

Latitudinal, habitat and substrate distribution patterns of freshwater ascomycetes in the Florida Peninsula

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Abstract Freshwater ascomycetes are important decomposers of dead woody and herbaceous debris in aquatic habitats. Despite evidence of their ecological importance, latitudinal, habitat and substrate distributional patterns of freshwater ascomycetes are poorly understood. In this study, we examined the latitudinal and habitat distributional patterns, and substrate recurrences of freshwater ascomycetes by collecting dead submerged woody and herbaceous debris in lentic and lotic habitats at five selected sites along a north-central-south, temperate–subtropical latitudinal ecotone in Florida. One hundred and thirty-two fungal taxa were collected during the study. Seventy-four were meiosporic and 56 were mitosporic ascomycetes, while two species were basidiomycetes. Canonical analyses of principal coordinates (CAP) and Sørensen’s similarity index of species based on presence/absence data revealed a high turnover in species composition between the northern and southern sites, indicating a change in species composition along the temperate–subtropical latitudinal ecotone of the Florida Peninsula. Results from the ordination analysis indicated that freshwater ascomycete community composition is not significantly different between lentic and lotic habitats in Florida. The geographically broadly distributed species and species commonly found in Florida occurred in both habitats, whereas a number of new or rare species occurred in either lentic or lotic habitats, but not both. The same freshwater ascomycete species did not necessarily occur on both woody and herbaceous debris; of the 132 taxa collected, 100 were reported only on woody debris; 14 species occurred exclusively on herbaceous debris; and 18 species were found on both woody and herbaceous debris in lentic or lotic habitats. Implications of data from this study to the conservation and knowledge of biodiversity for freshwater ascomycetes is discussed.

Keywords Aquatic habitats · Biogeography · Freshwater fungi

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Introduction

Freshwater ascomycetes are an ecological assemblage of fungi that occur on submerged or partially submerged substrates in aquatic habitats (Shearer 1993, 2001; Vijaykrishna et al. 2006). Beginning with the pioneering studies by Ingold (1951, 1954, 1955, 1959, 1961, 1966, 1968) and Ingold and Chapman (1952), this group of fungi has been studied only in the last 50 years (Dudka 1963, 1985; Shearer 1993; Hyde et al. 1997; Shearer 2001; Goh and Hyde 1996; Tsui and Hyde 2003; Cai et al. 2006a, b; Vijaykrishna and Hyde 2006; Shearer et al. 2007). Most other groups of organisms, including other fungal groups, have a much longer taxonomic and distributional history. Since the pioneering studies by C.T. Ingold, 123 new genera and about 261 species of freshwater ascomycetes have been described and currently, about 548 ascomycete species have been reported from freshwater habitats located mostly in Europe, North America, and South East Asia (for additional literature see <http://www.life.uiuc.edu/fungi/>). Although these studies have revealed the existence of a distinct freshwater ascomycota, there is a lack of knowledge about the geographical and habitat distribution patterns and substrate specificities for individual species (Shearer 1993, 2001; Cai et al. 2003, 2006a, b; Shearer et al. 2007).

Although latitude is known to influence the geographical distribution patterns of plants and animals (Rosenzweig 1995), similar information for most fungi (Arnolds 2007) and specifically the freshwater ascomycetes is lacking (Shearer 1993, 2001). In contrast, the marine ascomycetes are relatively well-studied with respect to their biogeography (Hughes 1974; Kohlmeyer and Kohlmeyer 1979; Hyde and Lee 1995; Kis-Papo 2005). Hughes (1974) compiled geographical information on higher marine fungi using range maps of species' distributions. He concluded that the most important environmental parameter in their latitudinal distribution is temperature. Booth and Kenkel (1986) used ordination methods and suggested that both temperature and salinity play an important role in the distribution of lignicolous marine fungi.

The geographical occurrences of Ingoldian mitosporic ascomycetes, viz (=anamorph or asexual fungi) are relatively well-studied compared to those of the freshwater meiosporic ascomycetes. The Ingoldian mitosporic fungi most commonly occur on autumn shed leaves in streams and rivers (Webster and Descals 1981; Bärlocher 1992) and a subset of these fungi are also known to occur on wood (Willoughby and Archer 1973; Sanders and Anderson 1979; Révay and Gönczöl 1990; Shearer and Webster 1991; Shearer 1992). These fungi have conidia that are mostly branched, tetradiate or long, narrow and sigmoidal; morphologies considered to be adapted for life in flowing water (Ingold 1953, 1954, 1966, 1975, Read 1990; Goh and Hyde 1996; Wong et al. 1998). Wood-Eggenschwiler and Bärlocher (1985) used distribution data for over 150 species of Ingoldian mitosporic ascomycetes obtained from the literature (Webster and Descals 1981) and computed Sørensen's similarity index based on species presence or absence data from various geographical locations. They found that there was a higher similarity in species composition of Ingoldian fungi between geographically distinct tropical locations (South America, West Africa) than between tropical and temperate regions that were located on the same continent, either African or North and South American. From their study, Wood-Eggenschwiler and Bärlocher (1985) concluded, "on a worldwide scale, temperature together with its influence on vegetation in different climatic regions is the major factor in determining distribution patterns of Ingoldian mitosporic fungi". Since a number of freshwater Ingoldian mitosporic fungi are asexual states of freshwater ascomycetes (Shearer 1993, 2001; Sivichai and Jones 2003; <http://www.life.uiuc.edu/fungi/>), one might expect distribution patterns of freshwater ascomycetes to be similar to those of Ingoldian mitosporic fungi.

The geographical distribution patterns of freshwater ascomycetes, at present, are linked largely to the geographical distribution of the few mycologists who study this ecological group and the places they have sampled (Shearer 1993; Hyde et al. 1997; Sivichai 1999; Shearer 2001; Vijaykrishna et al. 2006; Shearer et al. 2007). Some freshwater ascomycetes are cosmopolitan in distribution, while others are reported only from their type localities (Shearer 1993, 2001; Cai et al. 2006a, b; <http://www.life.uiuc.edu/fungi/>). About 65% of the ascomycetes reported from freshwater habitats have been reported only once (Shearer et al. 2007). The fact that they are reported only once cannot be interpreted as being absent from other geographical areas, unless those areas have been intensively sampled. Ho et al. (2001) compared lignicolous freshwater ascomycete communities in lentic (e.g., lakes, ponds, and swamps) and lotic (e.g., streams and rivers) habitats in Australia, Brunei, Hong Kong, Malaysia, Seychelles, South Africa, and the UK. The authors used multivariate analysis to visualize the fungal community and found that there were distinct fungal communities between the temperate site (UK), subtropical sites (Hong Kong, South Africa), and tropical sites (Australia, Brunei, Malaysia, and Seychelles). These comparisons were made from a single collection site each in Australia, Brunei, Malaysia, Seychelles, and the UK and from six collection sites in Hong Kong. Since the comparisons did not differentiate between lentic and lotic habitats in their analyses, the differences in species composition might be due in part to the effect of habitat type as well as geography. In addition, the study by Ho et al. (2001) was a literature study using published data from studies that were conducted at different times by different investigators.

Due to the lack of comprehensive, directly comparable studies from different geographical locations, little can be said about the broad geographical distribution patterns of freshwater ascomycetes. At present, there are no large or medium spatial scale freshwater mycogeographic studies in a single geographical area that have examined the effects of latitudinal change to determine how this factor influences geographical distribution patterns and community composition of freshwater ascomycetes. Understanding changes in species composition along environmental gradients such as latitude can reveal important information regarding species distribution patterns.

To better understand the distribution of organisms, it is also important to recognize and characterize their associations with different habitat types. Variation in habitat type is often known to affect the movement, settlement and community composition of plants and animals (Morin 1999), but the influence of habitat type on freshwater ascomycete community composition is unexplored and poorly understood. A number of studies on freshwater ascomycetes have been conducted at single, spatially limited sites that were either lentic (Shearer and Crane 1986; Hyde and Goh 1998a; Goh and Hyde 1999; Cai et al. 2002; Luo et al. 2004; see Wong et al. 1998) or lotic habitats (Lamore and Goos 1978; Shearer and Von Bodman 1983; Hyde and Goh 1997; Hyde et al. 1998; Hyde and Goh 1998b; Hyde and Goh 1999; Ho et al. 2002; Sivichai et al. 2000, 2002; Tsui et al. 2001, 2003; Tsui and Hyde 2004; Kane et al. 2002; Cai et al. 2003; Fryar et al. 2004; González and Chavarría 2005; Vijaykrishna et al. 2006; see Wong et al. 1998). However, thus far, no studies have examined distribution of freshwater ascomycetes simultaneously in both lotic and lentic habitats to compare species composition between habitat types.

Most collections of freshwater ascomycetes have been made from submerged woody debris (Dudka 1963; Shearer 1972; Willoughby and Archer 1973; Lamore and Goos 1978; Minoura and Muroi 1978; Shearer and von Bodman 1983; Ho et al. 2001; Kane et al. 2002; Tsui et al. 2000, 2001; Raja et al. 2003, 2005; Raja and Shearer 2008; Vijaykrishna and Hyde 2006; also see <http://fungi.life.uiuc.edu/>). In addition to woody debris, freshwater ascomycetes have also been collected from a variety of emergent aquatic macrophytes,

such as *Carex*, *Equisetum*, *Juncus*, *Phragmites*, *Scirpus*, and *Typha*, which are common in lentic habitats, and backwaters of rivers, bogs and swamps (Shearer 1993; Dudka 1985; Magnes and Hafellner 1991; Fallah and Shearer 2001; Van Ryckegem and Verbeken 2005). Of the 548 species of freshwater ascomycetes reported thus far (<http://fungi.life.uiuc.edu/>), 60% are reported only from submerged woody debris and about 30% are reported only from herbaceous substrates, while only about 9–10% species are reported from both submerged wood and herbaceous substrates. This suggests that some degree of substrate specialization occurs. However, few investigators have collected both submerged woody and herbaceous debris at the same time to compare species composition on different substrates. Fallah (1999) collected freshwater ascomycetes from submerged woody and herbaceous debris from seven north temperate LTER (Long Term Ecological Research) lakes in Wisconsin. He found that Sordariomycetes occurred on wood and Dothideomycetes were more prevalent on herbaceous debris. He also found that species distributions in the LTER lakes were related to the distribution of the macrophyte species on which they occurred. Species found on submerged wood were not found on herbaceous debris and vice versa. Cai et al. (2003) collected both submerged wood and dead decaying bamboo in a river in the Philippines and found that the community composition of meiosporic and mitosporic ascomycetes differed between the two substrates. Of the 80 species reported in their study, only 16 taxa occurred on both submerged wood and bamboo, and fewer taxa occurred on bamboo than on wood. A high similarity in species composition was found when Luo et al. (2004) compared occurrences of freshwater fungi on three different monocotyledon herbaceous substrates. However, Luo's study revealed differences in species relative abundance between the fungal communities on different herbaceous substrates. These foregoing studies suggest that substrate type is important in the distribution of freshwater ascomycetes, but additional comparative studies from different geographical areas are needed to better understand the role of substrate specificity in the geographical distribution patterns of freshwater ascomycetes.

Without adequate knowledge about the environmental factors that determine species distribution patterns, accurately assessing the diversity of freshwater ascomycetes is not possible. Efforts to develop rational plans to conserve this group of important saprobic fungi are hindered by this lack of information. To obtain baseline comparative distribution data, the following study was undertaken.

The objective of this study was to address the following questions about the distribution patterns of freshwater ascomycetes: (1) Does the species composition of freshwater ascomycete communities differ among sites at different latitudes along the temperate–subtropical ecotone of the Florida Peninsula? (2) Does the species composition of freshwater ascomycete communities differ between lentic and lotic habitats in Florida? (3) Do the same freshwater ascomycete species occur on both woody and herbaceous debris?

Methods

Description of study sites

The Florida Peninsula was selected as the location for this study because of its large number of freshwater lentic and lotic habitats, including 7,800 lakes and 1,700 rivers and streams (Whitney et al. 2004). In addition, the Florida Peninsula is a biotic transition zone between the warm temperate and subtropical zones based on climatic and biotic data (Henry et al. 1948). Because the peninsula is long, climatic conditions vary somewhat



Fig. 1 Study area. The *solid dots* indicate the locations of the five collection sites within the Florida Peninsula; *scale* indicates latitudes where sites were located

north to south. Florida lies within the temperate zone but the climate is subtropical in south Florida (Henry et al. 1948), providing a unique region to investigate hypotheses about freshwater fungal diversity and distribution. In addition, Florida is a known area of high biodiversity for other organisms (Whitney et al. 2004). Prior to this study, however, only three species of freshwater ascomycetes had been reported from Florida (Conway and Barr 1977; Shearer and Crane 1995; Anderson and Shearer 2002).

Five collection sites were chosen in north, central and south Florida based on a latitudinal ecotone along the Florida Peninsula (Fig. 1): (1) Blackwater River State Forest (BW) (30°N latitude), (2) Apalachicola National Forest (AP) (30°N latitude), (3) Ocala National Forest (OC) (29°N latitude), (4) Big Cypress National Preserve (BC) (25°N latitude), and (5) Everglades National Park (EV) (25°N latitude).

According to Platt and Schwartz (1990), the panhandle forests (BW and AP) are southern hardwood forests, the central peninsula forest (OC) is a temperate broad-leaved evergreen forest, and south Florida forests (BC and EV) are subtropical forests. Tropical hardwood hammocks are seen predominately in the BC and EV. These five sites were chosen because (a) they are located across a temperate and subtropical ecotone along the Florida Peninsula (Question 1), and (b) they are rich in a variety of lentic and lotic habitats, so collections can be made from both habitat types and woody and herbaceous debris can be collected within the same area in each site (Questions 2, 3). In addition, for the region where the study sites are located, Beaver et al. (1981) found that the lentic habitats differ on the basis of temperature and categorized these habitats by their thermal properties into north (warm temperate), central (transitional) and south (subtropical).

Sampling procedure

Submerged, dead woody and herbaceous debris was collected randomly from lentic and lotic habitats, four times over 2 years. Sampling times included two summer (wet season) and two winter (dry season) collections at the five sites within the Florida Peninsula from 2004 to 2006. Both woody and herbaceous debris (dead, decaying emergent macrophytes)

were collected. Equal amounts of debris were collected (about 15 pieces of each depending on availability) from each site. In lotic habitats, such as a stream or river, collections were made along an imaginary transect 100 meters upstream and downstream at a collection site. In lentic habitats, collections were made from around the littoral zone from depths of about 0.5–1.0 m. Efforts were made to identify and collect substrates that had been submerged in water for a considerable time. This was estimated by observation of the degree of softening by fungal soft-rot and colonization by other aquatic organisms. Samples were placed in zippered plastic bags containing moist paper towels and transported to the lab in an insulated cooler containing ice to reduce heat build-up and biological activity. Water temperature was recorded in the field with a thermometer; pH was measured with an IQ125 miniLab pH meter and Fisher pH strips; and latitude and longitude were measured using a Garmin global positioning system (GPS). In the lab, substrates were gently rinsed with tap water and incubated in plastic storage boxes with moistened paper towels at ambient temperatures (about 24°C) under 12/12 h (light/dark) conditions.

Morphological observations

Samples were examined with a dissecting microscope within one to two weeks of collection and periodically over 6–12 months (Shearer 1993; Shearer et al. 2004). After sporulating fungi were located on natural substrates or isolation media using the dissecting microscope, ascomata were opened in a drop of distilled water on a large (25 mm) cover slip on a slide using fine dissecting needles, and then covered with a second smaller (18 mm) cover slip. Ascomycetes were identified based on the morphology and anatomy of the ascomata and the morphology of the hamathecium, asci, and ascospores. Melzer's reagent (0.5 g iodine, 1.5 g KI, 20 g chloral hydrate, 20 ml distilled water), and aqueous cotton blue was used to determine staining reactions of the ascus apical apparatus. India ink or aqueous nigrosin was added to water mounts to reveal gelatinous sheaths on or around ascospores as well as gelatinous material surrounding the paraphyses or pseudoparaphyses. Mitosporic ascomycetes were identified using the type of conidiogenesis and conidial morphology. Measurements were made of material mounted in distilled water, glycerin (100%) or lactic acid containing azure A. Material mounted on slides was preserved with glycerin (100%) or lactic acid (85%) using the double cover glass method (Volkmann-Kohlmeyer and Kohlmeyer 1996). Whenever, possible freshwater ascomycetes were isolated in pure culture using procedures outlined in Fallah and Shearer (2001) and Shearer et al. (2004). Slides and specimens of fungi collected during the study are deposited in the Herbarium of the University of Illinois (ILL).

Data preparation

A site by species matrix based on presence or absence data was constructed. Within this matrix, sites (aquatic habitats) were the column variables and species were the row variables. Each cell contained "1" if a particular species was present at that site, and "0" if it was not. The matrix contained records of all the occurrences of 132 fungal species in 97 sites.

Multivariate statistical analysis

Data were analyzed using canonical analysis of principal coordinates (CAP; Anderson and Willis 2003). CAP is a multivariate constrained ordination technique in which an initial

principal coordinates analysis (PCO) is used to reduce the number of axes in the analysis. A further analysis is then conducted on the matrix produced by the PCO. A canonical discriminant functional analysis (=discriminant analysis) was used in this study for questions 1 and 2 to test if the data matrix is structured according to the grouping variables, representing either latitude (N–C–S) (Question 1) or habitat (lentic vs. lotic) (Question 2) as detailed below. One of the benefits of using CAP is that it uses permutation tests (trace statistic, 1st squared canonical correlation) to assign a *P*-value to the a-priori hypothesis by determining the probability that the grouping found in the final analysis could arise by chance alone. The CAP method, therefore, allows the objective evaluation of a hypothesis. In addition, a Canonical Correlation Analysis (CCA) was employed to test if variation in community composition is explained by water pH and/or latitude. The CCA analysis was part of the CAP ordination. Separate analyses were conducted for pH and latitude, followed by an analysis of the combined pH and latitude data. For the CCA analysis, pH values from different collection dates at a single site were transformed to log scale, averaged and then transformed to antilog and used in the CCA analysis. Canonical analysis of principal coordinates has been used recently for analyzing the distribution patterns of aquatic mangrove fungi (Schmit and Shearer 2004) and Ingoldian mitosporic ascomycetes (Nikolcheva and Bärlocher 2005).

All analyses were performed using CAP software, freely available at the Ecological Society of America's Ecological Archives (E084-011-S1; <http://esapubs.org/archive/ecol/E084/011/suppl-1.htm>). All analyses were performed using "Gower excluding double zero" (Gower 1971; Legendre and Legendre 1998) as the distance measure.

Latitudinal distribution

The CAP analysis was used to test the hypothesis that there are differences in the freshwater ascomycete fungal communities between sites at different latitudes (north, central and south) in Florida. A significant result indicates fungal communities differ along the latitudinal gradient sampled.

In addition to the CAP analysis, fungal similarity among different collections sites (N–C–S) was calculated using Sørensen's similarity index (Sørensen 1948; Magurran 1988, 2004).

Habitat distribution

The CAP was used to test the hypothesis that there are consistent differences in freshwater ascomycete species between lentic and lotic habitats. To test this hypothesis, lentic and lotic collection sites from north, central, and south Florida were analyzed with CAP. A significant result indicates that fungal communities differ between habitat types.

Two CAP analyses were performed. The first analysis contained species presence or absence data from all the 97 habitats sampled along the Florida Peninsula, with 26 lotic and 71 lentic habitats. Since the results of the CAP analyses containing an unequal number of habitats could bias the result of the ordination graph, a second analysis was performed in CAP using habitat data from BW and AP (northern collection sites) because approximately equal number of habitat types were sampled in these sites. In the second CAP analyses, presence or absence data of species from 21 lotic and 27 lentic habitats were included.

Results

A total of 97 habitats were sampled at the five collection sites in Florida. Appendix 1 shows the latitudes and longitudes, water temperatures and pH measured during the study. Maximum and minimum ranges of water temperature and pH values from the five collection sites are listed in Appendix 2. In both years of collection, the lowest water temperatures were recorded in winter at the northern sites, and the highest water temperatures were recorded for the southern sites. The water temperatures recorded at the central site were intermediate between those of the northern and southern sites. However, in summer, the water temperature differential along the latitudinal ecotone disappeared, probably due to the tropical circulation pattern of the Caribbean that influences the climate of the entire Florida Peninsula (Beaver et al. 1981), and the water temperature along the entire peninsula becomes generally warmer with an average of about 30°C.

One hundred and thirty-two species of fungi were collected during the study (Table 1). Seventy-four are meiosporic and 56 are mitosporic ascomycetes, while two species, *Rogersiomyces okefenokeensis* and *Ingoldiella hamata*, are basidiomycetes. Of the 74 meiosporic ascomycetes, 28 are Dothideomycetes, 44 are Sordariomycetes, and two taxa belong to the Leotiomycetes. Of the 132 taxa collected, 12 species and two genera were new to science (Raja and Shearer 2006a, b, 2007; Raja et al. 2008, in press; Raja and Shearer 2008), 26 taxa are new records for North America and 127 taxa are new records from aquatic habitats in Florida (Table 1). *Ayria appendiculata*, *Falciformispora lignatilis*, and *Trematosphaeria lineolatispora* are new records for fresh water.

Among the mitosporic ascomycetes collected, six species, *Brachiosphaera tropicalis*, *Condylospora* sp., *Dendrospora* sp., *Ingoldiella hamata*, *Nawawia filiformis*, and *Vari-cosporium* sp., are Ingoldian mitosporic ascomycetes; three species, *Cancellidium applanatum*, *Helicodendron* sp., and *Helicoon auratum* are aeroaquatic fungi, and the remaining 49 species belong to the miscellaneous mitosporic fungi (Shearer et al. 2007). All of the mitosporic fungi found belong to the ascomycetes, except *I. hamata*, which is a basidiomycete (Shaw 1972).

Distribution patterns along the latitudinal ecotone

Analysis using CAP revealed latitudinal structuring of freshwater fungal communities along the Florida Peninsula (Fig. 2). North, central and south sites in Florida formed three clusters on the ordination graph. The northern and central sites are slightly closer to one another than either is to the southern cluster. The analysis found two canonical axes. Permutation tests provided statistical support for the hypothesis of latitudinal structuring of freshwater fungal communities (trace statistic = 1.341, $P < 0.01$; 1st squared canonical correlation = 0.72, $P < 0.01$).

Sørensen's coefficient of similarity

Species similarity was greatest between the two northern sites (BW and AP 42%) and between the two southern sites (BC and EV 34%) (Table 2). The northern sites BW and AP also shared some similarity with the central site OC (31 and 32%, respectively). The least similarity (13%) occurred between the northernmost site (BW) and the two southern sites (BC and EV).

Table 1 Total numbers of fungal species and the number of times they were collected at each of the five sites along the Florida Peninsula

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Dothideomycetes</i>					
<i>Aliquandostipite minuta</i> Raja & Shearer ^a					1
<i>Aliquandostipite crystallinus</i> Raja, Ferrer & Shearer ^b					1
<i>Aliquandostipite khaoyaiensis</i> Inderb. ^c					1
<i>Aliquandostipite siamensiae</i> (Sivichai & E.B.G. Jones) J. Campbell, Raja, Ferrer, Sivichai & Shearer ^c					1
<i>Boerlagiomyces websteri</i> Shearer & J.L. Crane		2	1	6	2
<i>Caryospora obclavata</i> Raja & Shearer ^a		1			
<i>Caryospora langloisii</i> Ell. & Everh. ^b			1		
<i>Falciformispora lignatilis</i> K.D. Hyde ^b			1		1
<i>Jahmula aquatica</i> (Plöttner & Kirschst.) Kirschst. ^b			1		
<i>Jahmula australiensis</i> K.D. Hyde ^c				1	
<i>Jahmula bipileata</i> Raja & Shearer ^a	1	1			
<i>Jahmula bipolaris</i> (K.D. Hyde) K.D. Hyde ^c				1	
<i>Jahmula potamophila</i> K.D. Hyde & S.W. Wong ^c		1			
<i>Jahmula rostrata</i> Raja & Shearer ^a	1		2	1	1
<i>Jahmula sangamonensis</i> Shearer & Raja ^b		1		1	
<i>Kirschsteiniothelia elaterascus</i> Shearer ^b		1	1	1	1
<i>Lepidopterella palustris</i> Shearer & J.L. Crane ^b		2			
<i>Lepidopterella tangerina</i> Raja & Shearer ^a	1				
<i>Massarina bipolaris</i> K.D. Hyde ^c		1	2		1
<i>Massarina fronsisubmersa</i> K.D. Hyde ^c	1				
<i>Massarina ingoldiana</i> Shearer & K.D. Hyde ^b	1	8			
<i>Micropeltopsis</i> sp. F115	1				
<i>Ophiobolus shoemakeri</i> Raja & Shearer ^a			2		
<i>Trematosphaeria lineolatispora</i> K.D. Hyde ^b			1	4	1
Undescribed <i>Massarina</i> sp. F60		2			
Undescribed <i>Massarina</i> sp. F65					1
Undescribed <i>Massarina</i> sp. F80		1			
Undescribed genus F76		1	1		
<i>Leotiomyces</i>					
<i>Aquapoterium pinicola</i> Raja & Shearer ^d	3	1	2		
<i>Gorgoniceps</i> sp. F72					1
<i>Sordariomycetes</i>					
<i>Aniptodera aquadulcis</i> (S.Y. Hsieh, H.S. Chang & E.B.G. Jones) J. Campb., J. Anderson & Shearer ^b			1		
<i>Aniptodera chaesapeakensis</i> Shearer & Miller ^b			1		
<i>Aniptodera inflatiascigera</i> K.M. Tsui, K.D. Hyde & I.J. Hodgkiss ^c	1		3	1	
<i>Aniptodera lignatilis</i> K.D. Hyde ^c	2	3	1		
<i>Aniptodera megaloscocarpa</i> Raja & Shearer ^a			1		
<i>Aniptodera palmicola</i> K.D. Hyde, W.H. Ho & K.M. Tsui ^b			2	6	1

Table 1 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Annulatascus velatisporus</i> K.D. Hyde ^b	6	1	7	2	
<i>Arnium gigantosporum</i> Raja & Shearer ^a			1		
<i>Ascitendus austriacus</i> (Réblová, Winka & Jaklitsch) J. Campb. & Shearer ^b	3	3			
<i>Ascosacculus heteroguttulatus</i> (S.W. Wong, K.D. Hyde & E.B.G. Jones) J. Campb., J.L. Anderson & Shearer ^b	2	2	1		1
<i>Ascotaiwania hsilio</i> H.S. Chang & S.Y. Hsieh ^b	1			1	
<i>Ayria appendiculata</i> Fryar & K.D. Hyde ^c		1			
<i>Catactispora bipolaris</i> (K.D. Hyde) K.D. Hyde, S.W. Wong & E.B.G. Jones ^c			1		
<i>Cyanoannulus petersenii</i> Raja, J.Campb. & Shearer ^b	4	1			
<i>Fluviatispora reticulata</i> K.D. Hyde ^c	2	5	3		
<i>Flammispora pulchra</i> Raja & Shearer ^a			1		
<i>Hanliniomyces hyaloapicalis</i> Raja & Shearer ^d	2			1	
<i>Jobellisia luteola</i> (Ellis & Everh.) M.E. Barr ^b	3	3			
<i>Lockerbia striata</i> Raja & Shearer ^a	1	1			
<i>Luttrellia estuarina</i> Shearer ^b		1			
<i>Luttrellia</i> sp. F14			1		
<i>Lulworthia</i> sp. F54			1		
<i>Nais inornata</i> Kohlm.	1	5	3		1
<i>Natantispora retorquens</i> (Shearer & J.L. Crane) J. Campb., J.L. Anderson et Shearer ^b	2	1			
<i>Ophioceras commune</i> Shearer, J.L. Crane & Chen ^b		2	2		
<i>Phaeonectriella lignicola</i> R.A. Eaton & E.B.G. Jones ^b			2		
<i>Phomatospora triseptata</i> Raja & Shearer ^a				1	
<i>Pseudoproboscispora caudae-suis</i> (Ingold) J. Campbell & Shearer ^b	3				
<i>Physalospora limnetica</i> Raja & Shearer ^a		1			
<i>Savoryella aquatica</i> K.D. Hyde ^b			2	1	
<i>Savoryella fusiformis</i> W.H. Ho, K.D. Hyde & I.J. Hodgkiss ^c					2
<i>Submersisphaeria aquatica</i> K.D. Hyde ^b	15	6		1	
<i>Torrentispora fibrosa</i> K.D. Hyde, W.H. Ho, E.B.G. Jones, K.M. Tsui & S.W. Wong ^b	2	1	2		
<i>Verticicola caudatus</i> K.D. Hyde, S.W. Wong & V.M. Ranghoo ^b	1		1		
<i>Zopfiella latipes</i> (N. Lundq.) Malloch & Cain ^b	3		1	1	
<i>Zopfiella lundqvistii</i> Shearer & J.L. Crane ^b		2			
Unidentified ascomycete sp. F28		1			
Undescribed sp. F41		2			
Undescribed genus F44		1			
Undescribed genus F50		1			
Undescribed sp. F57	2				
Undescribed genus F99			1		
Undescribed sp. F100			1		
Undescribed sp. F107			2		
<i>Basidiomycetes</i>					

Table 1 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Rogersiomyces okefenokeensis</i> J.L. Crane & Schoknecht ^b			1		
<i>Mitosporic fungi</i>					
<i>Acrogenospora sphaerocephala</i> (Berk. and Broome) M. B. Ellis ^b	1	1	1		1
<i>Ardhachandra cristaspora</i> (Matsush.) Subram. & Sudha ^c			1		
<i>Bactrodesmium linderi</i> (J.L. Crane & Shearer) M.E. Palm & E.L. Stewart ^b		4	2	3	1
<i>Berkleasium concinnum</i> Berk. (S. Hughes) ^b			1		
<i>Brachiosphaera tropicalis</i> Nawawi ^c					1
<i>Brachysporium obovatum</i> Kiessl ^b			1		
<i>Cancellidium applanatum</i> Tubaki ^b	7	8	1		
<i>Canalisporium caribense</i> (Hol.-Jech. & Mercado) Nawawi & Kuthub. ^c					1
<i>Canalisporium kenyense</i> Goh, W.H. Ho, K.D. Hyde, S.R. Whitton & T.E. Umali ^b			1		
<i>Cacumisporium sigmoideum</i> Mercado & R.F. Castañeda ^b			3	1	
<i>Chaetospermum camelliae</i> Agnihotr. ^c			1	1	2
<i>Coleodictyospora micronesia</i> (Matsush.) Matsush.				1	1
<i>Cordana abramovii</i> Seman & Davydkina var. <i>seychellensis</i> K.D. Hyde & Goh ^b		1			
<i>Condylospora</i> sp. FH 34			1		
<i>Cryptophiale cucullata</i> Kuthub. ^b	1				
<i>Dactylaria hyalotunicata</i> K.M. Tsui, Goh & K. D. Hyde ^c	1	1			
<i>Dactylaria tunicata</i> Goh & K.D. Hyde ^b	6	1			
<i>Delortia palmicola</i> Pat. ^b			5		
<i>Dendrosporium lobatum</i> Plakidas & Edgerton ex J.L. Crane ^b			1		
<i>Dendrospora</i> sp. FH 87			1		
<i>Dictyosporium</i> sp. FH39	1				
<i>Dictyosporium digitatum</i> J.L. Chen, C.H. Hwang & S. S. Tzean ^c		2		2	3
<i>Dictyosporium elegans</i> Corda ^b		1			
<i>Dictyosporium giganticum</i> Goh & K.D. Hyde ^b					1
<i>Dictyosporium heptasporium</i> (Garov.) Damon ^b				1	
<i>Ellisembia abscondens</i> (Berk.) Subram. ^b		1	2		1
<i>Exserticlava globosa</i> Roa & de Hoog ^c		1			
<i>Exserticlava triseptata</i> (Matsush.) S. Hughes ^c		1	1		
<i>Exserticlava vasiformis</i> (Matsush.) S. Hughes ^c	2		3		
<i>Helicodendron</i> sp. FH38		3			
<i>Helicoon auratum</i> (Ellis) Morgan ^b		1			
<i>Helicomycetes roseus</i> Link ^b		3			1
<i>Helicosporium aureum</i> (Corda) Linder ^b			1		
<i>Helicosporium guianense</i> Linder ^b			1		
<i>Helicosporium gigasporum</i> K.M. Tsui, Goh, K.D. Hyde & Hodgkiss ^b		3	2		
<i>Helicosporium lubricopsis</i> Linder ^b			1		
<i>Humicola asteroidea</i> Udagawa & Y. Horie ^b	1				
<i>Ingoldiella hamata</i> D.E. Shaw ^c	1				
<i>Intercalarispora</i> sp. FH88		1			

Table 1 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Monacosporium ellipsosporum</i> (Preuss) R.C. Cooke & C.H. Dickinson ^b			2		
<i>Monotosporella</i> sp. FH20	3		1		
<i>Melanocephala australiensis</i> G.W. Beaton & M.B. Ellis ^b		1			
<i>Nawawia filiformis</i> (Nawawi) Marvanová ^c					1
<i>Pleurophragmium malaysianum</i> Matsush. ^c	9	2	2		
<i>Pleurothecium recurvatum</i> (Morgan) Höhn. ^b		1			
<i>Septonema hormiscium</i> Sacc. ^b	1	1			
<i>Speiropsis</i> sp. FH59			1		
<i>Sporidesmiella hyalosperma</i> var. <i>novae-zealandiae</i> ^b (S. Hughes). P.M. Kirk		1			
<i>Sporidesmium tropicale</i> M.B. Ellis ^b		1			
<i>Sporidesmium</i> sp. FH27		1			
<i>Sporoschisma saccardoii</i> Mason & S. Hughes ^b			1	1	
<i>Tetraploa aristata</i> Berk. & Broome					1
<i>Thozetella</i> sp.	1				
<i>Vargamyces</i> sp. FH86		1			
<i>Varicosporium</i> sp. FH22			1		
<i>Wiesneriomyces larinus</i> (Tassi) P.M. Kirk ^b			1	1	
<i>Xylomyces chlamydosporus</i> Goos, R.D. Brooks & Lamore ^b	1	3	3		
Total number of samples collected ^e	52	41	49	25	13
Species richness	41	59	63	33	19

BW Blackwater River State Forest, AP Apalachicola National Forest, OC Ocala National Forest, BC Big Cypress National Preserve, EV Everglades National Park

^a New species described in this study

^b New records for Florida

^c New records for North America and Florida

^d New genus described in this study

^e Each collection consisted of about 20–30 samples of wood and herbaceous debris depending on availability

Habitat distribution

Based on the presence or absence data in a site by species matrix, analyses using CAP provided some separation of freshwater fungal communities based on lentic and lotic sites, with some lentic habitats forming a separate cluster from the lotic habitats on the ordination graph (Fig. 3). However, there was not enough evidence to support distinct cluster formation between lentic and lotic habitats. The analysis found one canonical axis. Permutation tests did not provide statistical support for the hypothesis that fungal communities in lentic and lotic habitats are distinctly different (trace statistic = 0.5108, $P > 0.05$; 1st squared canonical correlation = 0.5108, $P > 0.05$). An additional CAP analysis between lentic and lotic habitats in northern Florida, where the number of lentic and lotic sites were more similar, also showed some separation between habitats (Fig. 4), but again, permutation tests did not provide statistical support. The analysis found a single

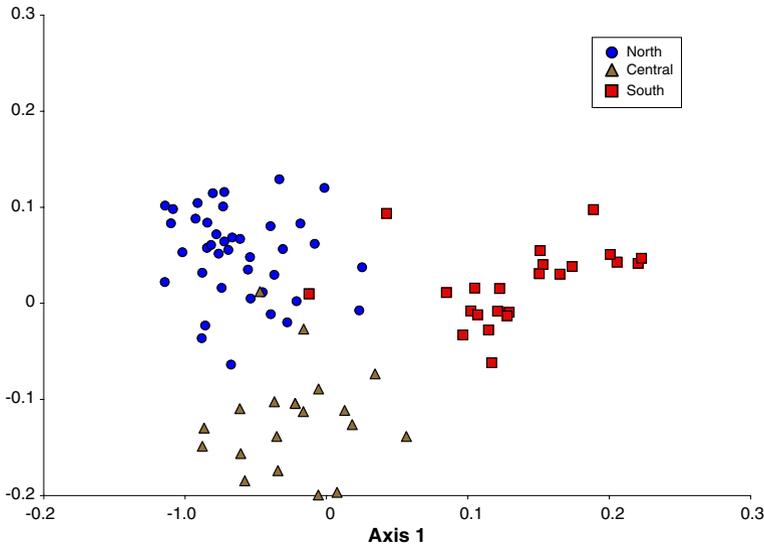


Fig. 2 Canonical analysis of principal coordinates (CAP) of fungal communities in freshwater habitats based on latitudinal ecotone along north, central and south Florida ($n = 97$)

Table 2 Index of Sørensen’s similarity among five collection sites

Sites	BW	AP	OC	BC	EV
BW	–	0.42	0.31	0.13	0.13
AP		–	0.32	0.17	0.20
OC			–	0.25	0.21
BC				–	0.34
EV					–

canonical axis (trace statistic = 0.4643, $P > 0.05$; 1st squared canonical correlation = 0.4643, $P > 0.05$).

Seventy-five species were collected only from lentic habitats, 16 species were collected only from lotic habitats, and 41 species were collected from both lentic and lotic habitats (Appendix 3). Numerous species of freshwater ascomycetes, including *Boerlagiomyces websteri*, *Jahnula rostrata*, *J. sangamonensis*, *Lepidopterella palustris*, *Trematosphaeria lineolatispora*, Undescribed *Massarina* sp. F60, *Aquapoterium pinicola*, *Aniptodera lignatilis*, *A. palmicola*, *Annulatascus velatisporus*, *Ascitendus austriacus*, *Ascosacculus heteroguttulatus*, *Cyanoannulus petersenii*, *Fluviatispora reticulata*, *Hanliniomyces hyaloapicalis*, *Nais inornata*, *Natantisporea retorquens*, *Ophioceras commune*, *Submersisphaeria aquatica*, *Torrentisporea fibrosa*, *Verticicola caudatus*, *Zopfella latipes*, and *Z. lundqvistii* occurred in both lentic and lotic habitats. A number of these species also occurred frequently and were reported from more than one collection site along the Florida Peninsula (Table 1; Appendix 3).

Aliquandostipite minuta, *Arnium gigantosporum*, *Caryospora obclavata*, *Flammispora pulchra*, *Lockerbia striata*, *Ophiobolus shoemakeri*, *Phomatospora triseptata*,

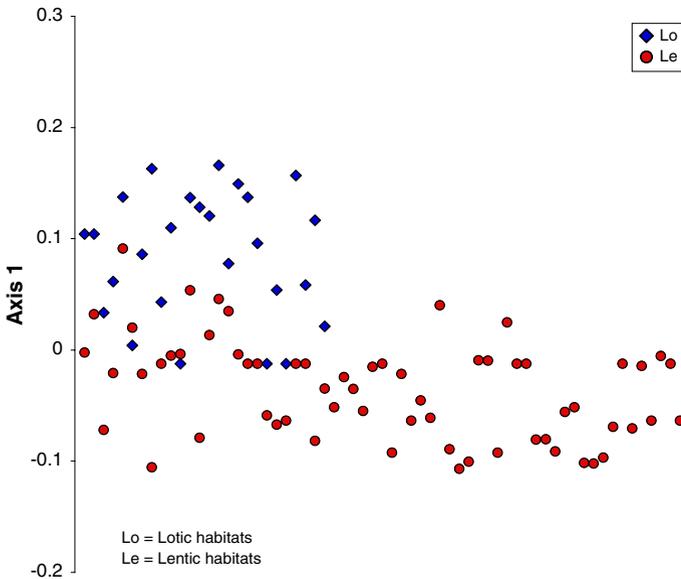


Fig. 3 Canonical analysis of principal coordinates (CAP) of fungal species in freshwater habitats based on lotic and lentic habitat type ($n = 97$). Lo = Lotic habitats, Le = Lentic habitats

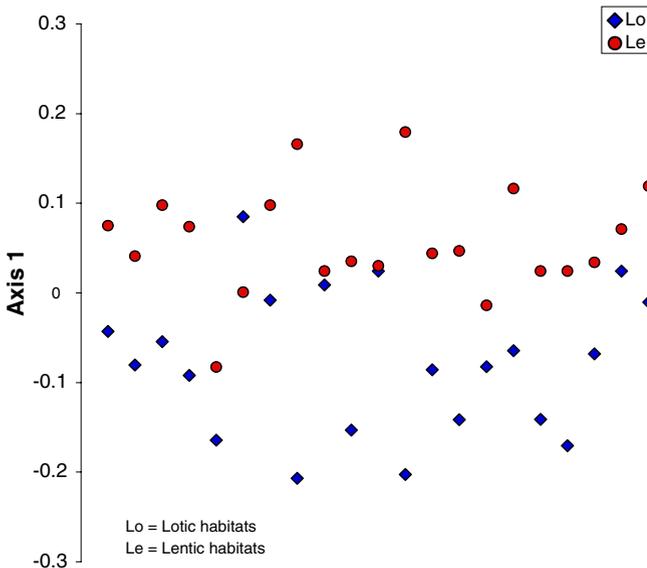


Fig. 4 Canonical analysis of principal coordinates (CAP) of fungal species in freshwater habitats based on lotic and lentic habitat type in north Florida ($n = 48$). Lo = Lotic habitats, Le = Lentic habitats

Physalospora limnetica, undescribed *Massarina* sp. F65, F80, undescribed sp. F41, F44, F99, F100, and F107 were collected only from lentic habitats. Whereas, two undescribed genera, F76 and F50, were collected exclusively from lotic habitats (Appendix 3).

Substrate distribution

One hundred of the 132 species collected from Florida were recorded only on woody debris, 14 species only on herbaceous debris, and 18 species occurred on both herbaceous and woody debris (Appendix 3). Freshwater ascomycetes, such as *O. shoemakeri* and *P. limnetica*, were collected exclusively from herbaceous debris in lentic habitats. *Aquapoterium pinicola*, collected only from pine needles, was found in both lentic and lotic habitats. Other taxa that occurred only on herbaceous debris include some freshwater mitosporic ascomycetes such as *Ardhachandra cristaspora*, *Coleodictyospora micronesia*, *Cryptophiale cucullata*, *Dendrosporium lobatum*, *Sporidesmium* sp., and *Tetraploa aristata*.

Eighteen species occurred on both herbaceous and woody debris and may be substrate generalists. Among these, *Annulatascus velatisporus*, *Ascitendus austriacus*, *Ascocaculus heteroguttulatus*, *Bactrodesmium linderi* and *Cancellidium applanatum* were the most commonly occurring species during the study and were found in more than two collection sites in both lentic and lotic habitats along the Florida Peninsula (Appendix 3). Species that occurred on both woody and herbaceous debris usually occurred on herbaceous debris in lentic habitats. Two exceptions are *A. austriacus* and a new undescribed fungus (F76) that occurred on herbaceous debris in lotic habitats.

Relationship of freshwater ascomycete community composition to pH and latitude

When community composition was examined as a function of latitude and pH separately (Figs. 5, 6), both these variables remained significant as determinants of variation in community composition. Canonical correspondence analyses with pH as the variable found one canonical axis (trace statistic = 0.462131, $P < 0.05$; 1st squared canonical correlation = 0.462131, $P < 0.05$) and pH explained about 40% of the variation (Fig. 5). Canonical correspondence analyses with latitude also found one canonical axis (trace

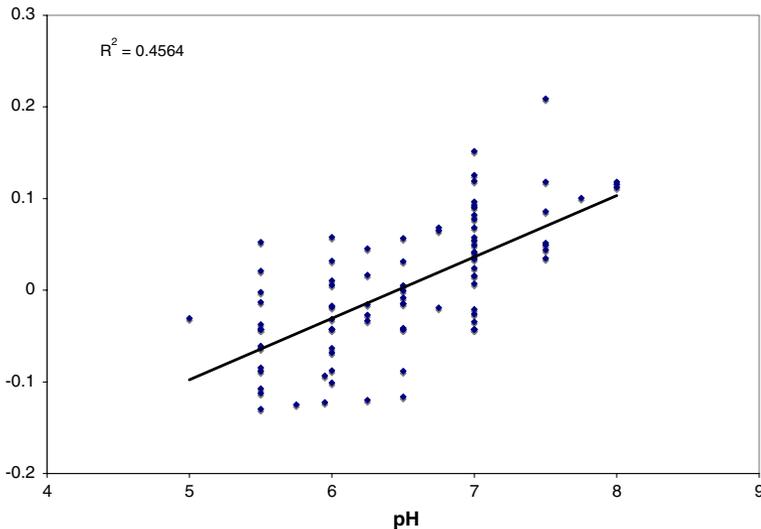


Fig. 5 Canonical correlation analysis using CAP to explain the relationship of freshwater fungal species with pH ($n = 97$)

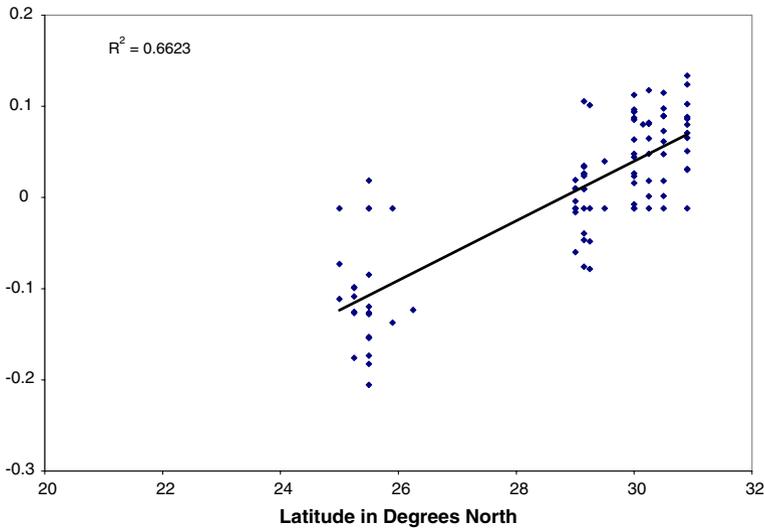


Fig. 6 Canonical correlation analysis using CAP to explain the relationship of freshwater fungal species with latitude ($n = 97$)

statistic = 0.620395, $P < 0.01$; 1st squared canonical correlation = 0.620395, $P < 0.01$) and latitude explained about 60% of the variation (Fig. 6). Ordination analysis also provided some evidence of interaction of both pH and latitude as explanatory variables in determining variation in community composition. The analysis found two canonical axes with significant statistical support (trace statistic = 1.123, $P < 0.01$; 1st squared canonical correlation = 0.664, $P < 0.01$). The freshwater fungal communities showed some separation based on both latitude (vertical axis) and pH (horizontal axis) on the ordination graph (Fig. 7). The southern sites formed a cluster distinct from the northern and central sites on axis 2 (vertical axis) and colors representing low pH values < 6.5 are at the top, the middle pH values are mostly in the middle and the high pH values are almost all at the bottom of the ordination graph (Fig. 7).

Discussion

Latitudinal distribution patterns along the temperate–subtropical ecotone in Florida

This study demonstrates that species composition of freshwater ascomycete communities differs along the temperate–subtropical ecotone in the Florida Peninsula. The differences in species composition are resolved in the ordination graph as three different clusters shown as north, central and south (Fig. 2). Species composition in the north and central sites are more similar to one another than either is to the southern sites. High turnover in species composition is indicated by the lower similarity values between the northern and southern sites, than between the northern and central sites (Table 2). The results of the canonical correspondence analysis for latitude (Fig. 7) are somewhat consistent with the results of discriminant function analysis (Fig. 2), which shows the freshwater fungal communities in north and central Florida are clustered closer together than to those in south Florida. For

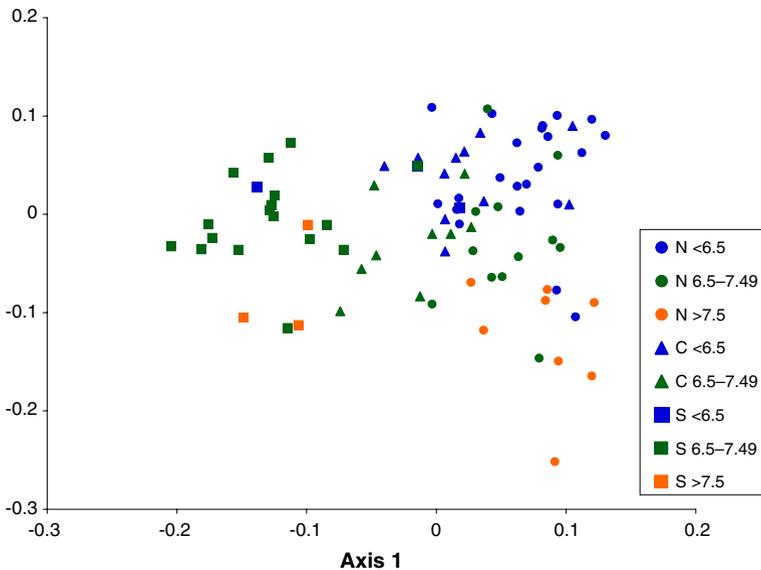


Fig. 7 Canonical correlation analysis (CCA) to explain the relationship of freshwater fungal species with pH and latitude ($n = 97$)

example, freshwater ascomycetes, *Lepidopterella palustris*, *L. tangerina*, *A. austriacus*, *Jobellisia luteloa*, *Lockerbia striata*, *Pseudoproboscispora caudae-suis*, F41, and F57 occurred only in north Florida sites, but were absent from south Florida. On the other hand, *Aliquandostipite minuta*, *A. khaoyaiensis*, *A. siamensis*, *Jahnula bipolaris*, and *J. australiensis*, and mitosporic ascomycetes, *Coleodictyospora micronesia*, *Canalisporium caribense*, *Brachiosphaera tropicalis*, *Dictyosporium heptasporum*, and *Nawawia filiformis* occurred in the southern sites, but were completely absent from the northern sites in Florida (Table 1). The above species recorded from south Florida have been reported previously from the paleotropics and subtropics as well as from freshwater habitats in the neotropics (<http://fungi.life.uiuc.edu/>).

Previous studies on aquatic fungi have also revealed differences in species composition along latitudinal zones that differ in climatic conditions. Miura (1974) conducted a study of freshwater Ingoldian mitosporic ascomycetes in Japan along a group of islands that were located along a latitudinal gradient from 45°N, 37°N, and 25°N and found that the species composition showed a pronounced change along the subtropical collection sites. He also found that the species composition of Ingoldian fungi in streams sampled at the northern latitudes were more similar to each other than either of them was to the southern subtropical region in Japan. Shearer and Burgos (1987) found a change in species composition of lignicolous marine fungi along collection sites between north, central and south Chile. They found that some species occurring in northern subtropical Chile did not occur in the anti-boreal southern part of Chile. For marine fungi studied along a wider latitudinal gradient, Hughes (1974) and Booth and Kenkel (1986) also found that temperature was an important environmental parameter in explaining the latitudinal distribution patterns of marine fungi. Similarly, Taylor et al. (2000) and Fröhlich and Hyde (2000) found the palm saprobes from sites of the same latitude/longitude were more similar than sites from different latitudes.

Differences in species composition observed in this study are also similar to patterns observed for other groups of organisms sampled along the temperate–subtropical ecotone of the Florida Peninsula. The northern and southern distributional limits of several vertebrate taxa in Florida (Whitaker 1968) show distinct patterns similar to those observed for the freshwater ascomycetes. A number of vertebrate taxa found commonly in eastern North America apparently do not occur in central and south Florida (Sprunt 1954; Whitaker 1968). Humphrey (1975) found that the common bat species *Lasiurus cinereus* and *L. borealis* are absent south of 29° latitude in Florida. In another study, Christman (1975) examined the distribution of snake species in Florida and concluded that seasonal temperature extremes were mainly responsible for a pronounced north–south replacement series along the Florida Peninsula. In a study conducted at the beginning of the 20th century, Brown (1909) delineated three forest regions for peninsular Florida as north Florida (29.5° latitude), transitional pine (27.5–29.5° latitude), and south Florida or Antillean (27.5° latitude) based on the distribution of tree species.

Our results support a previous study that showed greater similarity in species composition among sites located at similar latitudes than between species on the same continent found at different temperate and tropical latitudes (Wood-Eggenschwiler and Bärlocher 1985). For example, in our study several freshwater ascomycete species, such as *A. khayaiensis*, *J. australiensis*, *Massarina bipolaris*, *Aniptodera inflatiascigera*, *A. palmicola*, *Ayria appendiculata*, *Fluviatispora reticulata*, *Torrentispora fibrosa*, and *Vertexicola caudatus*, and mitosporic ascomycetes, *P. malaysianum* and *D. tunicata*, have been reported previously from southeastern Asian tropical and subtropical regions (Fryar and Hyde 2004; Hyde 1993, 1994, 1995; Hyde et al. 1999, 2000; Inderbitzin et al. 2001; Ranghoo et al. 2000; Tsui et al. 1997), but not from other states in USA north of Florida (Shearer 1993, 2001). Speculating on the latitudinal distribution of aquatic hyphomycetes, Ingold (1966) stated: “I think I could tell my latitude with an error of 15° by examining the aquatic spores in a sample of stream foam.”

An increase in species richness from higher latitudes (polar zones) towards lower latitudes (equatorial zones) is the oldest and most fundamental pattern concerning the distribution of life on earth and a widely documented macroecological pattern (see Rosenzweig 1995; Brown and Lomolino 1998; Gaston and Blackburn 2000). The latitudinal gradient in diversity and/or richness has been well documented for several groups of organisms in marine (Gray 2001), freshwater (France 1992), and terrestrial habitats (Stevens 1989; Blackburn and Gaston 1996; Ruggiero 1999). For freshwater ascomycetes sampled along the Florida Peninsula, however, there was no prominent richness gradient (Table 1), despite changes in species composition along the peninsula as discussed above. A total of 75 species were collected from north Florida (BW + AP) from 48 habitats sampled, 63 species were collected from central Florida (OC) from 24 habitats sampled, while only 43 species were collected from south Florida (BC + EV) from 25 habitats sampled. Since species richness is dependent, in part, on sampling effort (Magurran 2004), which to some extent was uneven among the collection sites in this study, further work along the Florida ecotone is needed to validate this pattern.

One reason for lower richness in the southern sites in this study might be due to the relatively homogenous vegetational composition at the BC site. Although extensive freshwater cypress swamps are present in BC, and EV is an extensive freshwater wetland (Kushlan 1990), the number of easily accessible discrete freshwater habitats such as lakes and streams are fewer in BC and EV compared to the other northern and central sites in the study. In addition, EV, is referred to as the “river of grass” (Douglas 1947), and one of the most abundant sedge species in the EV is a *Cladium* sp., commonly called saw grass. This

substrate is highly depauperate of fungal growth and we have found only a few fungal species colonizing submerged saw grass (H.A. Raja and C.A. Shearer, personal observation). Sampling of fungi in other freshwater habitats not colonized by saw grass, but still located at lower latitudes should be carried out in future studies to further resolve species richness patterns with respect to latitudinal distribution in the Florida Peninsula.

Reverse richness gradients have been observed previously in peninsulas and this pattern is so called the “peninsula effect” (Simpson 1964; and see Brown and Lomolino 1998). The peninsula effect is a pattern of diversity documented thus far mostly in terrestrial environments where species richness decreases along peninsulas with increasing distance from their continental attachments. The peninsula effect has been shown along Florida for herpetofauna (Means and Simberloff 1987) and for avian species (Robertson 1955; Robertson and Kushlan 1974). The above mentioned studies suggest that the decline in species richness occurs due to a combination of historical effects and decline in habitat for species to colonize the lower parts of the peninsula.

Data from this study suggest that the compression of latitudinal thermoclines along the temperate–subtropical ecotone in peninsular Florida may be an important driving force in shaping the species composition of freshwater ascomycete communities.

Habitat distribution

Although CAP showed some clustering of species from lentic habitats separated from lotic habitats based on comparisons of species collected in all lentic and lotic habitat types in Florida (Fig. 3), analyses showed that habitat was not a significant factor ($P > 0.05$) in explaining the distribution patterns of freshwater ascomycete species. The analyses comparing all lotic and lentic habitats might be biased from uneven sampling due to the larger number of lentic habitats sampled ($n = 71$) compared to lotic habitats ($n = 26$) in the study. Therefore, another CAP analysis was employed for lentic and lotic habitats in north Florida where the number of lotic ($n = 21$) and lentic ($n = 27$) habitats sampled were geographically closer to each other. The second CAP analysis (Fig. 4) revealed similar results to the first and showed that habitat was not a significant factor ($P > 0.05$). These data suggest that freshwater ascomycetes communities are not significantly different although some species appeared to be exclusive to one or the other habitat type.

Numerous species of freshwater ascomycetes, including *Boerlagiomyces websteri*, *Jahnula rostrata*, *J. sangamonensis*, *L. palustris*, *Trematosphaeria lineolatispora*, Undescribed *Massarina* sp. F60, *Aquapoterium pinicola*, *Aniptodera lignatilis*, *A. palmicola*, *Annulataascus velatisporus*, *Ascitendus austriacus*, *Ascosacculus heteroguttulatus*, *Cyanoannulus petersenii*, *F. reticulata*, *Hanliniomyces hyaloapicalis*, *Nais inornata*, *Natantispora retorquens*, *Ophioceras commune*, *Submersisphaeria aquatica*, *T. fibrosa*, *V. caudatus*, *Zopfiella latipes* and *Z. lundqvistii* occurred in both lentic and lotic habitats (Appendix 3). A number of these species also occurred frequently and were reported from more than one collection site along the Florida Peninsula and may be habitat generalists (Appendix 3).

Fourteen new taxa were collected only from lentic habitats, whereas only two new taxa were collected exclusively in lotic habitats (Appendix 3). Since lentic habitats are often spatially discrete, which can restrict gene flow between their respective fungal populations; the populations may be subjected to different selective pressures. This characteristic could lead to higher rates of speciation than non-discrete habitats such as streams and rivers. The above hypothesis might be one of several possible reasons why more new species were found in lentic habitats than in lotic habitats. Additional comparative collections of freshwater ascomycetes from lentic and lotic habitats and population level studies of lentic

and lotic species are needed to determine the importance of isolation as a mechanism of speciation in aquatic ascomycetes.

Comparison of the freshwater ascomycetes from Florida lakes to those collected by Fallah (1999) from north temperate lakes in Wisconsin showed that *P. caudae-suis* and *M. ingoldiana* were the only two species common to collections made in lentic habitats from Wisconsin and Florida. These two species are widely distributed in both lentic and lotic habitats in North America (Fallah and Shearer 2001; Shearer 2001; Campbell et al. 2003). Because there is a greater difference in the water temperature regimes between Wisconsin and Florida, differences in species composition between lakes in these two regions is not unexpected. Another factor that might contribute to the striking difference in fungal species composition between Wisconsin and Florida might be due to geological ages of lakes in the two regions. Lakes in the northern latitudes are geologically younger than those in Florida due to the most recent glaciation, which did not reach Florida (Brenner et al. 1990).

We also compared the species composition of freshwater fungi from Florida Lakes to that of a tropical lake in Australia (Hyde and Goh 1998a), and to subtropical lakes in China (Cai et al. 2002; Luo et al. 2004). About 10% of the freshwater meiosporic and mitosporic fungal species were similar with Lake Barrine in Australia, and approximately 10–12% species were similar to the lakes from China. Fungal taxa that showed overlap among the lakes in the three geographical areas are common species that are distributed worldwide, such as *Aniptodera chesapeakeensis*, *Kirschsteiniothelia elaterascus*, *Nais inornata*, *Sporoschisma saccardoi*, and *Zopfiella latipes* (see <http://fungi.life.uiuc.edu/>).

Water pH was shown to be significant in explaining the variation in community composition of freshwater fungi in Florida as fungal communities were divided into three more or less distinct groups based on pH values (Fig. 7). Water chemistry plays an important role in the distribution of freshwater organisms (Hynes 1970; Wetzel 2001). Previous studies of freshwater fungi have also shown that pH is an important factor in the distribution of freshwater ascomycetes (Fallah 1999), as well as freshwater Ingoldian mitosporic fungi (Wood-Eggenschwiler and Bärlocher 1983; Shearer and Webster 1985; Bärlocher 1987; Bärlocher and Rosset 1981). In a review of the effects of water chemistry on the distribution of freshwater Ingoldian mitosporic ascomycetes, Chamier (1992) concluded that pH may have an indirect effect on the distribution of freshwater mitosporic fungi by affecting the solubility of Al or other metals in freshwater habitats.

Substrate distribution

Eighteen of 132 taxa occurred on both herbaceous and woody debris and may be substrate and habitat generalists. Among these, *Annulatasacus velatisporus*, *A. austriacus*, *Ascosacculus heteroguttulatus*, *Bactrodesmium linderi* and *Cancellidium applanatum* were the most commonly occurring species and were found in more than two collection sites in both lentic and lotic habitats along the Florida Peninsula (Table 1; Appendix 3). Species that occurred on both woody and herbaceous debris usually occurred on herbaceous debris in lentic habitats. Two exceptions are *A. austriacus* and a new undescribed fungus (F76) that occurred on herbaceous debris in lotic habitats.

Freshwater ascomycetes that occur on herbaceous substrates are reported more frequently from lentic habitats probably because herbaceous macrophytes are much more common in lentic habitats than lotic habitats (Shearer 1993; Shearer 2001). Fallah (1999) found a number of freshwater ascomycetes exclusively on herbaceous material in lentic habitats. *Ascovaginospora stellipala* Fallah, Shearer & J.L. Crane, *Aquadulciospora*

rhomboidia Fallah & Shearer, *Phaeosphaeria barriae* Fallah & Shearer, *Phaeosphaeria vilasensis* Fallah, Shearer & Leuchtm. and *Phomatospora muskellungensis* Fallah & Shearer occurred only on herbaceous debris collected from lakes in Wisconsin (Fallah 1999). The above taxa have not been reported from wood in lentic or lotic habitats from other geographical locations thus far (<http://fungi.life.uiuc.edu/>) and may be specialists on herbaceous material. Whether or not these taxa might have adapted to freshwater with their plant hosts is an interesting question (Shearer 1993, 2001).

Aquapoterium pinicola and *Ophiobolus shoemakeri*, two species of freshwater meiotic ascomycetes reported only from herbaceous debris in this study, were tested for the production of extracellular enzymes in vitro and found positive for cellulase, endoglucanase, beta-glucosidase, xylanase and amylase (Simonis et al. 2008), enzymes important in decomposing herbaceous substrates. Although positive for xylanase, *A. pinicola* and *O. shoemakeri* were both negative for production of the lignin modifying enzymes, peroxidase and tyrosinase, and they did not cause soft-rot in balsa wood. It is plausible that lack of lignin modifying enzymes and inability to form soft-rot cavities may prevent species such as *A. pinicola* and *O. shoemakeri* from being competitive on woody substrates and thereby limit their occurrences to herbaceous debris.

Studies that have examined substrate specificity of mitosporic Ingoldian fungi (Gulis 2001; Nikolcheva and Bärlocher 2005) suggest that most aquatic hyphomycetes can colonize and grow on a wide range of substrate types (Webster and Descals 1981; Bärlocher 1992; Suberkropp 1992). However, relative frequencies of individual species may be influenced by the substrate (Bärlocher 2005). For example, Bärlocher (1982) found that the dominant species on conifer needles differ from the dominant species on deciduous leaf litter. Bärlocher and Graça (2002) showed that fungal communities of streams running through eucalyptus stands are more similar to each other than those running through mixed deciduous forest. Gulis (2001) conducted a study on Ingoldian mitosporic ascomycetes to test preferences among various substrate types such as leaf litter, woody debris and herbaceous debris (grass blades) and found that wood and grass blades had a distinct fungal assemblage clearly different from those supported by deciduous leaf litter. Ferreira et al. (2006) reported a clear preference of aquatic hyphomycete species towards either leaves or wood, they found that the fungal assemblage on leaves was different from those colonizing balsa wood veneers. On the other hand, Nikolcheva and Bärlocher (2005) did not find strict substrate preferences for Ingoldian mitosporic ascomycetes using both traditional and molecular techniques, and they concluded that strict exclusion of fungi by substrate type was rare, and that presence of different species or phylotypes was governed by seasonality in their study.

In our study, some differences were found in the freshwater ascomycete species colonizing herbaceous debris versus those found on woody debris, but, in general, except for *Aquapoterium pinicola*, *Ayria appendiculata*, *O. shoemakeri* and *Physalospora limnetica*, and other mitotic ascomycetes (Appendix 3) most species occurred on woody debris. Of the 548 species of freshwater meiotic ascomycetes reported in the literature, 375 were collected from wood and 173 were collected from herbaceous debris (<http://fungi.life.uiuc.edu/>) while in the present study, of the 74 freshwater meiotic ascomycetes, 61 species occurred only on woody debris, eight occurred on both substrate types, while only four occurred exclusively on herbaceous debris (Appendix 3). The occurrences of few meiotic ascomycetes on herbaceous debris might be due to some features of wood not characteristic of herbaceous debris, such as persistence over time (Shearer 1992) or nutrient content (higher carbon: nitrogen ratio) which may stimulate the production of sexual states.

Conclusions

1. Results from CAP analyses, and Sørensen's similarity index indicate that the freshwater ascomycete community composition differs between northern and southern sites along the temperate–subtropical latitudinal ecotone of the Florida Peninsula. Canonical correspondence analyses revealed that both latitude and pH are important factors in explaining the distribution patterns of freshwater ascomycetes. A number of freshwater ascomycete species from central and south Florida occur in the paleotropics as well as neotropics but have not been reported thus far from north Florida as well as other states north of Florida.
2. Ordination analysis of freshwater ascomycete communities indicated that lentic and lotic communities were not significantly different. Some geographically broadly distributed species and species commonly found in Florida occurred in both habitats whereas a number of rare species were collected either in lentic or lotic habitats.
3. Of the 132 taxa of meiosporic and mitosporic freshwater ascomycetes reported from Florida, 100 species were reported on woody debris, while only 14 species occurred exclusively on herbaceous debris. Eighteen species, of which some were commonly occurring taxa, were found on both woody and herbaceous debris. Most of the taxa reported from herbaceous debris were reported from lentic habitats. Species occurring on woody debris in lotic habitats were also found on wood in lentic habitats, but species found exclusively on herbaceous debris in lentic habitats were seldom found on wood or herbaceous debris in lotic habitats. This may reflect, to some degree, the absence of herbaceous substrates in many lotic habitats.
4. With respect to the conservation of freshwater ascomycetes, a broad latitudinal approach must be taken. Given the large number of new species discovered in this single study, additional geographically broad studies are warranted to fully understand the biodiversity of this group.

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Appendices

Appendix 1 List of habitats sampled with their water temperature and pH ranges as measured at the time of sample collection at five sites within the Florida Peninsula

Collection site	Latitude/longitude	Temperature (°C)	pH
<i>Blackwater River State Forest</i>			
Blackwater River	30°56'01"N, 86°44'07"W	11–27	5.5–7
Bone Creek	30°44'10"N, 86°43'56"W	25–27	5.5–6.7

Appendix 1 continued

Collection site	Latitude/longitude	Temperature (°C)	pH
Penny Creek	30°45'05"N, 86°46'54"W	23	6.6
Alligator Creek	30°44'39"N, 86°52'54"W	7–24	5.5–5.7
Juniper Creek	30°50'01"N, 86°54'11"W	11–24	5.5–6.3
Sweetwater Creek	30°51'21"N, 86°51'03"W	13–26	5.5–6.8
Coldwater Creek	30°52'59"N, 86°57'28"W	11–25	5.5–6.4
Pringle Branch	30°54'33"N, 86°58'04"W	11–23	5.5–6.4
Hurricane Creek	30°56'36"N, 86°44'50"W	30	8
Maria Branch	30°46'39"N, 86°54'42"W	7	5.5
Hawkins Creek	30°58'11"N, 86°59'43"W	30	5–5.5
Dixon Branch	30°54'50"N, 86°57'52"W	23	6.7
Horns Creek Swamp	30°46'31"N, 86°54'43"W	30	6
Pitman Creek Swamp	30°48'57"N, 86°55'31"W	27	5.7
Deaton Bridge Swamp	30°43'49"N, 86°52'29"W	36	6.3
Bear Lake	30°51'43"N, 86°49'56"W	11–34	6.5–7.6
Hurricane Lake	30°56'19"N, 86°45'12"W	11–36	5.5–8.7
Karick Lake	30°53'45"N, 86°38'30"W	13	5.5
Kennedy Branch Swamp	30°56'37"N, 86°44'49"W	11–12	5.5
Blackwater River Shingles Branch Swamp	30°43'30"N, 86°7'40"W	13	5.5
Calloway Swamp	30°53'28"N, 86°58'03"W	12	5.5
<i>Apalachicola National Forest</i>			
Big Gulley Creek	30°15'42"N, 85°00'46"W	27	6.6
Kennedy Creek	30°06'31"N, 85°03'37"W	27–28	7
Ochlockonee River	30°05'37"N, 84°37'42"W	24	5.5
Fisher Creek	30°18'51"N, 84°23'57"W	25–39	5.5–7.5
Syfreet Creek	30°05'02"N, 84°34'54"W	26	5.5–7.4
Little Gully Creek	30°15'39"N, 85°00'46"W	9–26	5.5
Rowletts Creek	30°51'30"N, 85°01'10"W	9–35	5.5
New Crossing Branch	30°13'08"N, 84°59'21"W	8	5.5
Apalachicola River	29°56'24"N, 85°00'41"W	9	6
Field Branch Creek	30°03'24"N, 85°03'36"W	30	7
Apalachicola River Swamp	29°56'20"N, 85°00'45"W	30	7.5
Owls Creek Swamp	30°03'31"N, 85°01'11"W	30	7.5
Leon Sinks	30°18'35"N, 84°20'46"W	21	8
Dog Pond	30°20'55"N, 84°24'41"W	30	5.5
Unnamed Pond	29°54'07"N, 84°20'36"W	30	6
Unnamed Swamp 1	30°17'02"N, 84°50'25"W	30	6.5
Andrew Lake	30°24'09"N, 30°24'09"N	33	6.5
Unnamed Lake	30°21'55"N, 84°22'54"W	30	6.5
Wood Lake	30°01'34"N, 84°33'57"W	30	6–8.5
Unnamed Swamp 2	29°49'42"N, 84°58'28"W	8	5.5
Unnamed Swamp 3	30°15'57"N, 84°48'53"W	9	6
Whitehead Lake	30°09'54"N, 84°40'30"W	12–29	6–7.5
Hitchcock Lake	30°04'54"N, 84°39'05"W	30	6

Appendix 1 continued

Collection site	Latitude/longitude	Temperature (°C)	pH
Wright Lake	30°00'02"N, 85°00'08"W	–	6
Long Bay Swamp	30°19'23"N, 84°37'23"W	21	5
Swamp at Fort Gadsden	29°55'07"N, 84°58'38"W	29	7.5
Camel Pond	30°16'36"N, 84°59'20"W	33	5.5
<i>Ocala National Forest</i>			
Alexander Springs	29°04'52"N, 81°33'57"W	18–27	7
Ocklawaha River	29°22'19"N, 81°53'56"W	19–25	7
Juniper Springs	29°10'59"N, 81°42'46"W	22–27	6–6.5
Redwater Lake	29°11'49"N, 81°53'28"W	35–36	5.5–6.4
Doe Lake	29°02'14"N, 81°49'09"W	30–34	5.5–6.3
Mary Lake	29°04'23"N, 81°49'57"W	30–37	5–5.7
Lake Dorr	29°00'50"N, 81°38'07"W	33–36	5–5.9
Bock Lake	29°05'52"N, 81°39'11"W	37	6.5
Faries Prairie	29°06'15"N, 81°40'27"W	39	6.5
South Grasshopper Lake	29°08'04"N, 81°37'11"W	27–37	6.5
Chain-O-Lake	29°07'57"N, 81°38'36"W	17–39	5.5–6.3
Beakman Lake	29°07'34"N, 81°37'14"W	36	6.5
Wildcat Lake	29°10'14"N, 81°37'40"W	35	6
Fore Lake	29°16'17"N, 81°55'03"W	18–37	5.5–7
Lake Eaton	29°15'18"N, 81°51'55"W	18–36	5.5–7
Half moon Lake	29°09'32"N, 81°49'17"W	19–34	5.5–6.9
Mill Dam Lake	29°10'42"N, 81°50'03"W	17–34	5.5–6.7
Lake Kerr	29°21'19"N, 81°48'45"W	21–39	6.7
Quarry Pond	29°12'45"N, 81°53'45"W	21	7
Little Lake Kerr	29°20'57"N, 81°43'49"W	21–32	7
Unnamed Pond 1	29°07'46"N, 81°37'34"W	15	5.5
Lake George	29°12'06"N, 81°34'40"W	38	7
Unnamed Pond 2	29°06'03"N, 81°32'52"W	18	7
Clearwater Lake	–	35	5.5
<i>Big Cypress National Preserve</i>			
Turner River Canal	25°54'21"N, 81°15'43"W	30	7
Pine Crest well head swamp	25°23'27"N, 80°47'56"W	27	7
Cypress Swamp 1	25°45'37"N, 81°00'50"W	30	7
Cypress Swamp 2	25°45'36"N, 81°02'07"W	25	7
Cypress Swamp 3	25°45'37"N, 81°03'18"W	25	7
Cypress Swamp 4	25°47'01"N, 81°05'39"W	25	7
Monument Lake	25°52'14"N, 81°06'51"W	20–30	6
Burns Lake	25°53'44"N, 81°13'49"W	21–33	7
Roadside Swamp	26°10'21"N, 81°16'00"W	26	8
East Hanson Swamp	26°11'06"N, 81°16'02"W	27	7
Tamiami Canal Swamp 1	25°52'36"N, 81°13'40"W	29	7
Tamiami Canal Swamp 2	–	–	7
Cypress Swamp 5	25°44'51"N, 80°57'24"W	18	7

Appendix 1 continued

Collection site	Latitude/longitude	Temperature (°C)	pH
Cypress Swamp 6	25°45'37"N, 81°02'09"W	–	7
Cypress Swamp 7	25°46'53"N, 81°05'31"W	20	7
Cypress Swamp 8	25°45'03"N, 80°58'02"W	25	7
Cypress Swamp 9	25°45'16"N, 80°58'42"W	25	6.5
Cypress Swamp 10	25°45'37"N, 81°02'54"W	27	6.5
Cypress Swamp 11	25°45'37"N, 81°03'18"W	27	6.5
Cypress Swamp 12	25°45'45"N, 80°55'09"W	30	6
<i>Everglades National Park</i>			
Mahogany Hammock	25°19'16"N, 80°49'33"W	20–35	7.5
Sisal Pond	25°23'28"N, 80°47'58"W	20–25	7
Paurotis Pond	25°16'56"N, 80°47'59"W	25	7
Long Key Pine Pond	25°24'02"N, 80°39'32"W	20–32	6–7
Royal Palm Pond	25°22'58"N, 80°36'36"W	20–30	7

Appendix 2 Ranges in water temperature and pH of all the freshwater habitats sampled during different seasons at the five collection sites

	BW		AP		OC		BC		EV	
	W	S	W	S	W	S	W	S	W	S
Temp	7–14	23–36	8–12	21–35	18–21	25–39	21–30	27–33	20–35	27–35
pH	5–8.5		5–8.5		5–6.5		6–8		7–8	

W winter; S summer; Temperature measured in degrees Celsius

BW Blackwater River State Forest, AP Apalachicola National Forest, OC Ocala National Forest, BC Big Cypress National Preserve, EV Everglades National Park

Appendix 3 Fungal species found on submerged woody or herbaceous debris in lentic or lotic habitats at each of the five sites along the Florida Peninsula

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Dothideomycetes</i>					
<i>Aliquandostipite minuta</i> Raja & Shearer				Le w	
<i>Aliquandostipite crystallinus</i> Raja, Ferrer & Shearer				Lo w	
<i>Aliquandostipite khaoyaiensis</i> Inderb.				Le w	
<i>Aliquandostipite siamensiae</i> (Sivichai & E.B.G. Jones) J. Campbell, Raja, Ferrer, Sivichai & Shearer				Le w	

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Boerlagiomyces websteri</i> Shearer & J.L. Crane		Lo w	Le w	Le w	Le h
<i>Caryospora obclavata</i> Raja & Shearer		Le w			
<i>Caryospora langliosii</i> Ell. & Everh.			Le w		
<i>Falciformispora lignatilis</i> K.D. Hyde			Le w		Le w
<i>Jahnula aquatica</i> (Plöttner & Kirschst.) Kirschst.			Lo w		
<i>Jahnula australiensis</i> K.D. Hyde				Le w	
<i>Jahnula bipileata</i> Raja & Shearer	Le w	Le w			
<i>Jahnula bipolaris</i> (K.D. Hyde) K.D. Hyde				Le w	
<i>Jahnula potamophila</i> K.D. Hyde & S.W. Wong		Le w			
<i>Jahnula rostrata</i> Raja & Shearer	Lo w		Le Lo w	Le w	Le w
<i>Jahnula sangamonensis</i> Shearer & Raja		Le w		Lo w	
<i>Kirschsteiniothelia elaterascus</i> Shearer		Le w	Le w	Le w	Le w
<i>Lepidopterella palustris</i> Shearer & J.L. Crane		Le Lo w			
<i>Lepidopterella tangerina</i> Raja & Shearer	Lo w				
<i>Massarina bipolaris</i> K.D. Hyde		Le w	Le w		Le w
<i>Massarina fronsisubmersa</i> K. D. Hyde	Lo w				
<i>Massarina ingoldiana</i> Shearer & K.D. Hyde	Le w	Le Lo w			
<i>Micropeltopsis</i> sp. F115	Le w				
<i>Ophiobolus shoemakeri</i> Raja & Shearer			Le h		
<i>Trematosphaeria lineolatipora</i> K.D. Hyde			Lo w	Lo Le w	Le h
Undescribed <i>Massarina</i> sp. F60		Le Lo w			

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
Undescribed <i>Massarina</i> sp. F65					Le w
Undescribed <i>Massarina</i> sp. F80		Le w			
Undescribed genus F76		Lo w	Lo h		
<i>Leotiomyces</i>					
<i>Aquapoterium pinicola</i> Raja & Shearer	Le Lo h	Le h	Le h		
<i>Gorgoniceps</i> sp. F72				Le w	
<i>Sordariomyces</i>					
<i>Aniptodera aquaduleis</i> (S.Y. Hsieh, H.S. Chang & E.B.G. Jones) J. Campb., J. Anderson & Shearer			Le w		
<i>Aniptodera chesapeakensis</i> Shearer & Miller			Le w		
<i>Aniptodera inflatiscigera</i> K.M. Tsui, K.D. Hyde & I.J. Hodgkiss	Le w		Le h	Le w	
<i>Aniptodera lignatilis</i> K.D. Hyde	Lo w	Le w	Lo w		
<i>Aniptodera megaloscarpa</i> Raja & Shearer			Le w		
<i>Aniptodera palmicola</i> K.D. Hyde, W.H. Ho & K.M. Tsui			Le Lo w	Le h w	Le w
<i>Annulatascus velatiporus</i> K.D. Hyde	Le Lo w	Le w	Le h	Le Lo w	
<i>Arnium gigantosporum</i> Raja & Shearer			Le w		
<i>Ascitendus austriacus</i> (Réblová, Winka & Jaklitsch) J. Campb. & Shearer	Lo Le h w	Le w			
<i>Ascocacculus heteroguttulatus</i> (S.W. Wong, K.D. Hyde & E.B.G. Jones) J. Campb., J.L. Anderson & Shearer	Le w	Le Lo w	Le w		Le h
<i>Ascotaiwania hsilio</i> H.S. Chang & S.Y. Hsieh	Lo w			Le w	
<i>Ayria appendiculata</i> Fryar & K.D. Hyde		Le h			
<i>Cataractispora bipolaris</i> (K.D. Hyde) K.D. Hyde, S.W. Wong & E.B.G. Jones			Le w		
<i>Cyanoannulus petersenii</i> Raja, J.Campb. & Shearer	Le Lo w	Lo w			

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Fluviatispora reticulata</i> K.D. Hyde	Le Lo w	Le Lo w	Le w		
<i>Flammispora pulchra</i> Raja & Shearer			Le w		
<i>Hanliniomyces hyaloapicalis</i> Raja & Shearer gen. nov	Lo w			Le w	
<i>Jobellisia luteola</i> (Ellis & Everh.) M.E. Barr	Le Lo w	Le Lo w			
<i>Lockerbia striata</i> Raja & Shearer	Le w	Le h			
<i>Luttrellia estuarina</i> Shearer		Lo w			
<i>Luttrellia</i> sp. F14			Le w		
<i>Lulworthia</i> sp. F54			Le w		
<i>Nais inornata</i> Kohlm.	Le w	Le Lo w	Le Lo w		Le w
<i>Natantispora retorquens</i> (Shearer & J.L. Crane) J. Campb., J.L. Anderson et Shearer	Lo Le w	Le w			
<i>Ophioceras commune</i> Shearer, J.L. Crane & Chen		Le w	Le Lo w		
<i>Phaeoectriella lignicola</i> R.A. Eaton & E.B.G. Jones			Lo w		
<i>Phomatospora triseptata</i> Raja & Shearer				Le w	
<i>Pseudoproboscispora caudae-suis</i> (Ingold) J. Campbell & Shearer	Lo w				
<i>Physalospora limnetica</i> Raja & Shearer		Le h			
<i>Savoryella aquatica</i> K.D. Hyde			Le w	Le w	
<i>Savoryella fusiformis</i> W.H. Ho, K.D. Hyde & I.J. Hodgkiss					Le w
<i>Submersisphaeria aquatica</i> K.D. Hyde	Le Lo w	Le Lo w		Le w	
<i>Torrentispora fibrosa</i> K.D. Hyde, W.H. Ho, E.B.G. Jones, K.M. Tsui & S.W. Wong	Lo w	Lo w	Le w		
<i>Verticicola caudatus</i> K.D. Hyde, S.W. Wong & V.M. Ranghoo	Lo w		Le w		

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Zopfiella latipes</i> (N. Lundq.) Malloch & Cain	Le Lo w		Le w	Le w	
<i>Zopfiella lundqvistii</i> Shearer & J.L. Crane		Le Lo w			
Unidentified ascomycete sp. F28		Le w			
Undescribed sp. F41		Le w			
Undescribed gen. F44		Le w			
Undescribed gen. F50	Lo w				
Undescribed sp. F57	Lo Le w				
Undescribed gen. F99			Le w		
Undescribed sp. F100			Le w		
Undescribed sp. F107			Le w		
BASIDIOMYCETES					
<i>Rogersiomyces okefenokeensis</i> J.L. Crane & Schoknecht		Le h			
<i>Mitosporic fungi</i>					
<i>Acrogenospora sphaerocephala</i> (Berk. and Broome) M. B. Ellis	Lo w	Le w	Lo w		Le w
<i>Ardhachandra cristaspora</i> (Matsush.) Subram. & Sudha			Le h		
<i>Bactrodesmium linderi</i> (J.L. Crane & Shearer) M.E. Palm & E.L. Stewart		Le Lo w	Le w	Le w	Le h
<i>Berkleasmium concinnum</i> Berk. (S. Hughes)			Lo w		
<i>Brachiosphaera tropicalis</i> Nawawi				Le w	
<i>Brachysporium obovatum</i> Kiessl			Le w		
<i>Cancellidium applanatum</i> Tubaki	Le Lo h w	Le Lo w	Le w		
<i>Canalisporium caribense</i> (Hol.-Jech. & Mercado) Nawawi & Kuthub.				Le w	

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Canalisporium kenyense</i> Goh, W. H. Ho, K. D. Hyde, S. R. Whitton & T.E. Umali			Le w		
<i>Cacumisporium sigmoideum</i> Mercado & R. F. Castañeda			Lo w	Le w	
<i>Chaetospermum camelliae</i> Agnihothr.			Le h	Le h	Le h w
<i>Coleodictyospora micronesia</i> (Matsush.) Matsush.				Le h	Le h
<i>Cordana abramovii</i> Seman & Davydkina var. <i>seychellensis</i> K. D. Hyde & Goh		Le w			
<i>Condylospora</i> sp. FH34			Le w		
<i>Cryptophiale cucullata</i> Kuthub.	Le h				
<i>Dactylaria hyalotunicata</i> K.M. Tsui, Goh & K.D. Hyde	Lo h w	Le w			
<i>Dactylaria tunicata</i> Goh & K.D. Hyde	Le Lo w	Le w			
<i>Delortia palmicola</i> Pat.			Le h w		
<i>Dendrosporium lobatum</i> Plakidas & Edgerton ex J.L. Crane			Le h		
<i>Dendrospora</i> sp. FH87			Le w		
<i>Dictyosporium</i> sp. FH39	Le w				
<i>Dictyosporium digitatum</i> J.L. Chen, C.H. Hwang & S.S. Tzean		Le h w		Le h	Le h
<i>Dictyosporium elegans</i> Corda		Lo w			
<i>Dictyosporium giganticum</i> Goh & K.D. Hyde					Le h
<i>Dictyosporium heptasporum</i> (Garov.) Damon				Le w	
<i>Ellisembia abscondens</i> (Berk.) Subram.		Lo w	Le Lo w		Le w
<i>Exserticlava globosa</i> Roa de Hoog		Le w			
<i>Exserticlava triseptata</i> (Matsush.) S. Hughes		Le w	Le w		

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Exserticlava vasiformis</i> (Matsush.) S. Hughes	Lo Le w		Le w		
<i>Helicodendron</i> sp. FH38		Le Lo w			
<i>Helicoon auratum</i> (Ellis) Morgan		Le w			
<i>Helicomycetes roseus</i> Link		Le Lo w		Le w	
<i>Helicosporium aureum</i> (Corda) Linder			Le w		
<i>Helicosporium guianense</i> Linder			Le w		
<i>Helicosporium gigasporum</i> K.M. Tsui, Goh, K.D. Hyde & Hodgkiss		Lo w	Le Lo w		
<i>Helicosporium lubricopsis</i> Linder			Le w		
<i>Humicola asteroidea</i> Udagawa & Y. Horie	Lo w				
<i>Ingoldiella hamata</i> D.E. Shaw	Lo h				
<i>Intercalarispora</i> sp. FH88		Lo w			
<i>Monacrosporium elliposporum</i> (Preuss) R.C. Cooke & C.H. Dickinson			Le h w		
<i>Monotosporella setosa</i> (Berk. & M.A. Curtis) S. Hughes	Lo Le w		Le w		
<i>Melanocephala australiensis</i> G.W. Beaton & M.B. Ellis		Lo w			
<i>Nawawia filiformis</i> (Nawawi) Marvanová				Le w	
<i>Pleurophragmium malaysianum</i> Matsush.	Le Lo w	Le w	Le w		
<i>Pleurothecium recurvatum</i> (Morgan) Höhn.		Le w			
<i>Septonema hormiscium</i> Sacc.	Le h	Le w			
<i>Speiropsis</i> sp. FH59			Le h		
<i>Sporidesmiella hyalosperma</i> var. <i>novae-zealandiae</i> (S. Hughes) P.M. Kirk		Le w			

Appendix 3 continued

Species	Collection sites				
	BW	AP	OC	BC	EV
<i>Sporidesmium tropicale</i> M.B. Ellis		Le w			
<i>Sporidesmium</i> sp. FH27		Le h			
<i>Sporoschisma saccardoii</i> Mason & S. Hughes			Le w	Le w	
<i>Tetraploa aristata</i> Berk. & Broome					Le h
<i>Thozetella</i> sp. FH37	Low				
<i>Vargamyces</i> sp. FH86		Le w			
<i>Varicosporium</i> sp. FH22			Le w		
<i>Wiesneriomyces larinus</i> (Tassi) P. M. Kirk			Le h	Le w	
<i>Xylomyces chlamydosporus</i> Goos, R.D. Brooks & Lamore	Lo w	Le Lo w	Le w		

Le lentic habitats (e.g., lakes, ponds, and swamps), *Lo* lotic habitats (e.g., streams and rivers), *w* woody debris, *h* herbaceous debris

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