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Chytrid Distribution in Diverse Boreal Manitoba Sites

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Soil samples were collected in thirteen Manitoba boreal forest sites. Spatial distribution of chytrids from diverse boreal forest microhabitats was investigated by baiting with jack pine pollen. After baiting, the pollen was surveyed for chytrids for a ten day period and individual species were counted. Total infestations of pollen by chytrids ranged from 5.8% to 90.2% from various soils. Each site with high infestation was characterized by litter with high needle content while mineral soil or soil with limited organic matter yielded low levels of pollen infestation. Species diversity tended to be higher in soils with higher pollen infestation and lower in soils with lower pollen infestation. Lower diversity was generally observed in mineral soils or soils with a limited organic horizon comprised, in part, of broad leaf litter. Based on coefficients of association and species in common among species across the collection sites, it was possible to relate dominant species assemblages in site groups. These species assemblages in the site groups suggest that the chytrids are distributed by litter and soil types. It can be concluded that the substratum characteristics of litter types and availability of litter may be important in describing chytrid distribution in boreal forest sites.

Although chytrids (Chytridiales, lower fungi) are ubiquitous and have been collected across Arctic to tropical latitudes, relatively little direct information exists regarding chytrid activity in boreal forest and bog habitats. Sphagnum bogs are considered to be harsh environments for organisms to survive in because of high acidity and limited amounts of naturally occurring substrates (Lund, 1934; Lange, 1978). Despite such limitations, bogs are one of the richest sources of bizarre types of chytrids (Sparrow, 1966). Furthermore, bogs are also high in chytrid diversity (Miller, 1965).

Subsequent to Sparrow (1952), a few papers dealing with chytrids from these habitats have been published. For example, chytrids were reported from forest and bog sites in the transition zone between mixed deciduous and boreal forests of northern Michigan (Johns, 1956; Sparrow and Koch, 1959; Sparrow et al., 1965; Gaertner and Sparrow, 1966; Dogma, 1969, 1970). Johnson and Howard reported zoosporic fungi from freshwater and bog habitats in Iceland and Norway (Howard, 1968; Howard and Johnson, 1969; Johnson, 1973, 1975, 1977). Booth (1969, 1971a, 1971b) studied zoosporic fungi in forest and bog soils of coastal British Columbia and Booth and Barrett (1971, 1976) reported chytrids from acidic soils of the Canadian high arctic. In general, systematic study of chytrids from boreal forest soils and microhabitats, other than bogs, are rare.

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Based on their nutritional capabilities, these fungi are important biodegraders of cellulose, chitin, and keratin, which are resistant to decay by many microorganisms (Powell, 1993; Wong et al., 1998). Pollen exine, readily available in boreal forest and bog habitats, is a particularly refractory substrate that chytrids are able to digest to gain access to nutrient-rich contents (Sparrow, 1960). A major chemical component of pollen wall is sporopollenin, which is composed of carotenoids and carotenoid esters. In a comprehensive investigation of pollen and spores degraded by chytrids, gymnosperm pollen (especially pine) walls were shown to be highly susceptible to local digestion (Goldstein, 1960).

Studies on the role of fungi in pollen degradation in forest soils are limited. Pollen may be considered as an important source of nutrients for tree growth and its degradation (hence, nutrient mobilization) in dry sites has been reported more effectively carried out by filamentous fungi than by chytrids (Stark, 1972). In fact, Stark suggested that chytrids were generally unimportant in pollen degradation in contrast to filamentous fungi. The activity of chytrids has not been systematically studied in the range of boreal forest micro-environments or in forest ecosystems in general thus, It is not known whether Stark's conclusion about pollen degradation by chytrids and filamentous fungi in dry sites is generally true. Furthermore, the role of pollen degradation in forest nutrition has yet to be elucidated.

This study reports on a spatial distribution of chytrids from thirteen selected boreal forest microhabitats. Specifically the aim of this study is; i) to record the levels

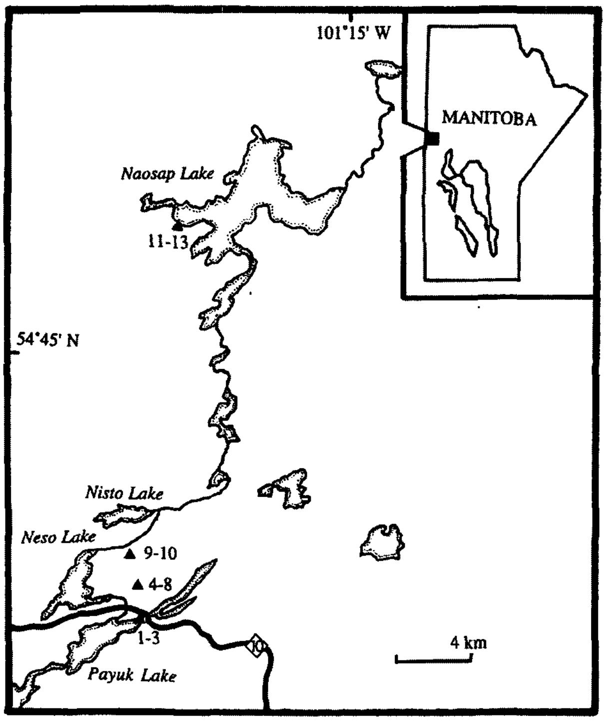

Fig. 1. Location of the study area (Mistik Creek) in west-central Manitoba, Canada. Sites are designated by numbers: 1, balsam fir; 2, mature pine; 3, poplar; 4, pine ridge; 5, spruce; 6, bog; 7, swale; 8, young pine; 10, bare sand; 11, Naosap forest; 12, Naosap riser; 13, Naosap beach. Closely approximated sites are mapped as groups indicated by triangles.

of chytrid infestation of pollen placed as bait with soils collected from selected diverse boreal Manitoba sites; ii) to observe distributional patterns of infesting chytrids across boreal forest sites; and iii) to describe the species composition of pollen inhabiting chytrids that occur in soils with different types of litter.

Methods and Materials

Study area

The Mistik Creek study area (Fig. 1) is located in west-central Manitoba, Canada (54°39′ to 54°50′ N; 101°27′ to 101°32′ W). The climate is sub-humid continental and prevailing winds are from the northwest. The growing season, based on a 4℃ index, lasts from early May to early October. Mean annual precipitation is 484 mm and mean annual temperature is -0.5℃. Average land elevation is about 300 m above sea level.

The region lies on the Canadian Precambrian Shield. As a result of intensive glaciation, relief is irregular with rocky parallel ridges separating poorly drained depressions and narrow lakes. Drift depositions on the uplands are thin in some places and absent in others where rock barrens of Precambrian granites and gneisses are exposed. Soil fertility is low with a weakly developed podzol profile.

The study area includes the northern coniferous section of the boreal forest (Rowe, 1972). Within the area, black spruce (*Picea mariana* [Mill.] BSP) is the dominant tree in poorly drained lowlands. Jack pine (*Pinus banksiana* Lamb.) stands are common on well-drained, sandy sites and on upland, rock outcrops. Mixed stands of white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), trembling aspen (*Populus tremuloides* Michx) and balsam poplar (*P. balsamifera* L.) tend to grow under more favorable soil conditions.

Soil collection, pollen baiting and laboratory observation

Soil samples were collected on August 21, 1993. The collections were made from the 3 cm top of litter and soil over 13 sites (Fig. 1). Detailed designations and descriptions of the thirteen sites are presented in Table 1. In each site, five replicate soil samples were collected. Direct observation counting of collected soil samples was made to determine litter types. Within 48 hours after soil collection, one gram of soil from each replicate was placed in an individual petri dish and covered to a depth of 1 cm with deionized water. Air dried jack pine pollen (*Pinus banksiana*), collected from the same region as the soil samples, was added to the water as bait. Baited samples were maintained at room temperature (ca. 21℃).

Table 1. Site numbers, designations, and descriptions of 13 sites in boreal Manitoba

No	Designations	Descriptions
1	Balsam Fir	Mixed litter (high needle content) on sand from a balsam fir and white spruce stand
2	Mature Pine	Mixed litter soil from a mature 65-yr old jack pine stand mixed with patches of alder and black spruce
3	Poplar	Mixed litter (high broad leaf content) soil from a trembling aspen and alder stand
4	Pine Ridge	Lichens and mixed litter (high needle content) soil from a jack pine ridge
5	Spruce	Mixed litter with some mosses and soil from a black spruce stand
6	Bog	Mosses and wet mixed litter soil from a black spruce and alder stand
7	Swale	Exposed soil from a willow and *Carex* swale
8	Alder	Mixed litter from an alder stand
9	Young Pine	Needle litter on sand from under trees in a young (25-yr) regenerating jack pine stand
10	Bare Sand	Sand from open areas (not under young trees and with sparse needle litter) in a young (25-yr) regenerating jack pine stand
11	Naosap Forest	Mixed litter (high needle content) soil from a jack pine stand along the margin (5 m from the beach) of Naosap lake (mixed with alder)
12	Naosap Riser	Mixed litter (high needle content on loam) from a riser edge located above (2 m) and away (2.5 m) from Naosap lake beach strand. Collections from a jack pine (mixed with alder) forest edge fronting lake beach
13	Naosap Beach	Unvegetated regosolic material (sands) from open washed beach

After baiting, the pollen was surveyed for chytrids every other day for a ten day period and individual species were noted (Repeated observation of developing and discharging chytrid thalli were required for identification of species). During the survey period, levels of pollen infestation (% of 100 grains surveyed) were determined and recorded for each observation date. Infestation by each taxon on the fifth observation date (at ten days) was used to represent the infestation levels by all the individual species. Pollen infestation levels from various soils were also determined at the date of fifth observation levels (after 10 d of incubation) and calculated as percentage of grains infested by all species. Species diversity was identified as the number of chytrid species occurring in each site. Species dominance for various soils was determined as the taxon with the highest pollen infestation levels relative to all other infesting species in each specific site.

Similarity of chytrid assemblages between sites

The V coefficient of association (Krebs, 1972) was calculated for between-site comparisons of fungal assemblages, as follows:

$$V = \frac{ad - bc}{\sqrt{(a+b)\ (c+d)\ (a+c)\ (b+d)}}$$

(a = the number of taxa common to sites 1 and 2, b = the number of taxa exclusive to site 1, c = the number of taxa exclusive to site 2, and d = the number of taxa excluded from both sites 1 and 2). A site with one chytrid species, Naosap beach sands, was excluded in this analysis because it did not have enough species to compare.

Results

Litter types

Four litter groups were recognized based on litter and soil types in the study area (Table 1). These included: i) mixed (leaf and needle pieces) litter with high needle content; ii) mixed litter with high broad leaf content; iii) loamy soil with broad leaf content characterized the Pine Ridge, Naosap Forest, and Naosap Riser sites. Mixed litter with broad leaf content was encountered in the Mature Pine, Poplar, Spruce, Bog, and Alder sites. Swale was in loamy soil with broad leaf litter. Needles on exposed sand were found in Young Pine, Bare Sand, and Balsam Fir sites.

Pollen infestation

Total infestations of pollen by chytrids ranged from 5.8% to 90.2% from various soils (Table 2). Three groups were designated based on pollen infestation (i.e. those with high, medium, and low pollen infestation levels). Pine, Naosap Forest, Bog, Naosap Riser, and Pine Ridge sites showed > 40% pollen infestation rates. Mature Pine, Balsam Fir, Alder, and Spruce sites showed 20 to 40%, Poplar, Naosap Beach, Swale, and Bare Sand sites showed < 20% pollen infestation rates.

Table 2. Infestation (% grains infested by chytrids after 10 d of incubation) of jack pine pollen added as bait to flooded soil samples collected in selected boreal Manitoba sites

Sites	Total grains infested (%, x ± SE)	Number of chytrid species
Young Pine	90.2 ± 2.5	4
Naosap Forest	79.4 ± 11.5	6
Bog	56.0 ± 10.6	5
Naosap Riser	52.0 ± 13.0	6
Pine Ridge	46.2 ± 17.7	6
Mature Pine	37.2 ± 19.0	3
Balsam Fir	34.4 ± 8.6	2
Alder	34.2 ± 12.6	5
Spruce	30.8 ± 14.8	4
Poplar	12.4 ± 6.3	2
Naosap Beach	11.4 ± 5.1	1
Swale	10.4 ± 4.5	4
Bare Sand	5.8 ± 2.3	2

The highest pollen infestation occurred in soils collected from the Young Pine site, with 90.2% of pollen bait infested by chytrids (Table 2). The second highest pollen infestation, 79.4%, was observed on pollen bait added to Naosap Forest soils. Both of these sites have a high needle content in the litter. Infestations by endobiotic chytrids (i.e. *Olpidium* spp.) were low in soil collections from all sites (0% to 9.6%). The highest endobiotic chytrid infestations were found in samples taken from the Poplar site.

Chytrid diversity and distribution

Species diversity tended to be higher in soils with higher pollen infestation and lower in soils with lower pollen infestation (Table 2). Soils with high infestation (> 40%) had 4 to 6 species from each collection site (mean ≈ 5 spp.). Soils with medium and low infestation (< 40%) had 1 to 5 species (mean ≈ 3 spp.). The greatest diversity (6 spp.) was observed in soils from sites with high needle litter content (Naosap Forest, Naosap Riser and Pine Ridge sites). Lower diversity was generally observed in mineral soils or soils with a limited organic horizon comprising, at least in part, broad leaf litter.

Specimens of *Olpidium* spp., the most wide-spread of the chytrids in this study, were observed in pollen bait placed with soil from 11 of the 13 sites. *Rhizophydium pollinis-pini* (Braun) Zopf and *Phlyctochytrium reinboldtae* Persiel were found from only four sites making them the most restricted in distribution (Table 3). *Rhizophydium pollinis-pini* was found in Spruce, Alder, Bog, and Poplar sites, which were typified by mixed litter with broad leaf content. *Phlyctochytrium reinboldtae* occurred in litter and soils from Swale, Naosap Forest, Naosap Riser, and Pine Ridge sites, all of which are high in needle litter content.

Table 3. Infestation (%) of pine pollen grains after 10 days of incubation by chytrid species placed with soils collected from the diverse sites in boreal Manitoba.

Site	Species							
	OL	CA	PP	RS	CP	RP	PR	TI
Young Pine	1.2	**68.0**	12.6	8.4	0	0	0	90.2
Naosap Forest	1.4	20.6	0.8	10.2	**46.0**	0	0.4	79.4
Bog	2.2	0.2	0.2	0	**40.4**	13.0	0	56.0
Naosap Riser	5.6	4.0	2.8	**27.0**	12.0	0	0.6	52.0
Pine Ridge	1.2	14.0	0.8	**27.8**	2.2	0	0.2	46.2
Mature Pine	0.2	0	2.0	0	**35.0**	0	0	37.2
Balsam Fir	0	6.2	0	**28.2**	0	0	0	34.4
Alder	1.6	7.8	0.8	0	**14.6**	9.4	0	34.2
Spruce	0.6	0	2.8	0	**26.4**	1.0	0	30.8
Poplar	**9.6**	0	0	0	0	2.8	0	12.4
Naosap Beach Sand	0	0	0	**11.4**	0	0	0	11.4
Swale	3.0	0	0	**5.8**	1.4	0	0.2	10.4
Bare Sand	0.2	0	0	**5.6**	0	0	0	5.8

Maximum infestation for each site is indicated in bold face. OL, *Olpidium* spp.; CA, *Chytriomyces annulatus*; PP, *Phlyctochytrium papillatum*; RS, *Rhizophydium sphaerotheca*; CP, *Chytriomyces poculatus*; RP, *Rhizophydium pollinis-pini*; PR, *Phlyctochytrium reinboldtae*; TI, Total infestation

Chytrid dominance

Four species showed maximum infestation of pollen over the 13 sites (Table 3). *Rhizophydium sphaerotheca* Zopf (*sensu* Booth, 1971b) dominated (relative frequency) in collections from Naosap Beach (100%), Bare Sand (96.6%), Mature Pine (94.1%), Balsam Fir (82%), Pine Ridge (60.2%), Swale (55.8%), and Naosap Risers (51.9%). *Chytriomyces annulatus* Dogma dominated in Young Pine (75%) samples. *Chytriomyces poculatus* Willoughby and Townley dominanced in peat or soils from Bog (72.1%) collections, Naosap Forest (57.9%), and Alder (42.7%) stands. *Olpidium* spp. dominated in soils of Poplar (77.4%) groves. High dominance (76 to 100%) was seen in low chytrid infestation sites with low diversity, while lower dominance ($\leq 75\%$) was observed in high infestation sites with high diversity.

Coefficients of association

Based on coefficients of association values (Fig. 2), three site groups are distinguishable. Young Pine, Bare Sand, and Balsam Fir represent the first associated group, which is characterized by exposed sand or needle litter on sand. (consult Table 1 for site description data). The second associated group includes Naosap Forest, Naosap Riser, and Pine Ridge sites, which are strongly tied by high needle litter content. Spruce, Mature Pine, Alder, and Bog sites represent the third associated group, which has mixed litter with alder litter content.

Species in common

Based on comparisons of chytrid assemblages in baited soils from selected sites in west-central boreal Manitoba, two major site groups can be recognized (Fig. 3). The first of these includes the Young Pine, Bare Sand, Balsam Fir, Naosap Forest, Naosap Riser, Pine Ridge, and Swale sites. *Rhizophydium sphaerotheca* is common to these sites. This group may be divided into two subgroups. The first subgroup includes Young Pine, Bare Sand, and Balsam Fir sites, having *R. sphaerotheca* in common, and the second subgroup includes Naosap Forest, Naosap Riser, Pine Ridge, and Swale sites with *R. sphaerotheca*, *Chyriomyces poculatus* and *Phlyctochytrium reinboldtae* in common.

	Bare Sand	Balsam Fir	Naosap Forest	Naosap Riser	Pine Ridge	Swale	Spruce	Mature Pine	Alder	Bog	Poplar
Young Pine	0.6	0.6	0.5	0.5	0.5	-0.2	-0.2	0.2	0.1	0.1	-0.1
Bare Sand		0.3	0.3	0.3	0.3	0.6	-0.1	0.1	-0.3	-0.3	0.3
Balsam Fir			0.3	0.3	0.3	-0.1	-0.7	-0.6	-0.3	-0.3	-0.4
Naosap Forest				1.0	1.0	0.5	-0.4	0.2	-0.6	-0.6	-0.1
Naosap Riser					1.0	0.5	-0.4	0.4	-0.3	-0.3	-0.7
Pine Ridge						0.5	-0.4	0.4	-0.3	-0.3	-0.7
Swale							-0.2	0.4	-0.3	-0.3	-0.7
Spruce								0.8	0.7	0.7	0.6
Mature Pine									0.6	-0.3	0.1
Alder										0.7	0.4
Bog											0.4

Fig. 2. Coefficients of association for fungal assemblages in site parings (A coefficient value of 0.6 is considered to indicate strong association).

	Bare Sand	Balsam Fir	Naosap Forest	Naosap Riser	Pine Ridge	Swale	Spruce	Mature Pine	Alder	Bog	Poplar
Young Pine	1 4	4 5	1 3 4 5	1 3 4 5	1 3 4 5	1 4	1 3	1 3	1 3 5	1 3 5	1
Bare Sand		4	1 4	1 4	1 4	1 4	1	1	1	1	1
Balsam Fir			4 5	4 5	4 5	4	-	-	5	5	-
Naosap Forest				1 2 3 4 5 6	1 2 3 4 5 6	1 2 3	1 2	1 2	1 2	1 2	1
Naosap Riser					1 2 3 4 5 6	1 2 4 6	1 2 3	1 2 3	1 2 3 5	1 2 3 5	1
Pine Ridge						1 2 4 6	1 2 3	1 2 3	1 2 3 5	1 2 3 5	1
Swale							1 2	1 2 3	1 2 3 5	1 2 3 5	1
Spruce								1 2 3	1 2 3 7	1 2 3 7	1 7
Mature Pine									1 2 3	1 2 3	1
Alder										1 2 3 5 7	1 7
Bog											1 7

Fig. 3. Chytrid species in common among site parings (n=66) of selected boreal Manitoba sites. 1, *Olpidium* spp.; 2, *Chytriomyces poculatus*; 3, *Phlyctochytrium papillatum*; 4, *Rhizophydium sphaerotheca*; 5, *Chytriomyces annulatus*; 6, *Phlyctochytrium reinboldtae*; 7, *Rhizophydium pollinis-pini*

Spruce, Mature Pine, Alder, Bog, and Poplar sites represent the second major group. This group is characterized by the presence of *Olpidium* spp. and *C. poculatus* along with the absence of *R. sphaerotheca*.

Discussion

Pollen infestation by site

In boreal sites, occurrence of increased organic matter in soils is reflected in pH values below neutrality. Soils rich in organic matter usually have an ameliorated moisture regime, whereas soils with an increased mineral content have pH values above neutrality and rapidly changing soil moisture regimes. As in previous studies (Remy, 1948; Willoughby, 1964, 1965; Booth, 1971c; Booth and Barrett, 1976), the results showed higher levels of pollen infestation in soils rich in organic matter and lower infestation levels in mineral soils. Each site with high infestation levels was characterized by litter with high needle content while medium infestations were in sites with mixed (needle and broad leaf) litter. Mineral soil or soil with limited organic matter yielded low levels of pollen infestation. In addition, the presence or absence of litter and the type of litter were correlated with levels of pollen infestation. These observations may reflect pH, moisture regimes or interactions of the chytrids with other abiotic and biotic elements.

Species diversity

During the summer ice wedge polygons are the most acidic, warmest and driest soils in the studied ecosystem (Booth and Barrett, 1976). The results substantiated the findings of the high-Arctic study with high diversity (6 spp.) in soils from warm and dry sites. The high needle content of warm and dry site suggests that they were also acidic. Observation of high diversity (5 spp.) in bog samples coincides with previous reports (Miller, 1965; Sparrow, 1966) of a substantial variety of chytrids in this ecosystem. Lower diversity of chytrids from mineral soils also has been previously observed (Gaertner, 1954). Species diversity in soils from Mistik Creek study region seems to be, in part, determined by types of litter and the presence or absence of litter.

Chytrid distribution and dominance

As observed in an earlier study (Booth, 1971c), *Rhizophydium sphaerotheca* Zopf was collected from mesic to xeric, middle to low pH, warm soils. This species also was widely distributed across soil and litter types (Booth, 1971c, 1979; Booth and Barrett, 1971, 1976).

The occurrence of *Chytriomyces poculatus*, from low pH soils in the Mistik Creek area confirmed the distribution pattern reported in the type description (Willoughby and Townley, 1961) and subsequent studies (Willoughby, 1965; Dogma, 1969; Booth and Barrett, 1971). *Chytriomyces annulatus*, which came from low pH litters on sands in my study area, was originally described (Dogma, 1969) from acidic soils and later found from leaf litter on regosolic sands (Booth and Barrett, 1976; Booth, 1979).

Originally isolated (Sparrow, 1952) from riverbank soils in a Michigan coniferous forest, *Phlyctochytrium papillatum* Sparrow is generally absent from mixed litter sites in the Mistik Creek region. *Rhizophydium pollini-pini* has been reported from mixed litter habitats (Booth and Barrett, 1971, 1976), as is the case in my study. Narrow in ecological range (Booth, 1979), *Phlyctochytrium reinboldtae* Persiel occurs in the dry sites of my study area that are high needle litter.

In Mistik Creek sites with high needle content or needles on sand, *Rhizophydium sphaerotheca* is generally the dominant species. The tendency for this chytrid to be dominant in acidic sites has been seen in the work of Booth and Barrett (1971, 1976). Originally reported from broad leaf litter (Willoughby and Townley, 1961), *Chytriomyces poculatus* is dominant in mixed litter with high content of angiospermous leaf pieces in my study area. Litter from these sites is less acidic than the high needle content litter.

Species assemblages and litter types

Based on coefficients of association and species in common among species across the collection sites, it is possible to relate dominant species to species assemblages in site groups. *Rhizophydium sphaerotheca* typifies site group I (Young Pine, Bare Sand, and Balsam Fir). *Chytriomyces poculatus*, *Phlyctochytrium reinboldtae* and *Rhizophydium sphaerotheca* are common to site group II (Naosap Forest, Naosap Riser, Pine Ridge, and Swale). Finally *Chytriomyces poculatus* and *Olpidium* spp. occur together in site group III (Alder, Bog, Mature Pine, Poplar, and Spruce).

These species assemblages in the site groups suggest that the chytrids are distributed by litter and soil types (cf. group I, needles on sands or sandy soils; group II, mixed litter high in needle content on loamy soils; group II, mixed litter with high angiospermous leaf content on loamy soils). Roberts (1963) pointed out that the type of decaying vegetation might represent a more decisive factor determining the distribution of zoosporic fungi than simple hydrogen ion content. Although hydrogen ion content has been demonstrated to be correlated with chytrid distribution (Willoughby, 1965, 1998; Booth and Barrett, 1976), it is possible that the substratum characteristics, e.g. broad leaf litter, mixed leaf litter or needle leaf litter, and availability of litter, may be as critical as pH in describing their distribution in boreal forest sites. Furthermore, it is possible that litter types and characteristics are more meaningful than simple pH in accounting for spatial distribution of chytrids in nature. A previous study on the ecology of lower saprophytic fungi indicated that distinct aquatic and terrestrial floras could be distinguished in the order Chytridiales (Willoughby, 1961). My study gave some indication that edaphic factors might control the chytrid distribution and explain the apparently discontinuous distribution of certain very common species. In conclusion the typical boreal forest chytrid species found in this study are characteristic of the micro-flora where soil pH is low and associated with ground litter types.

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