Ectomycota Associated with Hibernating Bats in Eastern Canadian Caves prior to the Emergence of White-nose Syndrome

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Abstract - The emergence of the fungal disease white-nose syndrome (WNS) among hibernating bats in North America and its causative pathogen, *Geomyces destructans*, underscores how little is known about fungi associated with bats and their subterranean environments. Investigating 8 caves and mines in New Brunswick, Canada, we cultured a diverse array of fungi from the fur and skin of apparently healthy, hibernating *Myotis lucifugus* (Little Brown Bat) and *M. septentrionalis* (Northern Long-eared Bat) in the year prior to the emergence of WNS in the province. Among the 117 isolated fungal taxa, we found an array of psychrophilic, psychrotrophic, keratinolytic, coprophilous, and saprobic fungi. The most common taxa were *Geomyces pannorum* sensu lato, *Penicillium* spp., *Mortierella* spp., *Mucor* spp., *Cephalotrichum stemonitis*, *Leuconeurospora* spp., *Penicillium solitum*, *Cladosporium* spp., and *Trichosporon dulcitum*. Each bat hosted 6.9 ± 3 (SD) fungal taxa, and 30.8 ± 5 taxa were isolated per hibernaculum. Number of taxa isolated per bat was positively correlated with mean and minimum winter temperatures in the dark zones of hibernacula. Forty-seven of the taxa have never been reported in caves, and an additional 31 taxa are new records for North American caves. The presence of *Geomyces pannorum* sensu lato on 70% of hibernating bats may complicate results of diagnostic techniques used for identifying *G. destructans*. Bats hibernating in eastern Canada harbor a rich reservoir of fungal species and probably play a role in moving fungal spores into and between hibernacula, as well as onto the landscape.

Introduction

Very little is known about the mycota associated with bats. The few existing studies have largely been done outside caves and outside the range of North American bats. These studies have mainly focused on fungi potentially pathogenic to humans or other wildlife and the role that bats play in the spread and propagation of pathogens (e.g., *Histoplasma capsulatum* Darling) (English 1966, Grose and Marinkelle 1966, Grose and Tamsitt 1965, Hoff and Bigler 1981, Hubalek et al. 1979, Kwong-Chung and Bennett 1992, Mok et al. 1982, Muotoe-Okafor and Gugnani 1993, Oyeka 1994, Reiss and Mok 1979, Ulloa et al. 2006). Only 2 studies specifically on the mycota associated with hibernating bats have been conducted: one in France, with 7 fungal genera isolated, (Larcher et al. 2003), and the other in Italy, with 12 fungal genera isolated (Voyron et al. 2011).

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Since its discovery in 2006 in a commercially operated cave in New York State, white-nose syndrome (WNS), an often fatal infection of hibernating bats caused by the fungus *Geomyces destructans* Blehert and Gargas (Lorch et al. 2011), has spread rapidly across eastern North America (Turner et al. 2011). The regional extinction of *Myotis lucifugus* LeConte (Little Brown Bat), one of the most common and widespread small mammals in North America, is predicted within 20 years (Frick et al. 2010). *Geomyces destructans* was probably introduced into North America from Europe, where it is seemingly native and widespread (Turner et al. 2011). For unknown reasons, no significant mortality or morbidity due to *G. destructans* has been documented in European bats (Puechmaille et al. 2010, 2011; Wibbelt et al. 2010). Among other hypotheses, it has been suggested the mycota on European bats or in the European cave environment has coevolved with *G. destructans* so as to render it a nonpathogenic part of the ecosystem (Wibbelt et al. 2010).

Incidental to recent searches for *G. destructans* in caves of New York State, several fungal taxa have been recorded from the skin of hibernating cave bats, including *Aspergillus terreus* Thom, *Candida glabrata* (H.W. Anderson) S.A. Mey. and Yarrow, *Cladosporium* sp., *Fusarium* sp., *Geomyces* spp., *Helicostylum elegans* Corda, *Mortierella* sp., *Mucor* sp., *Penicillium* sp., and *Trichophyton terrestre* Durie and D. Frey (Chaturvedi et al. 2010, Courtin et al. 2010, Veilleux 2008). Likewise, in the course of confirming the presence of *G. destructans* in Slovakia, Simonovicova et al. (2011) isolated *Isaria farinosa* (Holmsk.) Fr., *Cladosporium macrocarpum* Preuss, and *Alternaria tenuissima* (Nees) Wiltshire from hibernating cave bats.

We predicted, based on the low fungal diversity previously reported from hibernating bats, that overwintering bats in New Brunswick would host a small assemblage of fungal species adapted to the cold, oligotrophic cave environment, and that diversity might be influenced by rates of human visitation to sites. The study reported here examines ectomycotal diversity on apparently healthy bats (*Myotis* spp.) from caves in New Brunswick during 2010, one year before the confirmed arrival of WNS in the province. Coupled with similar post-WNS investigations now underway, these data may be helpful in guiding the development of management procedures for this new disease and in contributing to the conservation of bats that hibernate in North American caves.

Methods

Samples were taken from 6 caves and 2 long-abandoned manganese mines (length: $\bar{x}$ = 210 m ± 158 SD; n = 8) in southern New Brunswick, Canada (hereafter the word "cave" encompasses both natural solution caves and abandoned mines). Specific cave locations are shown in Vanderwolf et al. (2012). Although none of the caves in our study region was operated as a commercial show cave, one was used regularly for ecotours during the summer (until 2011), perhaps hosting several hundred people on multiple tours, and several sites are visited regularly by the local community, mainly outside the hibernation period. Our

initial attempts to code cave visitation on the basis of amounts of graffiti and refuse proved unsuccessful, and we eventually labeled two caves as high visitation (>100 person visits/year), based on our own knowledge of relative use and information from the New Brunswick Department of Natural Resources and R. Falkner of Baymount Outdoor Adventures, Inc. (Hillsborough, NB, Canada, pers. comm. to D.F. McAlpine). Other sites generally had fewer or no visitors annually, other than the authors.

Bats hibernating underground in New Brunswick consist mostly of *M. lucifugus* and *M. septentrionalis* Trouessart (Northern Long-eared Bat), with very few *Perimyotis subflavus* F. Cuvier (Tricolored Bat) (Vanderwolf et al. 2012). We sampled *Myotis* spp. for fungi between January and March 2010, and we followed the protocol of the United States Fish and Wildlife Service (2009) for minimizing the spread of WNS during all visits to caves. Necessary permits were obtained from the New Brunswick Department of Natural Resources.

At each hibernaculum, swabs were taken with a sterile, dry, cotton-tipped applicator from the dorsal fur or skin of live, apparently healthy bats; the term "skin" refers to the face, ears, patagium, and/or uropatagium, depending on which parts were within our reach. Swabs were obtained from 10 bats in each hibernaculum, resulting in samples from 43 *M. lucifugus* and 37 *M. septentrionalis*. Bats were swabbed while they were roosting and were not removed from cave walls.

After swabbing, the applicator was immediately streaked across an agar surface in a petri plate, and diluting streaks were completed in the hibernaculum within 3 h of the initial streak, after which plates were sealed in situ with parafilm (Pechiney Plastic Packaging, Chicago, IL). All streaks were made on plates containing either dextrose-peptone-yeast extract (DPYA) agar or Sabouraud-dextrose (SAB) agar, both of which were infused with the antibiotics chlortetracycline and streptomycin. Four swabs per bat were taken so that four plates, representing the four combinations of fur or skin on either SAB or DPYA, were obtained. A new applicator was used for each swab. DPYA was chosen because Papavizas and Davey (1958) found it to be a superior medium for both isolating maximum numbers of fungal genera and facilitating identification. SAB was selected because it is a standard medium currently used by WNS researchers (D.S. Blehert, USGS National Wildlife Health Center, Madison, WI, pers. comm. to K. Vanderwolf).

In the laboratory, samples were incubated, inverted, in the dark at 7 °C in a low-temperature incubator (Model 2015, VWR International, Mississauga, ON, Canada), to approximate the subterranean environment. We incubated at 7 °C instead of 5.1 °C (i.e., the average winter temperature of the hibernacula), to speed fungal growth while still providing a favorable environment for species of fungi that grow at the cool temperatures typical of caves. Samples were monitored over 4 months until no new cultures had appeared for 3 weeks on a plate or the plate had become overgrown with hyphae. Once fungi began growing on the plates, each distinct colony was subcultured to a new plate. DPYA without oxgall and sodium propionate was used for maintaining pure cultures.

Identifications were carried out by comparing the micro- and macromorphological characteristics of the microfungi to those traits appearing in the

taxonomic literature and compendia (Ahmed and Cain 1972, Carmichael et al. 1980, De Hoog 1972, Domsch et al. 1980, Hennebert and Desai 1974, Samson 1974, Van Oorschot 1980). Isolates were sent to taxonomic specialists for confirmation of identification, usually through a combination of morphological and molecular genetic techniques. Permanent cultures are housed in the University of Alberta Microfungus Collection and Herbarium (UAMH 11121, 11159–11164, 11182–11184, 11236–11251, 11296–11329, 11334–11345, 11379–11400, 11408–11436, 11438–11478, 11492–11496, 11499–11500, 11504–11516, 11528, 11529, 11594–11614, 11618, 11619, 11621–11626, 11639, 11642), and desiccant-dried samples are in the New Brunswick Museum (F-03425–F-03753, F-04306–F-04317).

The dimensions and layout of 7 of the study sites have previously been reported by Arsenault et al. (1997) and McAlpine (1976, 1982). Although all the hibernacula are characterized by high humidity and water seeping from walls and ceilings, 2 caves have large quantities of running water, and 1 has a large pool dominating the cave interior. The average winter air temperature in the dark zone of caves in New Brunswick that serve as bat hibernacula is 5.1 ± 1.1 °C (Vanderwolf et al. 2012), with winter defined as 1 November–30 April. Winter temperature range was calculated by subtracting the minimum winter temperature from the maximum. Methods for determining cave temperature and counting hibernating bats are detailed in Vanderwolf et al. (2012).

After verifying homogeneity of the variances and normality of the data, we used one-way ANOVAs to determine if the number of fungal taxa per bat differed between hibernacula, genders, species, high versus low rates of human visitation, sites with or without porcupine dung, and sites with or without substantive water. Environmental parameters were not normally distributed, even after transformation, so Spearman rank correlations were used to determine if the number of fungal taxa was correlated with selected features of the environment (Table 1). A chi-square test was used to determine if the number of fungi isolated differed when using SAB versus DPYA and fur versus skin. ANOVAs, Spearman rank correlations, and chi-square tests were done with Minitab® Statistical Software. Simpson's diversity index (D) was calculated for each hibernaculum with EstimateS software v.8.2 (Colwell 2009).

Table 1. Spearman rank correlations of the number of fungal taxa isolated with selected parameters of hibernacula in New Brunswick. All temperatures were measured in the dark zone where the bats roost (Vanderwolf et al. 2012). Temperature data were available for only 6 of the 8 caves.

	Number of fungal taxa	
Parameter	Per hibernaculum	Per bat
Number of bats in the hibernaculum	$r = -0.22$, $n = 8$, $P = 0.60$	$r = 0.01$, $n = 80$, $P = 0.92$
Length of hibernaculum	$r = 0.42$, $n = 8$, $P = 0.35$	$r = 0.10$, $n = 80$, $P = 0.45$
Mean annual temperature	$r = 0$, $n = 6$, $P = 1$	$r = -0.04$, $n = 60$, $P = 0.74$
Mean winter temperature	$r = 0.24$, $n = 6$, $P = 0.65$	$r = 0.27$, $n = 60$, $P = 0.03$
Winter temperature range	$r = 0$, $n = 6$, $P = 1$	$r = -0.07$, $n = 60$, $P = 0.59$
Minimum temperature	$r = 0.50$ $n = 6$, $P = 0.31$	$r = 0.40$, $n = 60$, $P = 0.002$

Results

Although 8 plates were damaged in the field and discarded, fungi were successfully cultured from all 80 bats and from 275 of 312 (88%) swabs, producing a total of 927 isolates. A mean of 6.9 ± 3 taxa (range: 1−15) were isolated from each bat. There was no significant difference in mean number of fungal taxa isolated between male (n = 52) and female (n = 22) bats ($F_{1,73}$ = 0.06, P = 0.81; 6 individuals were not sexed), *M. lucifugus* versus *M. septentrionalis* ($F_{1,79}$ = 0.17, P =0.68), sites with high versus low human visitation ($F_{1,79}$ = 0.91, P = 0.34), or among hibernacula ($F_{7,73}$ = 1.96, P = 0.07). However, bats harbored a greater number of fungal taxa in caves with porcupine dung ($F_{1,79}$ = 10.78, P = 0.002) and fewer fungal taxa in caves with substantive water ($F_{1,79}$ = 8.5, P = 0.005).

The number of fungal taxa isolated per bat was positively correlated with the mean and minimum temperatures in hibernacula (Table 1). No significant correlation was found between number of fungal taxa and number of bats present, length of hibernaculum, mean annual temperature, or winter temperature range. The correlation coefficients between environmental variables and number of fungal taxa isolated per hibernaculum generally mirrored those obtained per bat (Table 1).

During this study, 117 taxa in 74 genera, plus 11 sterile fungal morphs, were isolated from bat fur and skin (Appendix 1). A mean of 30.8 ± 5.4 taxa were isolated (excluding sterile taxa) per hibernaculum. Each hibernaculum had 1–7 unique genera, as well as unique species in shared genera. Fifty-six (48%) of the 117 taxa, as well as 10 of the sterile species, were found on only 1 of the 80 bats. Unidentified bacterial cultures also were isolated from bats, despite use of antibiotics in all agars.

The dominant families of fungi isolated from bats in New Brunswick were Trichocomaceae, Myxotrichaceae, and Microascacae. Of the species isolated from each bat, 77% were Ascomycota, 14% were Zygomycota, and 9% were Basidiomycota (we counted the occurrence of a fungal species on one bat as one occurrence of that phylum). Simpson's diversity index, which scales from 0 (diverse) to 1 (no diversity), was low (average 0.29 per hibernaculum), indicating that the fungal community was diversified and no single species was dominant. Forty-seven of the taxa isolated in this study have never previously been reported in caves, and an additional 31 taxa are new records for North American caves (Vanderwolf et al. 2013).

The most commonly isolated taxon was *Geomyces pannorum* sensu lato, which was found on 70% of swabbed bats. Despite the abundance of *Geomyces* spp., no isolate appeared to be *G. destructans*, based on morphology and genetic sequencing (L. Sigler, University of Alberta Microfungus Collection and Herbarium, Edmonton, AB, Canada, pers. comm. to K. Vanderwolf), and there was no evidence that this invasive species was present asymptomatically or had spread to the immediate region of our study sites during the course of our sampling. Other common taxa obtained from our swabs, along with *G. pannorum*, were *Penicillium* spp. (62% of bats), *Mortierella* spp. (48%), *Mucor* spp. (44%),

Cephalotrichum stemonitis (36%), *Leuconeurospora* spp. (35%), *Penicillium solitum* (31%), *Cladosporium* spp. (20%), and *Trichosporon dulcitum* (20%) (Appendix 1). Of these core taxa, 1 is coprophilous (*C. stemonitis*), 2 are of unknown ecology (*Leuconeurospora* spp. and *Trichosporon dulcitum*), and the remainder are cosmopolitan and widespread both inside and outside caves (Domsch et al. 1980, Vanderwolf et al. 2013). All these core fungi have been reported from caves previously except *Trichosporon dulcitum* and *Leuconeurospora* spp. There appears to be a secondary core group of 22 fungal species (present on 5–15 bats) of more limited distribution in the general cave environment (Appendix 1). The remaining species occur infrequently.

There was no difference in number of fungal taxa obtained from fur versus skin ($\chi^2 = 22.30$, df = 24, $P = 0.56$). Although type of agar appeared to be a significant variable in detecting taxonomic richness ($\chi^2 = 76.73$, df = 24, $P < 0.001$), results were not significant after removal of *Mortierella* spp. and *Mucor* spp. from the analysis ($\chi^2 = 31.44$, df = 22, $P = 0.09$). *Mortierella* spp. and *Mucor* spp. were isolated more frequently on SAB than DPYA (42 versus 6, and 38 versus 16 isolates, respectively), but other fungi were isolated more frequently from DPYA than SAB (367 versus 284 isolates). Thirty-two taxa were isolated exclusively on SAB, and 36 on DPYA. When only taxa isolated more than once are considered, 3 were isolated exclusively on SAB, and 10 on DPYA.

Discussion

We found that apparently healthy hibernating bats in caves in New Brunswick host a diverse reservoir of fungal species, representing an array of ecological strategies (Appendix 1). Many are saprobic, such as keratinolytic or coprophilous, and psychrophilic/psychrotropic. Most have been previously isolated from soil and plant debris, and some are entomophilous or phytophilous. Many of these fungal species probably originated outside the caves. Benoit et al. (2004) suggest that fungi present on the exoskeleton of cave crickets represent a subsample of the species present in the environment, and this is likely true for bats as well.

It appears that in most hibernacula in New Brunswick, a core group of 9, mainly cosmopolitan fungal taxa are present on the external surface of *Myotis* spp. Accompanying this core assemblage is a larger secondary group with more specialized niches, some of which appear to be adapted to the cold cave habitat. The remaining fungal species (74% of those isolated) can be characterized as rare because of their infrequent isolation in culture. Many of these are probably incidental acquisitions that will vary from cave to cave, even within a region. To some degree, the composition of this assemblage will be influenced by the aboveground habitat through which bats move as they enter or leave a hibernaculum, and this ability to acquire and transport a diverse array of fungal species emphasizes the role that bats can play as fungal vectors.

Human visitation did not appear to influence fungal diversity, but visitation frequencies at our study sites were likely below the necessary threshold to affect fungal richness. Previous studies that found increased diversity of fungi (or

yeasts) with increasing rates of human visitation compared tourist caves (i.e., 23 to >400,000 visitors per year) to caves closed to the public or those rarely used by spelunkers and scientists (Mosca and Campanino 1962, Vaughan-Martini et al. 2000, Wang et al. 2010).

The number of fungal taxa per bat was positively correlated with minimum and mean winter temperature (Table 1) and was greater in sites without substantive running water or pools and in hibernacula with porcupine dung. However, these variables are also correlated with each other, which complicates biological interpretation. These variables may correspond with population levels of terrestrial invertebrates. Mobile invertebrates (e.g., mites) that crawl across hibernating bats may be significant factors in fungal dispersion within caves. In soil outside caves, mites are thought to be vectors and distributors of microfungi (Ocak et al. 2008).

In New Brunswick, the external surface of living, apparently healthy bats overwintering in caves is dominated by Ascomycota, with less abundant Zygomycota and Basidiomycota (Appendix 1). In this respect, fungi found on healthy hibernating bats seem to track the broader fungal community of the cave environment (Cubbon 1976, Shapiro and Pringle 2010). In contrast, Voyron et al. (2011) cultured 59% Zygomycota, 35% Ascomycota, and 6% Basidiomycota from dead bats in an Italian cave. This difference is probably because Zygomycota grow on dead bats and produce abundant spores, masking other taxa. We found this masking effect apparent when culturing samples on SAB agar. Fast-growing Zygomycota tended to cover SAB plates with hyphae and spores, rendering slow-growing taxa undetectable. DPYA agar contains inhibitory ingredients that slow the growth of fungi, particularly Zygomycota, enabling the detection of slow-growing taxa. For this reason, we found DPYA a superior medium for detecting cave fungi.

This study cultured a greater diversity of fungi on live overwintering cave bats compared to previous studies done in France (Larcher et al. 2003) and Italy (Voyron et al. 2011). This increased diversity could be due to inherent geographic differences but is more likely due to differing methodologies. Fewer bats were swabbed in previous studies (Italy, $n = 20$; France, $n = 25$; this study $n = 80$), and plates were incubated at 10 °C and 24 °C for 2 weeks each in Italy, and at 28 °C for 4 weeks in France. These monitoring times may not have been sufficient to detect slow-growing species. We found the diameters of some cultures on modified DPYA agar after 42 days incubation at 7 °C were as little as 7 by 5 mm. Furthermore, the incubation temperatures of previous studies likely excluded some of the psychrophilic and psychrotrophic species that were relatively common on bats in New Brunswick. Five of the 7 fungal genera found by Larcher et al. (2003) in France and 9 of 12 genera found by Voyron et al. (2011) in Italy were also found in New Brunswick (Appendix 1). In particular, *Chrysosporium merdarium* was isolated on live bats from both New Brunswick and France (Larcher et al. 2003) and on dead bats in Italy (Voyron et al. 2011) and Hungary (Zeller 1966). This species is keratinophilic (Larcher et al. 2003) and may be of regular occurrence on the external surface of hibernating bats, although it was

only recorded on 2 bats in New Brunswick. Dermatophytes, while present on some bats, were not common (Appendix 1). However, variance in methodology does not explain the difference in diversity between our work and that of Lorch et al. (2012), the latter carried out in the northeastern US. Differences may indicate that the surface of live bats in caves harbor a greater diversity of fungal species than cave soil

No *G. destructans* was found in New Brunswick before winter 2011, which is consistent with the pattern of an introduced infectious agent spreading from a point source (Puechmaille et al. 2011, Wilder et al. 2011). However, the prevalence of *Geomyces pannorum* s.l. naturally occurring on apparently healthy hibernating bats in New Brunswick may complicate diagnoses for *G. destructans*. Several of our isolates, although morphologically distinct from *G. destructans*, are closely related genetically (S. Hambleton, Agriculture Canada, Ottawa, ON, Canada, and L. Sigler, pers. comm. to K. Vanderwolf). Preliminary internal transcribed spacer (ITS) sequences for all isolates identified as *G. pannorum* in this study, along with data for *G. pannorum* from a broad range of other substrates, indicate that they represent at least 10 closely related but distinct genetic groups. Two of these groups correspond to species in *Pseudogymnoascus* that have *Geomyces* anamorphs (S. Hambleton and L. Sigler, pers. comm. to K. Vanderwolf). *Geomyces pannorum* s.l., is a widespread psychrophilic fungus that is especially common in Arctic and Antarctic soils (Kochkina et al. 2007, Marshall 1998) and has also been found in caves (Bosák et al. 2001, Gunde-Cimerman et al. 1998, Nováková 2009, Volz and Yao 1991), on mammalian fur (Chabasse 1988, Hubalek et al. 1979), and as a rare animal pathogen in humans, cats, dogs, and zoo animals (Christen-Zaech et al. 2008, Erne et al. 2007, Gianni et al. 2003, Zelenkova 2006). However, *G. pannorum* is polyphyletic, and taxonomic revision of the genus is needed (S. Hambleton, pers. comm. to K. Vanderwolf).

Penicillium spp. and *Aspergillus* spp. are some of the most abundant taxa in cave environments (Vanderwolf et al. 2013). The current study found abundant *Penicillium* spp. but only 2 *Aspergillus* spp. The genus *Aspergillus* includes many thermotolerant and thermophilic species (Domsch et al. 1980), perhaps explaining why so few isolates were detected in caves in New Brunswick (mean temperature = 5.1 °C). Alternatively, our incubation temperature may have been too low for consistent detection of *Aspergillus* spp. The 2 *Aspergillus* spp. that we did isolate grew faster and were more robust at room temperature than at our routine incubation temperature of 7 °C.

None of the 17 phytophilous species was common on bats, but caves likely are not the natural habitat of these taxa, because no green plants grow in the dark zone of caves. These species were probably carried into the cave by air currents, water, insects, bats, or other animals. In many of the caves, roots of vascular plants penetrate and hang from the ceiling and may also be a source of phytophilous fungi on bats. The three entomophilous species that were isolated may have been associated with arthropod parasites on the bats or with other arthropods in the hibernacula.

Several taxa cultured from bats in New Brunswick are commonly reported from the Arctic and Antarctic. Because the average air temperature in the dark

zone of New Brunswick hibernacula throughout the year is 5.9 ± 1.4 °C (Vanderwolf et al. 2012), it is possible that this group of fungi represents indigenous mycota.

The mushrooms *Cerrena unicolor* and *Baeospora* sp. were isolated from bats roosting in a mine containing wooden support beams from the late 19th–early 20th century; multiple fruiting bodies were present on the beams, including those of *Baeospora* sp. and an unidentified species. The polypore *Trametes pubescens* was isolated from a cave containing woody debris with unidentified fruiting bodies. Bats may have acquired these macrofungal spores while flying within hibernacula.

We isolated several coprophilous species. Porcupine dung, present in 3 of our study caves, provides a rich fungal substrate, as evidenced by visible fungal growth on all deposits. We isolated some coprophilous species more commonly and some exclusively from bats in caves inhabited by porcupines. For example, *Phaeotrichum hystricinum* has been documented exclusively from porcupine dung (Cain 1956) and, during this study, was only isolated from caves containing this substrate. *Cephalotrichum stemonitis* was isolated from 24 bats in caves with porcupines and from 5 bats in caves without porcupines. We observed heavy sporulation of *C. stemonitis* on porcupine dung that was incubated in the lab, as well as spores of *P. hystricinum*. Dung from other vertebrates, although not observed in large quantities, likely also contributes appropriate substrate for coprophilous fungi.

Although several fungi cultured from bats are cosmopolitan, other species have rarely been reported from any environment. *Microascus caviariformis*, for example, has been detected only once, in a Belgian cave (Malloch and Hubart 1987). *Thelebolus globosus* also is rare and never before reported outside Antarctica (De Hoog et al. 2005). *Arthroderma silverae* is known from only a few specimens isolated from canine dung in the Arctic and Alberta, Canada (Currah et al. 1996); in New Brunswick, we isolated this species only from caves with porcupine dung.

It is not known whether any fungi isolated during this study are capable of growing on live bats or interacting with *G. destructans*. The keratinolytic species isolated from bats in this study are those most likely to be capable of becoming established and growing on live bat skin, although most of these species were rarely encountered. Bats are known to transport pollen, viruses, parasites, and the fungus *Histoplasma capsulatum* (Hoff and Bigler 1981, Kunz and Parsons 2009). It is believed that bats are responsible for much of the rapid spread of *G. destructans* across eastern North America (Turner et al. 2011). The rich reservoir of fungal species isolated from hibernating bats during this study suggests that bats may transport multiple fungal species, moving spores into and between hibernacula, as well as across the landscape.

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Appendix 1. Identification, frequency, and ecological/physiological characteristics of fungal taxa isolated from the external surface of hibernating bats (L = *M. lucifugus*; S = *M. septentrionalis*) in caves of New Brunswick. "Unknown" indicates that we could not confidently determine the ecological strategy or physiology of the taxa. The notation [R] indicates that the taxon has rarely been isolated before, with "rare" defined as ≤4 isolates present in the University of Alberta Microfungus Collection and Herbarium and the Centraalbureau voor Schimmelcultures of the Royal Netherlands Academy of Arts and Sciences collection combined. Live = Previously isolated from live bats in caves.[A] Dead = Previously isolated from dead bats in caves.[B]

	# of caves	# of bats	Live	Dead	Ecology/physiology
Ascomycota					
Acremonium berkeleyanum (P. Karst.) W. Gams	1	3L, 1S			Soil, ubiquitous
A. cereale (P. Karst.) W. Gams	1	1S			Soil
A. cf. *cereale*	1	1S			Soil
Acremonium type 6	1	1S			Unknown
Acremonium type 3	1	1S			Unknown
Acremonium type 7	1	1S			Unknown
Acrodontium crateriforme (J.F.H. Beyma) de Hoog	4	2L, 4S			Phylloplane
Aphanocladium album (Preuss) W. Gams	1	1S			Phytophilous
Arachniotus sp.	1	4L			Coprophilous
Arthrinium sphaerospermum Fuckel	1	1S			Phytophilous
Arthroderma sp. 2	2	1L, 1S			Keratinophilic
Arthroderma sp. 3	2	1L, 1S			Keratinophilic
Arthroderma sp. 4	1	1S			Keratinophilic
Arthroderma silverae Currah, S.P. Abbott and Sigler	2	2S			Coprophilous, psychrophilic/psychrotrophic [R]
Arthrographis sp.	1	1L, 1S	Yes		Unknown
Ascomycete unidentified	1	1L			Unknown
Aspergillus restrictus G. Sm.	1	1L	Yes	Yes	Cosmopolitan
A. versicolor (Vuill.) Tirab.	1	1S			Cosmopolitan
Beauveria bassiana (Bals.-Criv.) Vuill.	3	3L, 2S			Entomophilous
Candida sp.	1	1L	Yes	Yes	Psychrophilic/psychrotrophic
Cenococcum sp.	1	1S			Ectomycorrhizal
Cephalotrichum stemonitis (Pers.) Link	7	19L, 10S			Coprophilous
Ceratocystis autographa B.K. Bakshi	1	1L	Yes[C]		Phytophilous [R]
Chalara microspora (Corda) S. Hughes	1	1S			Phytophilous
Chrysosporium merdarium (Link) J.W. Carmich.	1	2L	Yes	Yes	Keratinophilic
C. pseudomerdarium Oorschot	1	1L			Keratinophilic
Cladosporium sp.	6	11L, 4S	Yes		Cosmopolitan
C. cladosporioides (Fresen.) G.A. de Vries	1	1S	Yes	Yes	Cosmopolitan
Coelomycete	1	1S			Unknown
Coelomycete unidentified	1	1L			Unknown
Hyphomycete unidentified	2	1L, 1S			Unknown
Cylindrocarpon sp.	3	2L, 4S			Phytophilous
C. destructans (Zinssm.) Scholten	1	1S			Phytophilous
Cylindrodendrum album Bonord.	1	1L			Phytophilous
Dictyosporium toruloides (Corda) Guég.	1	1L			Phytophilous [R]
Eremomyces sp.	1	1S			Dung, wood
Exophiala sp.	1	1S			General saprotroph; opportunistic pathogen on humans
Fusarium sp.	2	2S	Yes	Yes	Phytophilous

	# of caves	# of bats	Live	Dead	Ecology/physiology
Geomyces pannorum s.l. (Link) Sigler and J.W. Carmich.	8	29L, 25S			Keratinophilic, psychrophilic/psychrotrophic
Phialoconidial ascomycete	1	1S			Unknown
Gymnoascus intermedius G.F. Orr	1	1L			Keratinophilic [R]
Gymnostellatospora sp.	1	1L			Psychrophilic/psychrotrophic
Gymnostellatospora sp. type 2	1	3L			Psychrophilic/psychrotrophic
Humicola sp.	6	7L, 6S			Psychrophilic/psychrotrophic
Isaria farinosa (Holmsk.) Fr.	3	2L, 1S	Yes		Entomophilous
Leptodontidium cf. *elatius var. elatius* (F. Mangenot) de Hoog	1	1L			Phytophilous
Leuconeurospora sp. 1	5	17L, 7S			Unknown [R]
Leuconeurospora sp. 2	3	5L			Unknown [R]
Mammaria echinobotryoides Ces.	1	1S			Soil and plant materials
Microascus sp.	2	5L, 1S			Unknown [R]
Microascus caviariformis Malloch and Hubart	3	1L, 6S			Caves; proteolytic [R]
Myxotrichum sp.	2	2L			Keratinophilic
Oidiodendron sp.	4	2L, 3S			Psychrophilic/psychrotrophic
O. cf. *griseum* Robak	1	1L			Unknown
O. myxotrichoides M. Calduch, Gené and Guarro	2	2L, 3S			Psychrophilic/psychrotrophic [R]
O. truncatum G.L. Barron	5	12L, 1S			Psychrophilic/psychrotrophic
Paecilomyces sp.	2	2L			Unknown
P. inflatus (Burnside) J.W. Carmich.	1	1S			Thermotolerant
Penicillium sp.	2	1L, 1S	Yes	Yes	Cosmopolitan
P. chrysogenum Thom	1	1L			Cosmopolitan
P. citreonigrum Dierckx	2	4L, 7S			Soil and plant materials
P. concentricum Samson, Stolk and Hadlok	5	2L, 4S			Coprophilous
P. corylophilum Dierckx	5	12L, 4S			Cosmopolitan
P. fellutanum Biourge	2	3S			Cosmopolitan
P. miczynskii K.M. Zalessky	1	1S			Psychrophilic/psychrotrophic
P. solitum Westling	7	8L, 17S			Cosmopolitan
P. thomii Maire	3	4S			Soil and plant materials
P. vulpinum (Cooke and Massee) Seifert and Samson	5	8L, 2S			Coprophilous
Pestalotiopsis maculiformans (Guba and Zeller) Steyaert	1	1L			Phytophilous
Petriella cf. *boulangeri* Curzi	1	1L			Unknown [R]
Phaeotrichum hystricinum Cain and M.E. Barr	1	1L, 1S			Coprophilous [R]
Phialocephala sp.	1	1L			Phytophilous
Phialophora sp.	3	3S			Phytophilous, psychrophilic/psychrotrophic
P. cf. hyalina W. Gams	1	1L			Soil [R]
Phoma radicina (McAlpine) Boerema	1	1S			Phytophilous, psychrophilic/psychrotrophic [R]
Pleosporales unidentified	1	2L			Unknown
Preussia type 1	4	4L, 3S			Coprophilous
Pseudogymnoascus roseus Raillo	4	4L, 2S			Psychrophilic/psychrotrophic
Pyrenochaeta sp.	1	1L, 2S			Phytophilous
Sagenomella sp.	1	1S			Unknown
Septonema secedens Corda	1	1S			Aquatic [R]

	# of caves	# of bats	Live	Dead	Ecology/physiology
Shanorella sp.	1	1L			Unknown
Simplicillium lamellicola (F.E.V. Sm.) Zare and W. Gams	2	1L, 1S			Entomophilous
Sporothrix sp.	1	1S			Unknown
Tetracladium furcatum Descals	3	1L, 2S			Aquatic [R]
Thelebolus sp.	1	1S			Psychrophilic/psychrotrophic
T. crustaceus (Fuckel) Kimbr.	1	1S			Psychrophilic/psychrotrophic
T. globosus Brumm. and de Hoog	3	3L, 3S			Psychrophilic/psychrotrophic [R]
Thysanophora sp.	2	1L, 1S			Phytophilous
Tolypocladium inflatum W. Gams	3	5L, 2S			Psychrophilic/psychrotrophic
Trichocladium opacum (Corda) S. Hughes	1	1L			Soil and plant materials
Trichoderma sp.	6	5L, 7S			Mycoparasite
Trichophyton terrestre Durie and D. Frey	1	1S	Yes		Keratinophilic
Trichosporiella sp.	4	2L, 4S			Psychrophilic/psychrotrophic
T. multisporum Sigler and Currah	1	1S			Rhizosphere [R]
Tubercularia sp.	1	2S			Phytophilous [R]
Wardomyces sp.	3	4L, 2S			Coprophilous
W. humicola Hennebert and G.L. Barron	1	1S			Soil and plant materials
W. inflatus (Marchal) Hennebert	2	1L, 1S			Soil and plant materials
Zopfiella pleuropora Malloch and Cain	1	1S			Coprophilous [R]
Basidiomycota					
Asterotremella sp.	1	1L			On mushroom (*Asterophora*) [R]
Baeospora sp.	1	3L, 4S			Dead wood [R]
Basidiomycete unidentified	1	1S			Unknown
Cerrena unicolor (Bull.) Murrill	1	1S			Wood
Cystofilobasidium sp.	2	3S			Psychrophilic/psychrotrophic
Hormomyces aurantiacus Bonord.	1	1S			Decayed wood [R]
Leucosporidium fellii Gim.-Jurado and Uden	1	1L			Soil {R]
Pseudozyma sp.	1	1L, 1S			Unknown
Sporotrichum sp.	1	1L			Unknown
Trametes pubescens (Schumach.) Pilát	1	1L			Phytophilous [R]
Trichosporon sp.	3	4L, 1S	Yes	Yes	Psychrophilic/psychrotrophic
T. coprophilum Sugita, Takshima and Kikuchi	1	1S			Coprophilous [R]
T. dulcitum (Berkhout) Weijman	5	10L, 7S			Psychrophilic/psychrotrophic
T. lignicola var. *undulatum* (Diddens) Fell and Scorzetti	2	2L			Wood pulp [R]
Zygomycota					
Mortierella sp.	8	26L,12S	Yes	Yes	Cosmopolitan
Mucor sp.	7	25L, 11S	Yes	Yes	Cosmopolitan
Unidentified slime mold	3	3L			

[A]From Larcher et al. (2003), Chaturvedi et al. (2010), Courtin et al. (2010), Simonovicova et al. (2011), Veilleux (2008), and Voyron et al. (2011)
[B]From Zeller (1966) and Voyron et al. (2011)
[C]Genus only.