Inter- and intra stream variation of lignicolous freshwater fungi in tropical Australia

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Freshwater ecosystems are in a constant interaction with the terrestrial environment (riparian) surrounding them. Riparian vegetation is the major source of organic input into the stream ecosystem, which includes woody debris. The impact of the type of riparian vegetation on the biodiversity of lignicolous freshwater fungi in five tropical streams of the Barron River catchment area in Atherton Tablelands, Queensland, Australia was investigated. The collection sites were broadly classified in three types based on the kind of riparian vegetation; pristine, re-growth and agricultural zones. Fifty wood samples collected from each of 12 sites yielded 162 fungal taxa. The dominant fungi were species of *Annulatascus, Aquaticola* (*Annulatascaceae*), *Anthostomella* (*Xylariaceae*), *Massarina* (*Lophiostomataceae*) and *Savoryella* (*Sordariales incertae sedis*). The highest species diversity was found in the pristine forest zone, followed by agricultural zone, while the re-growth zone was least diverse. Species overlap was seen between all streams, and between the three types of riparian vegetation. The fungal species showed little habitat recurrence, however major changes were observed in species richness and abundance, with varying degrees of human disturbance.

Key words: ascomycetes, biodiversity, riparian vegetation, species abundance, submerged wood

Introduction

The riparian zone is a dynamic habitat characterised by material exchange between terrestrial and stream ecosystems (Wetzel, 2001). The input of organic matter (leaves, twigs, branches, whole trees) from riparian vegetation to streams is one of the most significant processes occurring at the interface of terrestrial and stream ecosystems (Dolloff and Webster, 2000), influencing stream food webs and total ecosystem functioning (Wallace *et al*., 1997). Woody debris deposited into stream ecosystems affects hydraulic conditions, defines channel morphology and provide habitats for various aquatic organisms (Keller and Swanson, 1979; Mosley, 1981; Harmon *et al*., 1986; Sedell *et al*., 1988). Leaves, small pieces of wood (< 2 mm) and

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reproductive structures of terrestrial plants account for more than 90% of the overall transport of organic matter downstream in temperate as well as tropical streams (Benson and Pearson, 1993). In contrast, larger woody substrates entering the stream from the riparian vegetation show little or no transport and limited breakdown (Webster *et al*., 1999). Even though the breakdown of wood is slower and its inputs are lower than that of leaf litter, their contributions to energy flux are higher. This is due to their resistance to downstream transport resulting in a relatively high standing stock (Díez *et al*., 2002). However, excessive amounts in stream ecosystems can have negative impacts, such as reduce dissolved oxygen and build up toxic levels of wood (Hicks, 1997). Therefore the decomposition of woody substrates into fine particulate organic matter (FPOM) that are easily transported and recycled is essential. The transport rates of FPOM resulting from wood breakdown (< 3 mm diam) have been shown to be substantially larger in tropical than those in temperate systems (Webster *et al*., 1995b).

Freshwater fungi play an important ecological role in tropical stream food webs as they enzymatically degrade allochthonous matter into more palatable forms, e.g. Ingoldian fungi are the dominant micro-organisms associated with decomposing leaf litter in stream ecosystems (Suberkropp, 1997; Abdel-Raheem and Shearer, 2002; Bucher *et al*., 2004; Gönczöl and Révay, 2004) and their biodiversity, distribution and ecological role in decaying leaves have been well investigated (Bärlocher, 1992; Suberkropp, 1997; Pascoal *et al*., 2005).

Studies on fungi inhabiting submerged plant debris and wood have been undertaken in temperate (Bärlocher, 1992; Shearer, 1993; Hyde and Goh, 1999a; Cai *et al*., 2002b; Van Ryckegem and Verbeken, 2005a,b) and tropical regions (Hyde and Goh, 1997, 1998a,b; Goh and Hyde, 1999, Tsui *et al*., 2000; Cai *et al*., 2002a, 2003a, 2005; Luo *et al*., 2004; Tsui and Hyde, 2004; Fryar *et al*., 2004, 2005), with the tropics exhibiting a greater diversity of aquatic fungi. More than 600 species, belonging to diverse taxonomic groups, have been described from woody substrates in freshwater ecosystems (see Shearer, 2001; Cai *et al*., 2003b, Goh and Tsui, 2003). Collection expeditions have resulted in a number of new taxa from freshwater samples in tropical Australia (Hyde *et al*., 1997; Goh and Hyde, 1999).

Fungi generally show recurrence in specific habitats and abundance of habitat therefore limits species abundance, and likely influences fungal communities (Lodge, 1997). Studies have shown significant correlations between certain attributes of stream habit and the local diversity of fungi (e.g. Tsui and Hyde, 2004). Thus, habitat modification resulting from human activities (e.g. riparian deforestation) should strongly influence the distribution

and abundance of freshwater fungi. However, habitat abundance relationships for lignicolous freshwater have rarely been conducted. This is particularly the case for tropical streams, where anthropogenic habitat modification has been shown to influence biodiversity of many other stream organisms (Dudgeon, 1999, 2000).

The aim of this study was to assess the impact of riparian forest disturbance on the diversity, richness and abundance of lignicolous freshwater fungi in tropical Australia. We compared the diversity of wood-inhabiting fungi from five tropical streams, with three different kinds of riparian vegetation (Primary forest, secondary/regrowth forest and cleared/agricultural riparian forests). The objectives are (1) to assess the biodiversity of fungi on submerged wood in a large tropical forest area, (2) to assess the inter- and intra- stream variation of fungi on submerged wood and (3) to characterise the effects of riparian forest cover on the diversity of fungi on wood logs and twigs.

Materials and methods

Site of study

This research was undertaken in the Atherton Tablelands, a high flat land in Queensland, northeastern Australia. The tableland rises gradually to the east and southeast, where Mount Bartle Frere, 5287 feet high, forms the highest point. The region receives a mean annual rainfall of 1200-4000 mm, over 60% of which falls in summer (December-March). The period of study was drier than average.

Experimental design

To examine the effect of riparian vegetation on the diversity of lignicolous freshwater fungi, stream sites were categorised into three types according to their riparian vegetation: pristine forest area, which is mostly undisturbed and lies within the World Heritage forest; secondary forest area comprising wood lands or a buffer forest area beside the stream, which are mostly part of National or State forests; and the agricultural riparian zone, which is in close proximity to agricultural fields and roads (Fig. 1).

The sampling was conducted during April 2002 and March 2003 (Table 1), when the temperatures ranged from an average of 17ºC at night to 26ºC in the day. The 12 study sites were separated by approximately 2 to 20 kms and included 5, third and fourth order streams, the Clohesy River, Davies Creek, Emerald, Kauri Creek and Tinaroo Creeks (Fig. 1).

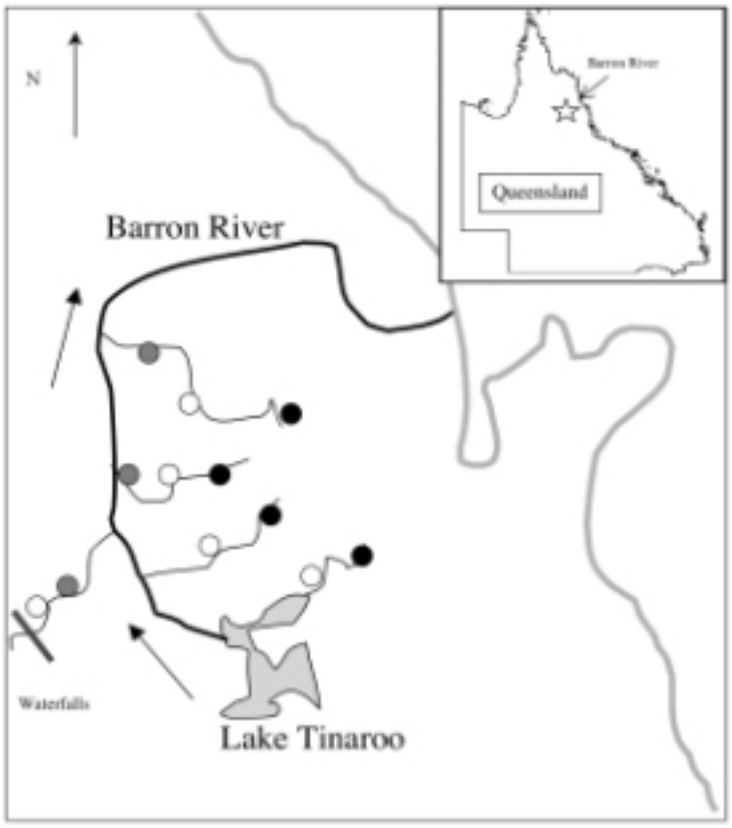

Fig. 1. The location of the 12 collection sites, on the 5 streams, flowing into the Barron River. Arrows indicate flow direction.

Methodology

Fifty submerged wood samples were randomly collected from a 100 m section of each stream site. The collection was carried out starting by walking upstream systematically in a zigzag fashion to randomise any bias associated with near-shore or midstream observations, and also pool and riffle effects. Utmost care was taken to collect only samples that had been submerged for a long period, by observing the degree of degradation. The collected samples included segments of trunks, branches and twigs from a variety of unidentified angiosperms. The size of the wood samples ranged from 15-30 cm long and 1-5 cm in diameter. All samples were placed in plastic bags in the field with moistened tissue paper, and returned to the laboratory in Hong Kong within 4 days. The samples were then incubated individually in sterile plastic boxes lined with moistened tissue paper at room temperature (22-24ºC). The woody substrates were examined under a dissecting microscope for fruiting bodies on

Table 1. Name, place and date of collection.

	Davies Creek	Clohesy River	Tinaroo Creek	Kauri Creek	Emerald Creek
Primary	Apr' 2002	Apr' 2002	NA	Mar' 2003	NA
Secondary	Apr' 2002	Apr' 2002	Mar' 2003	Mar' 2003	Mar' 2003
Agricultural	Apr' 2002	Apr' 2002	Mar' 2003	NA	Mar' 2003

Day one and at 7 days intervals thereafter until 9 months after collection. For identification, fungi were mounted in water and lactic acid. Measurements were made from fresh material mounted in water. Attempts were made to isolate single spore cultures of new and interesting fungi.

Number of species, and frequencies of occurrence of each species were recorded and calculated for each sampling site. Frequency of occurrence was calculated based on the following formula:

$$\frac{\text{Number of samples of wood that a particular fungal species occurred on}}{\text{Number of samples of wood examined}} \times 100\%$$

The number of species, their frequency and abundance was used to calculate the biodiversity index Brillouin (*HB*) (Magurran, 2004):

$$HB = \frac{\ln N! - \sum \ln n_i!}{N}$$

where n_i is the species abundance of the i^{th} species, and N the sum of abundance of all species in the community.

$$pi = \frac{ni}{\sum_{i=1}^{S} ni} \times 100\%, i = 1,2,3,...,S,$$

where p_i is percentage abundance of the i^{th} species, n_i is the number of samples with the i^{th} species, and S is the number of species in the community. Taxa with more than 3% abundance were classified as dominant fungi (Ho *et al.*, 2001). To compare community structure, all taxa were sorted in descending order by their abundance, and species-abundance distributions were plotted for each sample. To emphasise which were dominant and which were rare, taxa are presented in overall descending total abundance for the 12 sample sites.

Sørenson's similarity index was used to compare the fungal assemblages at different sites. Sørenson's similarity index expresses the measured species occurrences against the theoretically possible ones (Sørenson, 1948). Sørenson's index of similarity is calculated using the formula 2c/(a+b), where a = total number of species in the first community, b = total number of species in the second community, and c = number of species both communities have in common. Communities at all sites were first compared resulting in 66 combinations. This was followed by the comparison of the sites based on riparian vegetation resulting in 3 combinations.

Multivariate analysis (Kenkel and Booth, 1992) was performed to summarise and reveal underlying trends of fungal community structure to collection sites. To perform ordination of variables simultaneously (i.e. with variables positioned in the same ordination space), correspondence analyses were performed (Kenkel and Booth, 1992). A data matrix consisting of the numbers of colonised wood samples from each collection site and their frequencies of occurrence were subjected to correspondence analysis (Anon, 1995).

Results

Species diversity and richness

Fungal sporulation was observed from the first week until 9 months from the collection date. A total of 162 fungal taxa were recorded from 600 wood samples from the 12 sites within the Barron river catchment (Table 2), including 101 ascomycetes and 61 anamorphic fungi (56 hyphomycetes; 5 coelomycetes). An average of 2.03 taxa per woody substrate occurred at each site, with a range of 1.3 - 2.84 taxa per sample per site.

Most ascomycete species belonged to the families *Annulatascaceae* (20 species), *Halosphaeriaceae* (20 species) and *Lophiostomataceae sensu* Barr (1979) (10 species) and also many species whose taxonomic placement are uncertain (Table 3). *Annulatascus velatisporus* was most common, appearing in all the 12 sites, followed by *Canalisporium pulchrum, Massarina australiensis* and *Massarina thalassioidea* in 10 sites, followed by *Aquaticola hyalomura, Lophiostoma ingoldianum, Ophioceras dolichostomum* and *Savoryella lignicola* in 9 sites each.

Pristine and agricultural zones had higher species richness than regrowth sites, with >100 taxa (Table 2). The pristine zone at Kauri creek (KP) had the greatest species richness (142 taxa). In contrast, four out of five regrowth zones had <100 species, with the Clohesy regrowth site (CR) having the lowest species richness, 63 taxa (1.3 species per wood sample).

Table 2. Diversity and species richness of freshwater fungi at various sites.

	CP*	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV
Total number of species	35	31	39	61	45	51	32	29	56	41	36	25
Total number of isolates	114	63	120	107	91	100	72	110	142	89	111	102
Number of taxa per sample	2.28	1.3	2.4	2.14	1.82	2	1.44	2.2	2.84	1.78	2.22	2.04
Brillouin's index	1.25	1.21	1.29	1.47	1.34	1.4	1.22	1.21	2.03	1.35	1.27	1.26

*CP = Clohesy Pristine, CR = Clohesy Regrowth, CV = Clohesy Agricultural, DP = Davies Pristine, DR = Davies Regrowth, DV = Davies Agricultural, ER = Emerald Regrowth, EV = Emerald Agricultural, KP = Kauri Pristine, KR = Kauri Regrowth, TR = Tinaroo Regrowth and TV = Tinaroo Agricultural.

Dominance

Species-abundance distributions (Fig. 2) showed that only a few species dominated at each site (percentage abundance ≥ 3%). Among the 12 sites, the most abundant taxa were *Massarina australiensis* from Clohesy River Agricultural (CV) zone (15% of the total occurrence of the fungi from the site), followed by *Canalisporium pulchrum* from Clohesy Pristine (CP) zone (14%; Table 3). There was moderate overlap of dominant species among the sites. All sites had many rare taxa that appeared only once, except for the Tinaroo Creek Agricultural site (TV) where every taxon was recorded at least twice. There were also taxa with intermediate abundance (1-3% of the total occurrence of fungi) in all sites.

Similarity

Similarity indices were calculated among all 12 sites to evaluate the similarity of freshwater fungal communities at different sites (Table 4). Similarity was greatest between Emerald Creek regowth zones (ER) and Tinaroo creek Agricultural zone (TV) (36%) and lowest between Clohesy pristine (CR) and Tinaroo regrowth (TR) (5%), Clohesy regrowth (CR) and Tinaroo agricultural (TV) (5%). For sites on the same stream, similarity was greatest for Clohesy River (18% to 31%) and Davies creek (25% to 27%) sites. The least similarity between the sites on the same stream was for Tinaroo creek, where the regrowth zone (TR) and agricultural zone (TV) had a similarity of 16%.

Multivariate analysis

Multivariate analysis showed that samples from sites Davies Creek (DP, DR, DV) and Emerald Creek (ER, EV) grouped together, while in Clohesy Creek only the pristine and regrowth zones (CP, CV) grouped together.

Table 3. Average % abundance of lignicolous freshwater fungi in all the 12 sites, in decreasing order. See Table 2 for abbreviation.

Species Name	CP	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV	Average % abundance
Massarina australiensis	3.5	3.2	15	3.7	7.7	3	-	-	0.7	3.4	11.7	6.9	4.9
Annulatascus velatisporus	6.1	4.8	5.8	3.7	6.6	5	2.8	9.1	1.4	4.5	2.7	4.9	4.8
Canalisporium pulchrum	14	4.8	4.2	0.9	-	3	8.3	5.5	4.9	3.4	5.4	-	4.5
Lophiostoma ingoldianum	-	6.3	0.8	2.8	7.7	1	9.7	11.8	2.8	-	5.4	-	4
Massarina thalassioidea	-	11.1	0.8	0.9	2.2	1	5.6	5.5	10.6	1.1	4.5	-	3.6
Aquaticola ellipsoidea	-	6.3	-	2.8	2.2	3	-	-	3.5	5.6	2.7	5.9	2.7
Anthostomella aquatica	10.5	1.6	1.7	-	-	-	2.8	4.5	6.3	3.4	-	-	2.6
Acanthophysis-like taxon	6.1	7.9	-	6.5	2.2	-	2.8	-	2.1	-	-	-	2.3
Savoryella aquatica	3.5	4.8	-	2.8	1.1	1	-	5.5	-	4.5	3.6	-	2.2
Ophioceras dolichostomum	4.4	4.8	4.2	1.9	1.1	1	-	-	0.7	5.6	0.9	-	2
Lophiostoma bipolare	6.1	-	-	2.8	3.3	-	2.8	-	2.1	-	-	6.9	2
Helicomyces roseus	-	1.6	-	2.8	5.5	6	4.2	-	1.4	-	1.8	-	1.9
Annulatascus biatriisporus	1.8	1.6	3.3	-	1.1	-	-	4.5	-	-	6.3	3.9	1.9
Clohesyomyces aquaticus	-	-	5.8	4.7	1.1	3	1.4	-	-	2.2	-	2.9	1.8
Aquaphila albicans	-	-	-	5.6	2.2	1	4.2	-	-	3.4	4.5	-	1.7
Annulatascus triseptatus	-	-	-	1.9	1.1	-	-	-	0.7	3.4	9.9	2.9	1.7
Quintaria submersa	2.6	3.2	3.3	1.9	5.5	3	-	-	-	-	-	-	1.6
Sporoschisma nigroseptatum	0.9	-	-	0.9	4.4	1	-	0.9	-	4.5	0.9	5.9	1.6
Aquaticola hyalomura	3.5	3.2	-	2.8	1.1	1	-	-	1.4	3.4	0.9	2	1.6
Halosarpheia aquatica	-	1.6	6.7	-	-	2	1.4	5.5	-	1.1	-	-	1.5
Kirschsteiniothelia elaterascus	4.4	4.8	4.2	0.9	-	3	-	-	-	-	-	-	1.4
Quintaria sp.	-	-	-	-	-	-	8.3	8.2	-	-	-	-	1.4
Mamillisphaeria dimorphospora	-	-	-	-	-	7	1.4	-	-	-	5.4	2	1.3
Savoryella lignicola	0.9	-	-	1.9	1.1	4	1.4	-	1.4	1.1	0.9	2.9	1.3
Dactylaria tunicata	0.9	-	-	1.9	1.1	1	2.8	0.9	0.7	4.5	-	-	1.1
Xylomyces elegans	-	-	-	-	-	4	-	0.9	1.4	3.4	-	3.9	1.1
Rivulicola incrustata	0.9	-	-	0.9	4.4	-	-	0.9	-	-	5.4	-	1
Aniptodera lignatilis	-	-	-	0.9	1.1	1	1.4	5.5	1.4	1.1	-	-	1
Jahnula bipolaris	0.9	1.6	0.8	0.9	-	2	-	-	-	-	-	5.9	1
Aquaticola longicolla	3.5	3.2	-	-	-	-	-	-	0.7	4.5	-	-	1
Submersisphaeria aquatica	-	-	4.2	-	-	-	-	-	-	-	-	6.9	0.9
Cataractispora appendiculata	0.9	-	-	0.9	-	-	-	2.7	3.5	1.1	1.8	-	0.9
Savoryella fusiformis	-	-	-	-	-	-	8.3	-	1.4	-	-	-	0.8
Jahnula australiensis	3.5	3.2	-	0.9	-	2	-	-	-	-	-	-	0.8
Chaetosphaeriaceae sp.	-	-	-	1.9	-	2	-	-	3.5	-	-	2	0.8
Aniptodera chesapeakensis	-	-	-	-	-	-	1.4	4.5	2.1	1.1	-	-	0.8
Nais inornata	-	-	4.2	-	-	-	-	-	0.7	-	-	3.9	0.7
Helicosporium hiospiroides	-	-	-	-	-	-	5.6	0.9	-	2.2	-	-	0.7
Delortia palmicola	-	-	-	1.9	1.1	1	-	0.9	-	-	-	2.9	0.7
Acrogenospora sphaerocephala	-	-	-	0.9	-	-	-	5.5	1.4	-	-	-	0.6

Table 3. Average % abundance of lignicolous freshwater fungi in all the 12 sites.

Species Name	CP	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV	Average % abundance
Halosarpheia retorquens	-	-	-	-	-	-	-	1.8	0.7	2.2	-	2.9	0.6
Ellisembia leonense	0.9	1.6	1.7	-	-	-	-	-	3.5	-	-	-	0.6
Aniptodera lignicola	2.6	1.6	3.3	-	-	-	-	-	-	-	-	-	0.6
Tripterosporaceae sp.	-	-	-	0.9	1.1	-	-	-	-	4.5	0.9	-	0.6
Quintaria aquatica	0.9	-	-	1.9	-	1	2.8	-	-	-	0.9	-	0.6
Coelomycete sp. 1	-	-	-	-	-	-	2.8	-	1.4	2.2	0.9	-	0.6
Trichoderma sp.	2.6	3.2	-	-	-	-	1.4	-	-	-	-	-	0.6
Aquaticola tropica	-	-	-	-	-	2	1.4	3.6	-	-	-	-	0.6
Jahnula systyla	-	-	0.8	-	-	1	1.4	-	-	-	3.6	-	0.6
Xylomyces giganteus	-	-	-	-	-	-	-	-	5.6	1.1	-	-	0.6
Halosarpheia lotica	-	1.6	5	-	-	-	-	-	-	-	-	-	0.5
Massarina peerallyi	-	-	-	-	-	3	-	0.9	0.7	-	-	2	0.5
Tamsiniella labiosa	4.4	-	-	-	-	-	-	-	2.1	-	-	-	0.5
Canalisporium variabile	-	-	-	0.9	2.2	1	-	-	2.1	-	-	-	0.5
Ophioceras commune	0.9	1.6	0.8	-	-	-	-	-	0.7	1.1	0.9	-	0.5
Neta angliae	-	-	-	-	-	-	-	-	-	-	-	5.9	0.5
Sporoschisma juvenile	-	-	-	1.9	1.1	2	-	-	-	-	0.9	-	0.5
Sporormiella sp.	-	-	5.8	-	-	-	-	-	-	-	-	-	0.5
Pseudohalonectria lignicola	-	-	4.2	-	-	-	-	0.9	0.7	-	-	-	0.5
Sporoschisma saccardoi	-	-	-	-	1.1	-	-	-	-	3.4	0.9	-	0.4
Lophiostoma lunisporum	1.8	1.6	-	0.9	-	1	-	-	-	-	-	-	0.4
Bactrodesmium longisporum	-	-	-	0.9	3.3	-	-	-	-	-	0.9	-	0.4
Coniochaeta sp.	-	-	-	-	-	5	-	-	-	-	-	-	0.4
Dictyosporium elegans	-	-	-	-	-	-	-	-	-	-	-	4.9	0.4
Quintaria lignatilis	-	-	-	1.9	-	3	-	-	-	-	-	-	0.4
Aquasphaeria dimorphospora	-	-	-	0.9	2.2	1	-	-	0.7	-	-	-	0.4
Coelomycete sp. 2	-	-	-	-	-	2	-	2.7	-	-	-	-	0.4
Jahnula aquatica	-	-	0.8	0.9	-	-	2.8	-	-	-	-	-	0.4
Annulatascus fusiformis	-	-	-	0.9	3.3	-	-	-	-	-	-	-	0.4
Dictyosporium sp.	-	1.6	1.7	-	-	-	-	-	0.7	-	-	-	0.3
Trematosphaeria confusa	-	-	0.8	-	2.2	-	-	0.9	-	-	-	-	0.3
Dactylaria uniseptata	-	-	-	-	-	-	-	-	-	-	-	3.9	0.3
Hyphomycete sp.	-	-	-	-	2.2	1	-	-	0.7	-	-	-	0.3
Ellisembia opaca	-	-	-	-	-	-	-	-	-	1.1	2.7	-	0.3
Micropeltopsis quinquecladiopsis	-	-	-	-	-	-	-	-	-	1.1	2.7	-	0.3
Clohesyomyces sp.	-	-	-	-	-	1	-	2.7	-	-	-	-	0.3
Digitodesmium recurvum	-	-	-	-	-	-	-	-	-	-	3.6	-	0.3
Cryptophiale multiseptata	-	-	0.8	-	1.1	-	-	0.9	0.7	-	-	-	0.3
Nectria sp.	-	-	-	-	-	-	-	-	3.5	-	-	-	0.3
Helicosporium gigaspora	-	-	-	-	1.1	1	1.4	-	-	-	-	-	0.3
Helicosporium griseum	-	1.6	0.8	0.9	-	-	-	-	-	-	-	-	0.3

Table 3. Average % abundance of lignicolous freshwater fungi in all the 12 sites.

Species Name	CP	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV	Average % abundance
Rivulicola aquatica	-	-	3.3	-	-	-	-	-	-	-	-	-	0.3
Savoryella longispora	0.9	1.6	0.8	-	-	-	-	-	-	-	-	-	0.3
Helicosporium decumbens	-	-	-	-	-	-	-	-	2.1	1.1	-	-	0.3
Sporoschisma uniseptatum	0.9	-	-	-	1.1	1	-	-	-	-	-	-	0.2
Ellisembia opaca	-	-	-	-	-	-	-	-	-	-	-	2.9	0.2
Tiarosporella paludosa	-	-	-	-	-	-	-	-	-	-	-	2.9	0.2
Lophiosphaeria sp.	-	-	-	0.9	-	2	-	-	-	-	-	-	0.2
Ophioceras arcuatisporum	-	-	-	1.9	-	1	-	-	-	-	-	-	0.2
Melanomma sp.	-	-	-	-	-	-	2.8	-	-	-	-	-	0.2
Cancellidium applanatum	0.9	-	-	1.9	-	-	-	-	-	-	-	-	0.2
Herpotrichia sp.	-	-	-	0.9	1.1	-	-	-	0.7	-	-	-	0.2
Stilbella fusca	-	1.6	-	-	-	-	-	-	-	1.1	-	-	0.2
Lophiostoma frondisubmersum	0.9	-	0.8	0.9	-	-	-	-	-	-	-	-	0.2
Paraniesslia tuberculata	-	-	-	0.9	-	-	-	-	0.7	-	0.9	-	0.2
Massarina corticola	0.9	1.6	-	-	-	-	-	-	-	-	-	-	0.2
Nais aquatica	-	-	-	-	-	-	-	-	1.4	-	0.9	-	0.2
Vaginatispora aquatica	-	-	-	-	-	-	1.4	0.9	-	-	-	-	0.2
Annulatascus lamtuensis	-	-	-	-	-	-	-	-	-	2.2	-	-	0.2
Phaeosphaeria culmorum	-	-	-	-	-	-	-	-	-	2.2	-	-	0.2
Chloridium sp.	-	-	-	-	2.2	-	-	-	-	-	-	-	0.2
Ophioceras venezuelense	-	-	-	-	-	-	-	-	2.1	-	-	-	0.2
Helicomyces torquatus	-	-	-	-	1.1	1	-	-	-	-	-	-	0.2
Paecilomyces sp.	-	-	-	0.9	-	-	-	-	-	1.1	-	-	0.2
Torrentispora fibrosa	-	-	-	0.9	1.1	-	-	-	-	-	-	-	0.2
Aquaticola rhomboidea	-	-	-	-	-	-	-	-	-	1.1	0.9	-	0.2
Glomerella sp.	-	-	-	-	-	-	-	-	-	1.1	0.9	-	0.2
Nectria cinnabarina	-	-	-	-	-	-	-	-	-	1.1	0.9	-	0.2
Hymenoscyphus varicosporoides	-	-	-	-	-	-	-	-	-	-	-	2	0.2
Aquaticola lignicola	-	-	-	0.9	-	1	-	-	-	-	-	-	0.2
Annulatascus aquaticus	-	-	-	1.9	-	-	-	-	-	-	-	-	0.2
Aquaticola lutea	-	-	-	1.9	-	-	-	-	-	-	-	-	0.2
Chalara sp.	0.9	-	-	0.9	-	-	-	-	-	-	-	-	0.2
Halosarpheia viscosa	-	-	-	-	-	1	-	-	0.7	-	-	-	0.1
Cataractispora aquatica	-	-	-	0.9	-	-	-	-	0.7	-	-	-	0.1
Immersiella immersa	-	-	-	-	-	-	-	-	0.7	-	0.9	-	0.1
Sporidesmium hyalospermum	-	1.6	-	-	-	-	-	-	-	-	-	-	0.1
Monotosporella sphaerocephala	-	-	0.8	-	-	-	-	-	0.7	-	-	-	0.1
Ascomycete sp.	-	-	-	-	-	-	-	-	1.4	-	-	-	0.1
Astrosphaeriella maquilingiana	-	-	-	-	-	-	-	-	1.4	-	-	-	0.1
Cataractispora bipolaris	-	-	-	-	-	-	-	-	1.4	-	-	-	0.1
Lollipopaia sp.	-	-	-	-	-	-	-	-	1.4	-	-	-	0.1

Table 3. Average % abundance of lignicolous freshwater fungi in all the 12 sites.

Species Name	CP	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV	Average % abundance
Astrosphaeriella trochus	-	-	-	-	-	-	1.4	-	-	-	-	-	0.1
Clohesia aquatica	-	-	-	-	-	-	1.4	-	-	-	-	-	0.1
Phaeonectriella appendiculata	-	-	-	-	-	-	1.4	-	-	-	-	-	0.1
Pseudoproboscispora caudae-suis	-	-	-	-	-	-	1.4	-	-	-	-	-	0.1
Halosarpheia aquadulcus	-	-	-	-	-	-	-	-	-	1.1	-	-	0.1
Helicoon gigantisporum	-	-	-	-	-	-	-	-	-	1.1	-	-	0.1
Tiarosporella sp.	-	-	-	-	-	-	-	-	-	1.1	-	-	0.1
Annulatascus tropicalis	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Dictyosporium giganticum	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Diplodia sp.	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Glonium sp.	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Iodosphaeria aquatica	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Melanomma australiense	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Saccardoella minuta	-	-	-	-	1.1	-	-	-	-	-	-	-	0.1
Ascotaiwania pallida	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Massarina aquatica	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Oxydothis sp.	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Sporidesmium sp.	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Sporormiella minima	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Sporoschisma parcicuneatum	-	-	-	-	-	1	-	-	-	-	-	-	0.1
Aqualignicola hyalina	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Aquaticola trisepata	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Candelosynnema ranunculosporum	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Cataractispora viscosa	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Dictyochaeta daphnioides	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Gonytrichum caesium	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Massarina purpurascens	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Sporoschismopsis australiensis	-	-	-	0.9	-	-	-	-	-	-	-	-	0.1
Dictyosporium digitatum	-	-	-	-	-	-	-	0.9	-	-	-	-	0.1
Monodictys putredinis	-	-	-	-	-	-	-	-	-	-	0.9	-	0.1
Digitodesmium elegans	0.9	-	-	-	-	-	-	-	-	-	-	-	0.1
Spadicoides sp.	0.9	-	-	-	-	-	-	-	-	-	-	-	0.1
Janetia curviapices	-	-	0.8	-	-	-	-	-	-	-	-	-	0.1
Phaeosphaeria sylvatica	-	-	0.8	-	-	-	-	-	-	-	-	-	0.1
Phomatospora aquatica	-	-	0.8	-	-	-	-	-	-	-	-	-	0.1
Ascitendus austriaca	-	-	-	-	-	-	-	-	0.7	-	-	-	0.1
Eutypa sp.	-	-	-	-	-	-	-	-	0.7	-	-	-	0.1
Lasiosphaeria sp.	-	-	-	-	-	-	-	-	0.7	-	-	-	0.1
Phomatospora berkeleyi	-	-	-	-	-	-	-	-	0.7	-	-	-	0.1
Pleurophragmium malayense		-	-	-	-	-	-	-	0.7	-	-	-	0.1

Clohesy creek agricultural zone (CV), Kauri pristine (KP) and Tinaroo agricultural (TV) were quite far removed from the rest of the collection (Fig. 3). In ecological terms, fungal assemblages on submerged wood in the sites within the same stream, had more similarity and the type of riparian zone had lesser effect on the species assemblages.

Discussion

Number of species

This is the first large-scale study (12 sites spread across 5 streams) of lignicolous freshwater fungi in the wet heritage tropical forests of Australia. An average of 40 species was collected from a total of 50 woody substrates at each site. Within a given stream, higher numbers of species were observed at pristine zones, with 35, 61 and 56 at the Clohesy (CP), Davies (DP) and Kauri (KP) sites respectively (Table 2). Earlier, studies at Mt. Lewis and Lake Barrine, Queensland, Australia (Hyde and Goh, 1997, 1998a) produced similar results. Several studies of freshwater fungi, have been carried out on naturally occurring submerged woody substrates around the world, and the numbers of taxa identified from single collections varies from as low as 28 taxa from River Coln, Britain (Hyde and Goh, 1998a) to more than 100 fungal taxa from the USA (Shearer and Crane, 1986) and Hong Kong (Ho *et al*., 2001, Tsui *et al*., 2000). Differences in the number of taxa recorded have been attributed to geographical variations such as temperate/tropical conditions or isolation of islands, physical attributes such as temperature, concentration of dissolved oxygen, perennial state of the water body, size of the stream, degree of shading by riparian vegetation (Ho *et al*., 2001, 2002), and period of incubation of collected substrates (Tsui *et al*., 2000). The lower biodiversity in tropical Australia streams, in comparison to other sub-tropical regions, may be because sub-tropical regions can harbor both temperate and tropical species (Ho *et al*., 2001).

Number of fungi per sample

In general, species richness declines with increase in habitat modification. In this study, there was a remarkable difference in species richness at different sites on the same stream and a general trend was observed in all streams: species richness was highest in the pristine zone (average taxa per woody substrate, 2.42), where shading by riparian vegetation and organic input was highest, whereas regrowth zones, which had moderate riparian cover and moderate organic input, had the lowest species richness (average taxa per

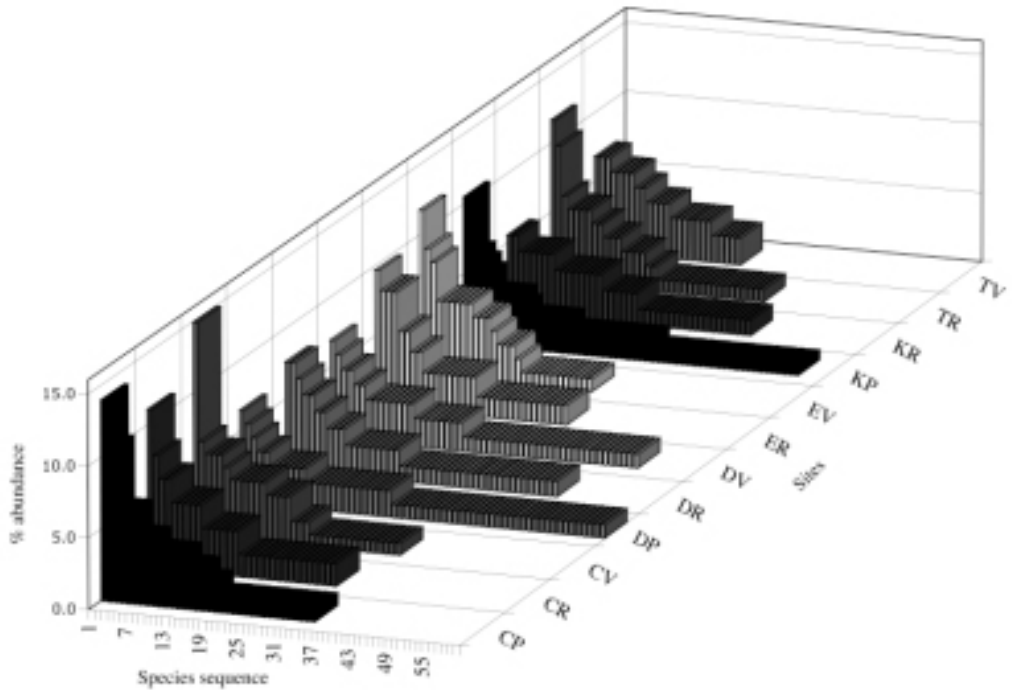

Fig. 2. Species-abundance distributions of lignicolous freshwater fungi collected from various sites. See Table 2 for abbreviation.

woody substrate, 1.71). The reduction of species richness is positively correlated with the reduction of organic input. However, the agricultural zone with the least riparian cover had a higher species richness (average taxa per woody substrate, 2.16) than the regrowth zone. The increase in species richness at the agricultural zones may be attributed to the replacement of organic input from allochthonous to autochthonous sources, as there is more light, due to the reduced riparian cover, which enables growth of plants in the stream (Bärlocher, 1992). Alternatively, due to the presence of herbaceous plants and the reduced speed of water currents, there is an increased trapping of organic material, therefore increasing fungal species richness. These results should be interpreted with caution, due to the lack of information on water quality at the time of collection. Given that the data collected were at the same geographical location in the same season, the likelihood that geographical separation, isolation, and seasonal changes may have effect on the species richness of freshwater fungi, is minimal.

Table 4. Sorenson's similarity index showing similarity indices within 12 sites. Shaded values represent similarities greater than 25%.

	CP	CR	CV	DP	DR	DV	ER	EV	KP	KR	TR	TV
CP		0.31	0.18	0.19	0.15	0.17	0.10	0.14	0.15	0.14	0.05	0.10
CR			0.26	0.17	0.15	0.19	0.13	0.13	0.16	0.17	0.15	0.05
CV				0.13	0.10	0.14	0.10	0.14	0.14	0.11	0.08	0.10
DP					0.25	0.27	0.13	0.10	0.17	0.18	0.21	0.11
DR						0.25	0.14	0.14	0.18	0.17	0.22	0.13
DV							0.18	0.15	0.15	0.15	0.18	0.14
ER								0.19	0.14	0.18	0.13	0.36
EV									0.16	0.17	0.09	0.09
KP										0.19	0.13	0.08
KR											0.23	0.12
TR												0.16
TV												

Species abundance

The relative abundance distribution describes how the individual in a community are partitioned among rare and common species (Fig. 2). A community containing many rare species and relatively few common species is associated with a community in equilibrium. Likewise, an equitable share of individuals amongst species groups is associated with non-equilibrium behaviour resulting from perturbation due to disturbance, pollution or immigration (Pachepsky *et al*., 2001). A total of 29 taxa were found dominant in more than 2 sites. All sites with the exception of Tinaroo Creek agricultural zone (TV) had a majority of rare taxa (Fig. 2). Higher evenness was recorded at TV (Fig. 2). At TV, a majority of the wood substrates collected were black, covered with carbon, which might be due to a wildfire near that region (Vijaykrishna pers. obs), which can be attributed to the non-equilibrium or high evenness of the fungal communities at the site.

Diversity

Shannon's index of diversity is the most popular choice of diversity index for various biodiversity studies, and has been mainly used for studying freshwater fungal communities. However, when the randomness of the sample cannot be guaranteed (Southwood and Henderson, 2000), or if the community is completely censured and every individual accounted for, the Brillouin index, is the appropriate form of the information index (Pielou, 1969, 1975) and has often been used (Lo *et al*., 1998; Dans *et al*., 1999; Ito and Imai, 2000). In this

study, at the Emerald creek regrowth (ER) site, the number of wood pieces was comparatively lesser than the other sites. This might have been due to rapid flow of water from the waterfall at its immediate vicinity, and therefore random selection of samples was impossible. Brillouin's index (Magurran, 2004) was therefore deemed appropriate for this study. Brillouin's index of diversity shows the diversity of the actual collection, therefore statistical tests are not necessary (Magurran, 2004), and is mathematically superior (Laxton, 1978).

The uniqueness of Kauri Creek pristine zone (KP), is shown by a higher diversity, which is directly proportional to the highest species richness. In comparison to other sites, KP was at the highest altitude, with comparatively higher riparian vegetation and shade. The extent of shade provided by the riparian vegetation has shown to affect invertebrate community (Dudgeon, 1989; Dudgeon and Corlett, 1994) and also fungi (Tsui *et al*. 2000).

Correspondence analysis, involving fungal species and their frequencies show higher similarity of taxa along the same stream (Fig. 3a,b), especially in the Clohesy River, Davies Creek and Emerald Creek. This is also due to high species similarity between the sites on the same stream (Table 4). Due to the unidirectional movement of water, the upstream communities (pristine) should have an influence on species composition of the downstream communities (regrowth, agricultural).

Composition of fungal groups

One of the most striking results of this study when compared to earlier studies of lignicolous freshwater fungi in both tropical and temperate regions is the teleomorph anamorph ratio. A surprisingly high number of ascomycetes (teleomorphic fruiting bodies) as compared to anamorphic spores (101: 59) were recorded from submerged samples in this study. In a comparative study of fungal communities on submerged wood in tropical regions and sub tropical regions, Ho *et al.,* (2001) showed that, except in Malaysia, the number of ascomycetes were always lower than the anamorphic taxa in submerged samples. However the reason for the ratio of more teleomorphic stages in this study as compared to other studies in freshwater habitats is unknown. Shearer (1992) commented that wood may play an important role as a site for genetic recombination in aquatic hyphomycetes, and a number of sexual states for these fungi have been found on wood (Webster, 1992).

Among the teleomorphs, pyrenomycetes and loculoascomycetes dominate the ascomycete assemblage, with representatives in the families *Annulatascaceae*, *Halosphaeriaceae* and *Lophiostomataceae*. It is not surprising, that in this study only one discomycete (*Hymenoscyphus*

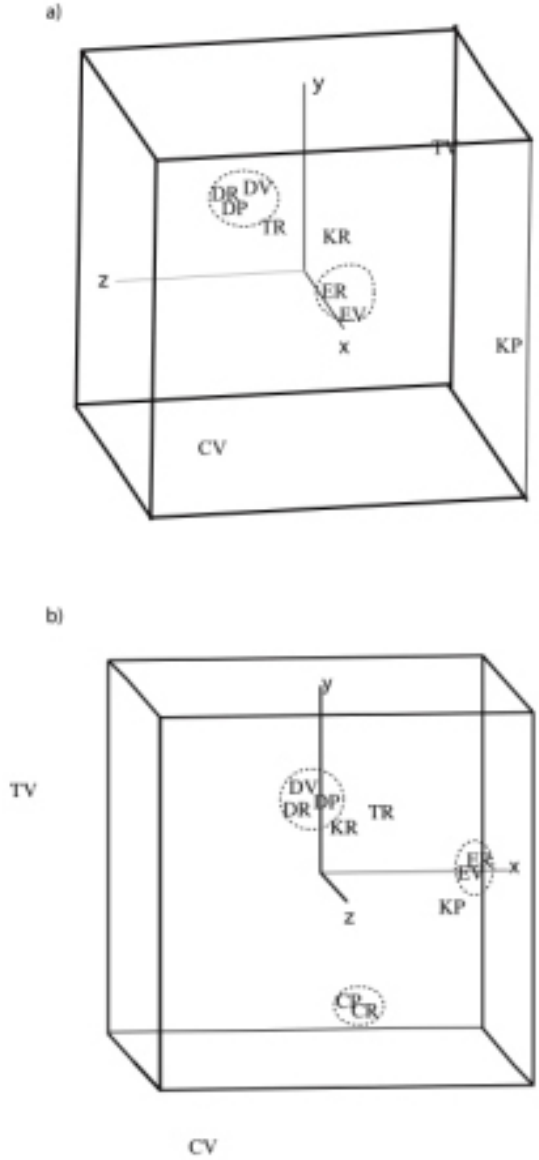

Fig. 3. Three dimentional correspondence ordination of taxa and fungal communities recorded from submerged wood from various sites. For site codes see Fig. 2.

varicosporoides) was recorded from Tinaroo Agricultural. Out of a total 111 discomycetes recorded from submerged wood worldwide, only *Hymenoscyphus malawiensis*, *Pezoloma rhodocarpus*, *Cudoniella indica*, *Saccobolus beckii* (Fisher and Spooner, 1987; Udaiyan, 1989; Webster *et al*., 1995a) and more recently *Hymenoscyphus varicosporoides* (Sivichai *et al.*, 2003) have been reported from the tropics. Hyde *et al.,* (1997) commented that the lack of discomycetes in tropical streams is most striking. It has been argued

that most of the discomycetes from temperate regions occur on graminaceous substrata (Shearer, 1993), and those substrates have been poorly studied in the tropics. However recently, studies on grasses and sedges in freshwater habitats of Hong Kong yielded no discomycetes (Wong and Hyde, 2001), indicating scarcity of this group of fungi in the tropics (Cai *et al*., 2003b).

The interpretation of lack of discomycetes in freshwater habitats should be noted with caution, as studies on freshwater fungi in the tropics have largely been conducted on naturally occurring submerged wood and wood baits immersed in streams. Sivichai and Jones (2003) noted that the majority of Ingoldian fungi (hyphomycetes actively growing and sporulating under water) have ascomycete connections, and with the highest species number in the genus *Hymenoscyphus* (discomycete). Furthermore, it has been shown that after several months of incubation discomycetes, produce their teleomorphic fruiting structures on wood (Sivichai *et al*., 2003). A large number of Ingoldian fungi are found on submerged leaves and spores trapped in air bubbles in streams (Bärlocher, 1992), and many have been recorded from tropical and subtropical regions (Bhat and Chien, 1990; Au *et al*., 1992a,b; Chan *et al*., 2000a,b). Sivichai *et al.,* (2003) suggested the use of different techniques to survey for tropical freshwater discomycetes might yield a wide range of species.

Impact of riparian vegetation

Statistical comparison of species from different sites using the Multivariate Correspondence analyses (Figs. 4a,b) does not provide any clear evidence of impact of riparian vegetation on the species composition. However, the similarity in species composition within streams is recognised, which is also shown in the Sørenson's similarity index (Table 4), with high similarity between species isolated from different sites from the same stream. This shows that fungal species of the higher reaches of the stream, obviously have an effect on the establishment of fungal communities down stream. Furthermore, the frequent identification of apparently same fungal taxa from different riparian zones suggests that riparian habitat preference of individual taxa is minimum. Major changes in overall abundance, and species richness was observed. A general trend with decrease of species abundance and richness with increased anthropogenic changes on the riparian zone is observed.

Conclusions

To examine the effects of riparian vegetation on taxonomic composition and distribution of lignicolous freshwater fungi, we studied fungal

communities in three different kinds of riparian vegetation. Results indicate that the type of riparian vegetation is a factor that determines species richness of lignicolous freshwater fungi. A clear trend was observed in all streams. There was a decline in species richness with increased habitat exploitation. Decomposition of organic matter has shown to decrease with decline in species richness, which might indirectly affect the overall biodiversity of the ecosystem (McGrady-Steed *et al*., 1997). Therefore, these results provide additional reasons for conserving species richness in relatively intact ecosystems and restoring diversity in degraded systems. An extension of the results obtained through this study would be to understand the effects of decline in fungal species richness to other communities, especially organisms that feed on woody debris and other organic matter (e.g. invertebrates). Also to further understand the reasons for variation in species richness manipulative experiments involving the terrestrial detritus input would provide valuable information regarding stream ecology.

In this study we also found that the type of riparian vegetation has little effect on the taxonomic composition of lignicolous freshwater fungi. Similarity between different sites of the same stream demonstrate that the fungal communities from the upper reaches of the stream have obvious effects in determining the taxonomic composition of downstream communities. It is intriguing, how the upper reaches of the stream continue to maintain fungal populations, with a constant drainage of spores and hyphae downstream, due to the unidirectional rapid flow of water in small streams (Bärlocher, 1992). Comparative studies of fungal assemblages from both submerged wood within the stream and decaying wood beside the stream would probably provide evidence of a vessel for the continued occurrence of fungal assemblages in the upper reaches of the stream.

Most dominant fungal taxa identified in this study belonged to the families *Annulatascaceae* and *Lophiostomataceae*. The diversity estimates of the present study relied on the production of fruiting structures under incubation, which might, however, underestimate the actual species composition present on submerged wood. This is because certain fungi may not sporulate when removed from their natural habitat. PCR based identification methods, which have primarily been used for bacteria, has gained popularity in fungal ecology (Nikolcheva *et al*., 2003). Future studies involving the combination of traditional methods and PCR based methods (e.g. DGGE) should be used in order to provide additional insight in to the ecology of fungi on submerged wood.

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References

Abdel-Raheem, A. and Shearer, C.A. (2002). Extracellular enzyme production by freshwater ascomycetes. Fungal Diversity 11: 1-19.

Anon. (1995). *JMP® Statistics and Graphics Guide*. Version 3.1. SAS Institute, Cary NC.

Au, D.W.T., Hodgkiss, I.J., and Vrimoed, L.L.P. (1992a). Decomposition of *Bauhinia purpurea* leaf litter in a polluted and unpolluted Hong Kong waterway. Canadian Journal of Botany 70: 1061-1070.

Au, D.W.T., Hodgkiss, I.J., and Vrimoed, L.L.P. (1992b). Fungi and cellulolytic activity associated with decomposition of *Bauhinia purpurea* leaf litter in a polluted and unpolluted waterway. Canadian Journal of Botany 70: 1071-1079.

Bärlocher, F. (1992). *The Ecology of Aquatic Hyphomycetes*. Berlin: Springer-Verlag.

Barr, M. E. (1979). A classification of Loculoascomycetes. Mycologia 71: 935-957.

Benson, L.J. and Pearson, R.G. (1993). Litter inputs to a tropical Australian rainforest stream. Australian Journal of Ecology 18: 377-383.

Bhat, D.J. and Chien, C.Y. (1990). Water-Borne hyphomycetes found in Ethiopia. Transactions of the Mycological society of Japan 31: 147-158.

Bucher, V.V.C., Hyde, K.D., Pointing, S.B., and Reddy, C.A. (2004). Production of wood decay enzymes mass loss and lignin solubilization in wood by marine ascomycetes and their anamorphs. Fungal Diversity 15: 1-14.

Cai, L., Lumyong, P., Zhang, K.Q. and Hyde, K.D. (2002a). New species of *Annulatascus* and *Saccardoella* from the Philippines. Mycotaxon 84: 255-263.

Cai, L., Tsui, C.K.M., Zhang, K.Q., and Hyde, K.D. (2002b). Aquatic fungi from Lake Fuxian, Yunnan, China. Fungal Diversity 9: 57-70.

Cai, L., Zhang, K.Q., McKenzie, E.H.C. and Hyde, K.D. (2003a). Freshwater fungi from bamboo and wood submerged in the Liput River in the Philippines. Fungal Diversity 13: 1-12.

Cai, L., Zhang, K.Q. and Hyde, K.D. (2003b). Freshwater Ascomycetes. Fungal Diversity Research Series 10: 275-324.

Cai, L., Zhang, K.Q. and Hyde, K.D. (2005). *Ascoyunnania chameleonia* gen. et sp. nov. a freshwater fungus collected from China and its microcyclic conidiation. Fungal Diversity 18: 1-8

Chan, S.Y., Goh, T.K, and Hyde, K.D. (2000a). Ingoldian fungi in Hong Kong. Fungal Diversity 5: 89-107.

Chan, S.Y., Goh, T.K, and Hyde, K.D. (2000b). Ingoldian fungi in Lam Tsuen River and Tai Po Kau Forest Stream, Hong Kong. Fungal Diversity 5: 109-118.

Dans, S.L., Reyes, L.M., Pedraza, S.N., Raga, J.A. and Crespo, E.A. (1999). Gastrointestinal helminths of the dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1928), off Patagonia in the southwestern Atlantic. Marine Mammal Science 15: 649-660.

Díez, J., Elosegi, A., Chauvet, E. and Pozo, J. (2002). Breakdown of wood in the Agera stream.

Freshwater Biology 47: 2205-2215.
Dolloff, C.A. and Webster, J.R. (2000). Particulate organic contributions from forests to streams: debris isn't so bad. In: *Riparian Management in Forests of the Continental eastern United States* (eds. E.S. Verry, J.W. Hombeck and C.A. Dolloff). Lewis Publishers, Boca Raton, Florida: 125-138.
Dudgeon, D. (1989). The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. Hydrobiologia 179:183-194.
Dudgeon, D. (1999). *Tropical Asian Streams*. Hong Kong University Press, Hong Kong.
Dudgeon, D. (2000). The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. Annual Review of Ecology and Systematics 31: 239-263.
Dudgeon, D. and Corlett, R. (1994). *Hills and Streams: an ecology of Hong Kong*. Hong Kong University Press, Hong Kong.
Fisher, P.J. and Spooner, B. (1987). Two new ascomycetes from Malawi. Transactions of the British Mycological Society 75: 201-206.
Fryar, S.C., Booth, W., Davies, J., Hodgkiss, I.J. and Hyde, K.D. (2004). Distribution of fungi on wood in the Tutong River, Brunei. Fungal Diversity 17: 17-38.
Fryar, S.C., Booth, W., Davies, J., Hodgkiss, I.J. and Hyde**,** K.D. (2005). Evidence of *in situ* competition between fungi in freshwater. Fungal Diversity 18: 59-71.
Goh, T.K. and Hyde, K.D. (1999). Fungi on submerged wood and bamboo in the Plover Cove Reservoir, Hong Kong. Fungal Diversity 3:57-85.
Goh, T.K. and Tsui, C.K.M. (2003). Key to common dematiaceous hyphomycetes from freshwater. Fungal Diversity Research Series 10: 325-343.
Gönczöl, J. and Révay, Á (2004). Fungal spores in rainwater: stemflow, throughfall and gutter conidial assemblages. Fungal Diversity 16: 67- 86.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, O., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.J., Sedell, J.R., Lienkaemper, G.W., Cromack, K. and Cummins, K.W. (1986). Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.
Hicks, B.J. (1997). Food webs in forest and pasture streams in the Waikato region: a study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. New Zealand Journal of Marine and Freshwater Research 31:651-664.
Ho, W.H., Hyde, K.D., Hodgkiss, I.J. and Yanna (2001). Fungal communities on submerged wood from streams in Brunei, Hong Kong and Malaysia. Mycological Research 105: 1492-1501.
Ho, W.H., Yanna, Hyde, K.D. and Hodgkiss, I.J. (2002). Seasonality and sequencial occurrence of fungi on wood submerged in Tai Po forest stream, Hong Kong. Fungal Diversity 10:21-43.
Hyde, K.D. and Goh, T.K. (1997). Fungi on submerged wood in a small stream on Mt Lewis, North Queensland, Australia. Muerllera 10: 145-157.
Hyde, K.D. and Goh, T.K. (1998a). Fungi on submerged wood in Lake Barrine, North Queensland, Australia. Mycological Research 102: 739-749.
Hyde, K.D. and Goh, T.K. (1998b). Fungi on submerged wood in the Riviere St Marie-Louis, The Seychelles. South African Journal of Botany 64: 330-336.
Hyde, K.D. and Goh, T.K. (1999a). Fungi on submerged wood from River Coln, England. Mycological Research 103:1561-1574.
Hyde, K.D., Wong, S.W. and Jones, E.B.G. (1997). Freshwater ascomycetes. In: *Biodiversity of Tropical Microfungi* (ed. K.D. Hyde). Hong Kong University Press, Hong Kong: 179-189.
Ito, A. and Imai, S. (2000). Ciliates from the cecum of capybara (*Hydrocheorus hydrochaeris*)

in Bolivia 2. The family Cycloposthiidae. Europian Journal of Protistology 36: 169-200.
Keller, E.A. and Swanson, F.J. (1979). Effects of large organic material on channel form and fluvial processes. Earth Surface Processes 4: 361-380.
Kenkel, N.C. and Booth, T. (1992). Multivariate analysis in fungal ecology. In: *The fungal Community: its organization and role in the ecosystem*. *2nd edn*. (eds. G.C. Carroll and D.T. Wicklow). Marcel Dekker, New York: 209-227
Laxton, R.R. (1978). The measure of diversity. Journal of Theoretical Biology 70: 51-67.
Lo, C.M., Morand, S. and Galzin, R. (1998). Parasite diversity and size relationship in three coral-reef fishes from French Polynesia. International Journal of Parasitology 28: 1695-1708.
Lodge, D.J. (1997). Factors related to diversity of decomposer fungi in tropical forests. Biodiversity and Conservation 6: 681-688.
Ludwig, J.A. and Reynolds, F.F. (1998). *Statistical Ecology: a primer on methods and computing*. John Wiley and Sons, Inc. New York.
Luo, J., Yin, J.F., Cai, L., Zhang, K. and Hyde, K.D. (2004). Freshwater fungi in Lake Dianchi, a heavily polluted lake in Yunnan, China. Fungal Diversity 16: 93-112.
Magurran, A.E. (2004). *Measuring Biological Diversity*. Blackwell Science, Oxford.
McGrady-Steed, J., Harris, P.M. and Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. Nature 390: 162-165.
Mosley, P.M. (1981). The influence of organic debris on channel morphology and bedload transport in a New Zealand forest stream. Earth surface Processes and Landforms 6: 571-579.
Nikolcheva, L.G., Cockshutt, A.M. and Bärlocher, F. (2003). Determining diversity of freshwater fungi on decaying leaves: comparison of traditional and molecular approaches. Applied and Environmental Microbiology 69: 2548-2554.
Pachepsky, E., Crawford, J.W., Brown, J.L. and Squire, G. (2001). Towards a general theory of biodiversity. Nature 410: 923-926.
Pascoal, C., Marvanová, L. and Cássio, F. (2005). Aquatic hyphomycete diversity in streams of Northwest Portugal. Fungal Diversity 19: 109-128.
Pielou, E.C. (1969). *An Introduction to Mathematical Ecology*. Wiley, New York.
Pielou, E.C. (1975). *Ecological Diversity*. Wiley InterScience, New York.
Sedell, J.R., Bisson, P.A., Swanson, F.J. and Gregory, S.V. (1988). What we know about large trees that fall in streams and rivers. In: *From the Forest to the Sea: a story of fallen trees* (eds. C. Maser, R.F. Tarrant, J.M. Trappe, and J.F. Franklin). General Technical Report PNW-GTR-229, USDA Forest Service, Pacific northwest Research Station; U.S. Department of the Interior Bureau of Land Management, Portland, Oregon: 47-81.
Sivichai, S. and Jones, E.B.G. (2003). Teleomorphic-anamorphic connections of freshwater fungi. Freshwater mycology. Fungal Diversity Research Series 10: 259-274.
Sivichai, S., Jones, E.B.G. and Hewyl-Jones, N.L. (2003). Lignicolous freshwater Ascomycota from Thailand: *Hymenoscyphus varicosporoides* and its *Tricladium* anamorph. Mycological Research 95: 340-346.
Shearer, C.A. (1992). The role of woody debris. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer Verlag, Berlin: 1-77.
Shearer, C.A. (1993). The freshwater ascomycetes. Nova Hedwigia 56: 1-33.
Shearer, C.A. (2001). The distribution of freshwater filamentous ascomycetes. In: *Trichomycetes and other Fungal Groups: Robert W. Lichtwardt Commemoration* (eds. J.K. Misra and B.W. Horn). Science Publishers, Inc. Enfield, New Hampshire: 225-292.
Shearer, C.A. and Crane, J.L. (1986). Illinios fungi XII Fungi and Myxomycetes from wood and leaves submerged in a freshwater swamp. Mycotaxon 25: 527-538.

Southwood, R. and Henderson, P.A. (2000). *Ecological Methods*. Blackwell Science, Oxford.
Sørenson, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Biologiske Skrifter Kongelige Danske Videnskabernes Selskab 5: 1-34.
Suberkropp, K. (1997). Annual production of leaf-decaying fungi in a woodland stream. Freshwater Biology 38: 169-178.
Tsui, C.K.M. and Hyde, K.D. (2004). Biodiversity of fungi on submerged wood in a stream and estuary in the Tai Ho Bay, Hong Kong. Fungal Diversity 15: 205-220.
Tsui, C.K.M., Hyde, K.D, and Hodgkiss, I.J. (2000). Biodiversity of fungi on submerged wood in Hong Kong streams. Aquatic Microbial Ecology 21: 289-298.
Udaiyan, K. (1989). Some interesting ascomycetes from water-cooling towers. Kavaka 17: 11-16.
Van Ryckegem, G. and Verbeken, A. (2005). Fungal ecology and succession on *Phragmites australis* in a blackish tidal marsh. I Leaf sheaths. Fungal Diversity 19: 157-187.
Van Ryckegem, G. and Verbeken, A. (2005). Fungal ecology and succession on *Phragmites australis* in a blackish tidal marsh. II Stems. Fungal Diversity 20: 209-233.
Wallace, J.B., Eggert, S.L., Meyer, J.L. and Webster, J.R. (1997). Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102-104.
Webster, J. (1992). Anamorph-teleomorph relationships. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer Verlag, Berlin Press, Berlin: 99-117.
Webster, J., Eicher, A. and Spooner, B.M. (1995a). *Cudoniella indica* sp. nov. (Ascomycetes, Leotiales), the teleomorph of *Tricladium indicum*, an aquatic fungus isolated from a South African river. Nova Hedwigia 60: 493-498.
Webster, J.R., Wallace, J.B. and Benfield, E.F. (1995b). Organic processes in streams of the eastern United States. In: *Ecosystems of the World*, *Vol. 22. River and Stream Ecosystems* (eds. C.E. Cushing, K.W. Cummins and G.W. Minshall). Elsevier, Amsterdam: 117-187.
Webster, J.R., Benfield, E.F., Ehrman, T.P., Schaeffer, M.A., Tank, J.L., Hutchens, J.J. and DíAngelo, D.J. (1999). What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41: 687-705.
Wetzel, R.G. (2001). *Limnology*, *Lake and River Ecosystems*. Academic Press, San Diego, CA.
Wong, S.W. and Hyde, K.D. (2001). Diversity of fungi on six species of Gramineae and one species of Cyperaceae in Hong Kong. Mycological Research 105: 1485-1491.

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