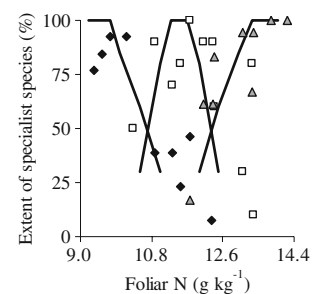
Fig. 5 The extent of specialist EMF species per plot as a percent of the total for each nutrient regime (oligotrophic = *black diamonds*; mesotrophic = *open squares*; eutrophic = *gray triangles*) in relation to *A. lasiocarpa* foliar N concentrations (g kg^{-1}). Distribution curves idealized to show nutrient regimes covering 40% of the foliar N gradient

The large number of infrequent and possibly transient satellite species is a common feature of EMF communities (Smith et al. 2002; Richard et al. 2004), and the positive correlation with productivity might be due to the greater microsite (wet depressions to raised mounds) and N diversity (organic N, NH_4^+, NO_3^-) found on very rich-Devil's club sites. The role of satellite species is perhaps not immediately measureable by ecosystem production, but plant ecologists suggest these rarer species likely provide future recruitment potential into the core community (Grime 1998; Gibson et al. 1999). Thus, in the long term, these satellite EMF species might play an intermittent yet important role in providing a species reservoir for ingress in response to ongoing pedogenic processes (podzolization, nutrient sequestration) or possible changes in climatic regime and host species distribution.

A specialization in EMF communities by site type would arguably provide some of the adaptations required for relatively few tree species to occupy vast complex landscapes. Diverse ectomycorrhizal fungal communities with an array of distribution classes likely support this ecosystem productivity and resiliency (Perry and Amaranthus 1997), but under widespread stressors, some fragmentation of these communities may occur, as indicated perhaps by a greater prevalence of broadly tolerant EMF species at the expense of specialist species. Changes in EMF communities of this nature could represent a loss in ecosystem integrity, which can be briefly defined here as the capacity of an ecosystem to support and maintain a balanced, integrated, adaptive community of organisms similar to undisturbed ecosystems of a region (Frego 2007). The focus in ecosystem monitoring could include attributes related to functional organization, such as the total number of EMF species by genera, the proportion of species per distribution class, and the ratio of satellite to core species. Given the challenges in sampling infrequent EMF species belowground, we would suggest there are unlikely to be any simple surrogates of ecosystem integrity related to EMF communities that does not involve surveys of fruiting bodies.

Conclusions

Similar to plants as bioindicators (Klinka et al. 1989), the potential of epigeous EMF fruiting bodies to provide sensitive indicators of soil fertility was well supported by the approximately 40 specialist species that were collectively aligned by simply presence or absence to the N status of these boreal ecosystems. Corresponding indicator species for related landscapes would require site-specific community data, however, since EMF species composition would undoubtedly vary a considerable degree across biomes (Dahlberg et al. 1997; Peter et al. 2001b). Where appropriate (e.g., common host species, uniform stand ages), a monitoring program of EMF fruiting bodies could be a relatively inexpensive, nondestructive, and thorough indication of functional changes in soil fertility and associated N cycles that might arise under anthropogenic activity. In addition, epigeous EMF species richness and the distribution of tolerant, specialist, and satellite species could provide useful indicators of functional organization for evaluating ecosystem integrity. The EMF macrofungi communities of late-seral forests under current environmental conditions should therefore become especially important reference benchmarks given the possible widespread altered forest landscapes of the future (Hamann and Wang 2006).

Appendix

Table 3 Mean abundance (% frequency in brackets) of EMF species among the four plant associations

Ectomycorrhizal fungal species	Poor-Cladonia (n=4)	Medium-Huckleberry (n=4)	Rich-Oak fern (n=4)	Very rich-Devil's club (n=4)	GenBank accession #
Broadly tolerant					
Chroogomphus vinicolor	2.7 (100)	5.4 (100)	6.3 (100)	4.0 (50)	FJ845402
Cortinarius acutus	0.4 (50)	2.9 (75)	4.0 (100)	2.9 (100)	FJ039609
Cortinarius brunneus grp	2.5 (100)	4.6 (100)	3.3 (100)	1.9 (100)	FJ039682
Cortinarius cinnamomeus	1.3 (75)	12.9 (100)	9.2 (100)	2.9 (100)	FJ845396

Table 3 (continued)

Ectomycorrhizal fungal species	Poor-Cladonia (n=4)	Medium-Huckleberry (n=4)	Rich-Oak fern (n=4)	Very rich-Devil's club (n=4)	GenBank accession #
Cortinarius croceus	2.1 (75)	10.2 (100)	1.3 (75)	1.0 (75)	FJ845399
Cortinarius flexipes grp	0.6 (75)	2.9 (75)	4.2 (100)	5.8 (100)	FJ845398
Cortinarius laniger	1.3 (75)	2.3 (100)	4.8 (100)	1.0 (75)	FJ039557
Cortinarius obtusus	1.5 (100)	3.5 (100)	6.3 (100)	0.6 (50)	FJ039610
Cortinarius paragaudis	0.4 (50)	3.5 (100)	4.8 (100)	1.3 (100)	FJ039675
Cortinarius triformis	1.0 (50)	1.0 (100)	0.4 (50)	0.4 (50)	FJ039573
Cortinarius vibratilis	2.3 (100)	6.0 (100)	3.1 (75)	2.9 (100)	
Hebeloma crustiliniforme	0.4 (50)	2.1 (100)	8.8 (100)	4.2 (100)	FJ845403
Hydnum repandum	0.6 (50)	0.6 (50)	2.3 (100)	0.6 (50)	FJ845406
Laccaria bicolor	0.4 (50)	2.7 (75)	1.7 (75)	0.8 (75)	FJ845417
Laccaria laccata	2.3 (75)	11.3 (100)	6.3 (100)	3.5 (100)	FJ845416
Lactarius deliciosus	0.6 (50)	2.9 (75)	3.3 (100)	1.7 (100)	FJ845418
Lactarius rufus	11.5 (100)	17.5 (100)	5.8 (75)	2.3 (75)	
Russula gracilis[a]	0.4 (50)	0.2 (25)	1.0 (100)	3.5 (100)	FJ845431
Russula cf *vinosa*	1.3 (50)	3.1 (100)	2.5 (75)	0.4 (50)	FJ845428
Russula xerampelina grp[a]	1.0 (75)	–	0.8 (50)	1.7 (75)	FJ845433
Suillus brevipes	2.3 (100)	1.9 (75)	2.1 (75)	1.5 (100)	FJ845440
Suillus flavidus	9.4 (100)	14.2 (100)	12.9 (75)	4.4 (50)	FJ845439
Suillus tomentosus	21.3 (100)	12.5 (100)	2.7 (100)	1.0 (50)	FJ845441
Tricholoma saponaceum	1.3 (100)	3.1 (100)	3.5 (75)	1.7 (50)	FJ845442
Intolerant of richest soils					
Cortinarius boulderensis	0.6 (75)	2.3 (100)	0.6 (50)	0.2 (25)	FJ039558
Cortinarius cacoacolor	1.3 (75)	1.0 (75)	0.6 (75)	0.2 (25)	FJ039677
Cortinarius clandestinus	3.8 (100)	3.8 (100)	5.2 (100)	0.4 (25)	FJ039583
Cortinarius gentilis	14.2 (100)	3.3 (100)	0.8 (75)	–	FJ039686
Cortinarius muscigenus	2.9 (100)	2.1 (100)	1.5 (75)	0.2 (25)	FJ039578
Cortinarius niveoglobosus	0.4 (50)	0.4 (50)	0.2 (25)	–	FJ039676
Cortinarius phoenicius	2.3 (100)	1.3 (75)	0.6 (75)	0.2 (25)	FJ039599
Cortinarius pluvius	0.4 (50)	0.4 (50)	0.2 (25)	–	
Cortinarius semisanguineus	17.1 (100)	10.8 (100)	2.5 (75)	–	FJ039598
Hydnellum peckii	6.0 (100)	1.9 (75)	0.4 (50)	–	FJ845405
Hygrophorus hypothejus	7.5 (100)	5.4 (100)	0.4 (50)	–	FJ845409
Leccinum aurantiacum	2.9 (100)	1.7 (100)	0.8 (50)	–	FJ845423
Intolerant of poorest soils					
Clavariadelphous pistillaris	–	2.7 (100)	4.0 (100)	2.9 (100)	
Cortinarius aureofulvous	–	0.6 (50)	0.6 (75)	0.6 (50)	FJ039644
Cortinarius argutus	–	0.2 (25)	1.5 (75)	0.8 (75)	FJ039662
Cortinarius calochrous grp	–	0.6 (50)	6.0 (100)	1.3 (75)	FJ039639
Cortinarius calopus	–	4.4 (75)	3.8 (100)	1.9 (75)	FJ039572
Cortinarius cana-barba	–	0.4 (50)	1.7 (100)	0.8 (75)	FJ039562
Cortinarius evernius	–	1.3 (75)	1.0 (75)	0.8 (75)	FJ039684
Cortinarius cf *flos-paludis*	0.2 (25)	3.3 (75)	2.3 (100)	2.7 (100)	FJ039560
Cortinarius hemictricus	–	3.5 (100)	6.0 (100)	5.0 (100)	FJ039543
Cortinarius sodagnitus	–	0.6 (50)	3.8 (100)	2.9 (100)	FJ039638
Cortinarius spilomeus	0.2 (25)	0.8 (75)	5.4 (100)	4.4 (100)	FJ039659
Cortinarius cf *pini*	–	0.2 (25)	0.6 (75)	0.4 (50)	FJ039614
Hebeloma mesophaeum	–	1.0 (75)	3.5 (100)	3.1 (100)	FJ845404
Hygrophorus pudorinus	–	0.4 (50)	1.9 (50)	1.0 (50)	FJ845408

Table 3 (continued)

Ectomycorrhizal fungal species	Poor-Cladonia (*n*=4)	Medium-Huckleberry (*n*=4)	Rich-Oak fern (*n*=4)	Very rich-Devil's club (*n*=4)	GenBank accession #
Inocybe lanuginosa	–	1.3 (50)	1.5 (50)	1.3 (50)	FJ845415
Inocybe pseudoastospora	–	0.4 (50)	1.5 (50)	1.0 (50)	
Lactarius caespitosus	–	2.7 (75)	2.3 (100)	0.8 (75)	FJ845421
Ramaria rasilispora	–	0.2 (25)	0.2 (25)	1.3 (75)	
Russula aeruginea	–	0.2 (25)	0.2 (25)	1.9 (100)	
Russula bicolor	–	10.0 (100)	18.3 (100)	6.3 (100)	FJ845435
Russula sanguinea	–	0.4 (25)	0.4 (25)	1.5 (50)	FJ845434
Russula silvicola	–	0.8 (75)	0.8 (75)	1.0 (100)	
Tricholoma platyphyllum	–	2.7 (100)	2.9 (100)	1.0 (75)	FJ845445
Tricholoma vaccinum	–	0.6 (75)	1.9 (50)	0.4 (50)	FJ845444
Intolerant of extremes					
Chroogomphus ochraceus	1.0 (50)	3.5 (75)	2.5 (75)	0.4 (25)	
Cortinarius anomalus	0.2 (25)	1.3 (75)	1.3 (50)	0.8 (75)	FJ039605
Cortinarius biformis	0.2 (25)	0.6 (50)	0.6 (75)	0.6 (50)	FJ039574
Cortinarius renidens	0.2 (25)	1.9 (100)	5.2 (100)	0.8 (50)	FJ039665
Hygrophorus camarophylus	0.2 (25)	0.6 (75)	0.2 (25)	0.2 (25)	
Hygrophorus piceae	0.4 (25)	9.0 (100)	4.4 (100)	0.8 (25)	FJ845411
Lactarius kaufmanii	0.4 (25)	6.0 (100)	8.8 (100)	0.8 (50)	FJ845422
Rozites caperata	0.2 (25)	6.7 (100)	4.2 (75)	0.8 (75)	FJ845425
Sarcodon imbricatus	0.4 (25)	0.6 (50)	2.7 (50)	0.4 (25)	FJ845438
Oligotrophic					
Boletopsis subsquamosa	1.3 (75)	–	–	–	FJ845401
Cortinarius pinophilous	7.9 (100)	1.3 (100)	–	–	FJ157123
Cortinarius traganus	1.3 (50)	0.2 (25)	–	–	FJ039570
Hygrophorus purpurescens	1.7 (75)	0.2 (25)	0.2 (25)	–	
Phellodon tomentosus	6.5 (100)	0.8 (100)	–	–	FJ845424
Russula cascadensis	9.6 (100)	0.2 (25)	–	–	FJ845426
Russula decolorans	6.5 (75)	0.6 (50)	–	–	FJ845432
Russula densifolia	5.2 (100)	–	–	–	FJ845430
Sarcodon scabrosum	4.2 (100)	–	–	–	
Suillus glandulosipes	1.3 (100)	1.0 (25)	–	–	
Tricholoma focale	1.5 (100)	1.0 (25)	–	–	FJ845447
Tricholoma magnivelare	0.6 (75)	–	–	–	
Tricholoma sejunctum	1.7 (75)	2.0 (100)	–	–	FJ845448
Mesotrophic					
Cortinarius alboviolaceus	–	1.5 (100)	0.4 (50)	0.4 (25)	FJ039575
Cortinarius camphoratus	–	0.6 (25)	2.7 (50)	–	FJ039626
Cortinarius ochrophyllus	0.4 (25)	0.8 (75)	0.4 (50)	–	FJ039604
Cortinarius purpurascens	–	0.8 (75)	1.0 (100)	0.2 (25)	FJ039660
Cortinarius scaurus	–	0.6 (75)	0.4 (50)	–	FJ039621
Hygrophorus erubescens	0.2 (25)	0.4 (50)	1.7 (100)	–	
Hygrophorus saxatilis	0.2 (25)	5.6 (100)	2.7 (100)	–	FJ845407
Russula occidentalis	0.2 (25)	2.9 (100)	0.4 (50)	–	FJ845436
Russula raoultii	–	0.6 (50)	1.5 (75)	0.6 (25)	
Tricholoma atrosquamosum	–	0.6 (50)	2.1 (75)	0.2 (25)	
Eutrophic					
Clavariadelphous truncatus	–	–	1.7 (75)	1.3 (75)	
Cortinarius elegantior	–	–	3.1 (100)	2.9 (100)	FJ845397

Table 3 (continued)

Ectomycorrhizal fungal species	Poor-Cladonia (n=4)	Medium-Huckleberry (n=4)	Rich-Oak fern (n=4)	Very rich-Devil's club (n=4)	GenBank accession #
Cortinarius guttatus	–	–	0.6 (75)	0.4 (50)	FJ039646
Cortinarius venetus	–	–	1.3 (75)	1.5 (50)	FJ039688
Hebeloma saarchiolens	–	–	0.8 (50)	0.8 (100)	
Hygrophorus chrysodon	–	–	0.2 (25)	0.8 (75)	
Hygrophorus olivaceoalbus	–	–	0.2 (25)	2.3 (75)	FJ845410
Hygrophorus pustulatus	–	0.2 (25)	5.2 (75)	1.9 (100)	FJ845412
Inocybe cf *friesii*	–	–	2.3 (50)	10.2 (100)	FJ845413
Inocybe geophylla	–	–	8.3 (100)	18.8 (100)	FJ845414
Inocybe rimosa	–	–	0.4 (25)	4.4 (100)	
Lactarius hepaticus	–	–	0.6 (50)	2.7 (75)	FJ845420
Russula cf *amydagloides*	–	–	0.2 (25)	1.7 (100)	
Russula brevipes	–	–	–	1.3 (75)	FJ845429
Russula cessans	–	–	2.1 (100)	7.5 (100)	FJ845437
Russula cf *placita*	–	–	0.4 (25)	1.3 (100)	
Russula puellaris	–	0.2 (25)	1.0 (75)	1.0 (100)	
Tricholoma myomyces	–	–	0.8 (75)	1.0 (75)	FJ845443
Satellite species					
Albatrellus ovinus	0.2 (25)	0.8 (50)	–	–	FJ845400
Amanita constricta	–	–	–	1.0 (50)	
Amanita pachycolea	–	–	–	0.2 (25)	
Catethelasma imperialis	–	–	0.4 (25)	–	
Clavaria purpurescens	–	–	–	0.2 (25)	
Cortinarius cf *amurceus*	–	0.4 (25)	–	–	FJ039627
Cortinarius balteatus	0.2 (25)	0.2 (25)			FJ039613
Cortinarius causticus	0.2 (25)	0.4 (50)	–	0.2 (25)	FJ039636
Cortinarius cf *comptulus*	–	–	0.2 (25)	–	
Cortinarius cf *decoloratus*	–	0.2 (25)	–	–	
Cortinarius delibutus	–	0.2 (25)	0.6 (50)	–	
Cortinarius eburneus	–	0.2 (25)	–	–	
Cortinarius fulvochrascens	–	–	0.4 (25)	0.2 (25)	FJ039689
Cortinarius glaucopus	–	–	1.3 (25)	–	FJ039616
Cortinarius humolens	–	–	–	0.2 (25)	FJ039640
Cortinarius infractus	–	0.4 (25)	–	0.2 (25)	FJ039612
Cortinarius cf *largus*	–	–	0.8 (25)	–	
Cortinarius limonius	–	0.4 (50)	0.4 (25)	0.4 (25)	FJ039667
Cortinarius melanotus	–	0.2 (25)	–	–	
Cortinarius mucosus	0.4 (25)	–	–	–	FJ039581
Cortinarius multiformis	–	0.8 (50)	0.2 (25)	0.4 (25)	FJ039635
Cortinarius nanceiensis	–	–	0.2 (25)	–	FJ039670
Cortinarius papulosus	0.2 (25)	1.3 (50)	–	–	FJ039669
Cortinarius percomis	–	0.2 (25)	–	–	FJ039657
Cortinarius pseudoglaucopus	–	–	0.2 (25)	0.2 (25)	FJ039641
Cortinarius cf *rheubarbarinus*	0.2 (25)	–	–	–	
Cortinarius rufo-olivaceous	–	–	0.2 (25)	–	FJ039645
Cortinarius salor	–	–	–	0.2 (25)	FJ039600
Cortinarius scutulatus	0.2 (25)	0.2 (25)	–	0.2 (25)	
Cortinarius talus	–	0.2 (25)	–	0.6 (50)	
Cortinarius cf *turibulosus*	–	0.4 (50)	–	–	FJ039673

Table 3 (continued)

Ectomycorrhizal fungal species	Poor-Cladonia (n=4)	Medium-Huckleberry (n=4)	Rich-Oak fern (n=4)	Very rich-Devil's club (n=4)	GenBank accession #
Cortinarius cf *variecolor*	–	0.4 (25)	0.2 (25)	0.2 (25)	FJ039633
Cortinarius cf *variegatus*	–	–	–	0.2 (25)	
Cortinarius violaceus	–	0.2 (25)	–	1.3 (50)	FJ039649
Cortinarius viridipes	–	0.2 (25)	0.2 (25)	0.4 (25)	FJ039683
Hydnellum aurantiacum	–	0.2 (25)	–	–	
Hydnellum scrobiculatum	–	–	0.2 (25)	–	
Hygrophorus hyacinthinus	–	–	1.3 (25)	0.4 (25)	
Hygrophorus monticola	–	0.8 (25)	0.2 (25)	–	
Hygrophorus odoratus	–	0.4 (25)	0.2 (25)	–	
Inocybe albodisca	–	–	1.0 (25)	1.0 (50)	
Inocybe geophylla var lilacina	–	–	0.4 (50)	0.2 (25)	
Inocybe griseolilacina	–	–	–	0.4 (50)	
Lactarius circellatus	–	–	–	0.2 (25)	
Lactarius luculentus	–	–	–	2.5 (50)	FJ845419
Lactarius olympianus	–	–	–	1.9 (50)	
Lactarius resimus	0.4 (50)	–	–	–	
Lactarius cf *olivinus*	–	–	0.4 (25)	–	
Limacella illinata	–	–	–	0.2 (25)	
Polyzellus multiplex	–	–	0.4 (25)	–	
Russula abietina	0.8 (25)	0.2 (25)	–	1.3 (50)	
Russula borealis	–	0.2 (25)	0.2 (25)	0.2 (25)	
Russula cf *integra*	0.2 (25)	–	–	–	
Russula cf *consobrina*	0.2 (25)	–	–	–	
Russula foetens	–	–	2.3 (25)	2.1 (25)	FJ845427
Russula paludosa	–	0.6 (25)	2.7 (25)	0.4 (25)	
Russula parazurea	–	0.2 (25)	–	–	
Russula unknown sp	0.2 (25)				
Thaxtergaster pingua	–	–	0.6 (50)	–	
Tricholoma flavovirens	0.2 (25)	0.2 (25)	–	–	
Tricholoma intermedium	–	–	0.2 (25)	–	
Tricholoma pessundatum	–	0.4 (25)	1.0 (50)	0.6 (25)	FJ845446
Tricholoma portentosum	0.4 (25)	–	–	–	
Tricholoma sulphureum	–	–	0.4 (25)	–	
Tricholoma virgatum	–	–	1.0 (25)	0.2 (25)	
Tricholoma unknown sp.	0.4 (25)	–	–	–	

Species are listed alphabetically within distribution categories of broadly tolerant, partially intolerant (poor, rich, and extremes), specialist (oligotrophic, mesotrophic, and eutrophic), and satellite species

[a] Exceptions in the criteria for broadly tolerant were made for these species which were more uncommon on medium sites than the gradient extremes

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