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Diversity patterns of leaf-associated aquatic hyphomycetes along a broad latitudinal gradient

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A B S T R A C T

Information about the global distribution of aquatic hyphomycetes is scarce, despite the primary importance of these fungi in stream ecosystem functioning. In particular, the relationship between their diversity and latitude remains unclear, due to a lack of coordinated surveys across broad latitudinal ranges. This study is a first report on latitudinal patterns of aquatic hyphomycete diversity associated with native leaf-litter species in five streams located along a gradient extending from the subarctic to the tropics. Exposure of leaf litter in mesh bags of three different mesh sizes facilitated assessing the effects of including or excluding different size-classes of litter-consuming invertebrates. Aquatic hyphomycete evenness was notably constant across all sites, whereas species richness and diversity, expressed as the Hill number, reached a maximum at mid-latitudes (Mediterranean and temperate streams). These latitudinal patterns were consistent across litter species, despite a notable influence of litter identity on fungal communities at the local scale. As a result, the bell-shaped distribution of species richness and Hill diversity deviated markedly from the latitudinal patterns of most other groups of organisms. Differences in the body-size distribution of invertebrate communities colonizing the leaves had no

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Plant litter
Species richness

effect on aquatic hyphomycete species richness, Hill diversity or evenness, but invertebrates could still influence fungal communities by depleting litter, an effect that was not captured by the design of our experiment.

Introduction

Global species diversity patterns of many taxonomic groups exhibit maxima at low latitudes in both terrestrial and marine ecosystems (Pianka 1966; Rosenzweig 1995; Gaston 2000; Hillebrand 2004). Though the mechanisms underlying this pattern are still not fully understood, several mutually non-exclusive hypotheses have been proposed (Rohde 1992; Rosenzweig 1995; Colwell & Lees 2000; Allen *et al.* 2002). In fresh waters, a meta-analysis encompassing a broad range of taxonomic groups has revealed a weaker increase in animal diversity with decreasing latitude compared with terrestrial and marine environments (Hillebrand 2004). Overall, however, the distribution of diversity in fresh waters has received less attention than in other ecosystems, and the existing data show conflicting gradients (Vinson & Hawkins 1998; González-Bergonzoni *et al.* 2012; Boyero *et al.* 2012).

Furthermore, very few studies have focused on aquatic fungal diversity patterns at large spatial scales (Ho *et al.* 2001; Arnolds 2007; Raja *et al.* 2009). Based on a compilation of data extracted from the literature, Shearer *et al.* (2007) concluded that the species richness of aquatic hyphomycetes in streams appeared to exhibit maxima in temperate rather than tropical climates, and suggested that this pattern might be driven by more varied ecological niches in temperate climates, resulting from stronger seasonality than in the tropics. It remains unknown, however, to what extent the latitudinal pattern identified by Shearer *et al.* (2007) reflected a geographical bias in the collection effort, since sampling of fresh water fungi in temperate regions has been much more intense than elsewhere. Studies encompassing broad geographical ranges across latitudinal gradients are restricted to literature analyses (Wood-Eggenschwiler & Bärlocher 1985; Shearer *et al.* 2007), since broad-scale coordinated surveys using identical methods have not been conducted.

Aquatic hyphomycetes, or Ingoldian fungi, are one of the most prominent groups of fresh water fungi (Bärlocher 1992a). As major drivers of leaf-litter decomposition, they are of primary importance in the functioning of forested stream ecosystems (Gessner *et al.* 2007). Notably, their productivity can be extraordinarily high (Suberkropp *et al.* 2010), in some cases resulting in more than 15 % fungal biomass in decomposing leaf litter (Gessner & Chauvet 1994). In addition, aquatic hyphomycetes stimulate litter consumption by detritivorous macroinvertebrates through the enzymatic 'conditioning' of leaf tissues (Bärlocher & Kendrick 1975; Suberkropp 1992). In turn, the feeding activity of these invertebrates could structure aquatic hyphomycete communities (Suberkropp 1992). Leaf-consuming invertebrates in streams often exhibit pronounced feeding preferences for particular fungal species (Arsuffi & Suberkropp 1985), which vary across invertebrate taxa (Arsuffi & Suberkropp 1989) and potentially alter fungal community composition or the relative abundances of species in a community. Smaller invertebrates, including early instars of litter-consuming detritivore larvae (Chung & Suberkropp 2009), may rely even more strongly on fungal hyphae rather than leaf tissue, and thereby could influence fungal communities as well. However, there is little information overall about how the feeding activity of invertebrates may affect the structure and composition of leaf-associated fungal communities in streams (Bärlocher 1980; Howe & Suberkropp 1994; Chung & Suberkropp 2008).

In the present study, we investigated aquatic hyphomycete communities colonizing leaf litter deployed in five streams located along a broad latitudinal gradient ranging from the subarctic to the tropics. By using strictly standardized procedures across locations we aimed at elucidating whether aquatic hyphomycete diversity in decomposing leaves can peak at mid-latitudes, as reported by Shearer *et al.* (2007). We expected fungal communities to vary across and within streams according to litter quality. Within locations, we varied litter quality by selecting native litter species belonging to four plant litter functional types. Furthermore, by enclosing litter in bags with one of three different mesh sizes, we tested whether the effects of litter consumers depend on the presence and size-class distribution of detritivorous invertebrates. We expected effects of invertebrates on fungal communities to be stronger for high-quality litter because of more intensive feeding. The influence of small invertebrates was expected to depend less on litter quality, because their feeding is likely to be mostly restricted to the litter surface. Exclusion of invertebrates by small mesh sizes also allowed us to assess interactions with latitude, as expected due to the scarcity of large detritivores in the tropics (Irons *et al.* 1994; Boyero *et al.* 2011, 2012).

Materials and methods

Study sites and litter functional types

We examined aquatic hyphomycete communities associated with native litter from five different forested low-order streams located across a 62° latitudinal range (Table 1): subarctic (Kopparåsen, Sweden), boreal (Krycklan, Sweden), temperate (Mosbeek, The Netherlands), Mediterranean (Maureillas, France), and tropical (Petit Saut, French Guyana). Stream characteristics are summarized in Table 1. To reflect locally available resource supply, four native litter species were selected in each location to represent four litter functional types: evergreen, nitrogen fixer, fast-decomposing deciduous and slow-decomposing deciduous (Table 2), which enabled comparisons of native plant litter species exhibiting similar sets of litter traits across sites (Fig S1;

Table 1 – Stream characteristics. Water samples for dissolved N and P determinations were filtered through 0.45-μm membrane filters, transported in a cooler to the laboratory, frozen, and later analyzed according to standard methods. SRP = soluble reactive phosphorus ≈ ortho-phosphate

	Subarctic	Boreal	Temperate	Mediterranean	Tropical
Stream	Kopperåsen, Sweden	Krycklan, Sweden	Mosbeek, The Netherlands	Maureillas, France	Petit Saut, French Guiana
Coordinates	68°26′N, 18°28′E	64°16′N, 19°50′E	52°26′N, 5°32′E	42°28′N, 2°48′E	5°04′N, 53°00′W
Dominant tree cover	*Betula pubescens*	*Betula pubescens*, *Picea abies*, *Alnus incana*	*Fagus sylvatica*	*Quercus ilex*, *Corylus avellana*, *Alnus glutinosa*	140 different canopy species
Incubation start	27/07/07	11/09/07	18/10/07	16/11/07	09/05/07
Incubation duration (days)	76	63	56	48	97
Altitude (m a.s.l.)	445	200	37	180	35
Stream order	1	3	2	3	2
Mean annual air temperature (°C)	0.9	1.8	10.2	15.4	25.4
Mean annual precipitation (mm)	352	643	814	766	2 519
Mean stream temperature during the experiment (°C)	6.4	4.6	7.2	5.7	24.4
Conductivity (μS/cm)	122	19	233	190	19
pH	7.3	7.1	6.8	7.9	7.7
Dissolved oxygen (mg/L)	9.3	11.0	11.3	11.4	n.d.
Alkalinity (μmol/L)	70.6	49.7	29.8	119.8	20.7
$N-NO_3^-$ (mg/L)	0.02	0.27	7.45	0.18	<0.02
$N-NH_4^+$ (mg/L)	n.d.	<0.020	0.154	0.020	<0.005
SRP (μg/L)	<2	18	16	18	<1

Table S1). In addition, we used *Ailanthus altissima* as a standard litter species at all sites. *A. altissima* is not native in any of the locations, and thus enabled comparison of fungal communities unconfounded by differences in litter quality across sites. Litter was collected shortly after natural abscission and was air-dried prior to the experiment. An exception was *Ilex aquifolium* litter, which was obtained by cutting branches in the field and simulating senescence in the laboratory for 3 weeks. Litter was collected during periods of most intense natural leaf abscission, which was normally in fall 2006, except for the tropical site (winter 2006) and *Quercus ilex* (summer 2007).

Experimental design

Air-dried leaf litter was weighed in batches of 5.0 ± 0.1 g, moistened with water using a spray bottle to make the leaves pliant, and enclosed in litter bags (15 × 20 cm). Three different mesh sizes were used to control access of invertebrates differing in body size. Coarse-mesh (5 mm) bags allowed access of all invertebrates to the leaf litter while limiting losses of leaf fragments, whereas a medium-sized mesh (1 mm) excluded larger invertebrates but allowed access to medium-sized invertebrates. Finally, fine mesh (0.25 mm) excluded both large and medium-sized invertebrates while allowing small invertebrates and micro-organisms to access the litter. The experiment was fully replicated in each stream using five spatially distinct blocks, corresponding to stream reaches at least 20 m apart. Each block contained one replicate of each litter species in each type of mesh bag, resulting in 75 litter bags per stream or 375 litter bags in total.

The experiment in each stream ran until the fast-decomposing deciduous litter species in coarse-mesh bags had lost about 50–60 % of its initial mass. The exact incubation times in each site are given in Table 1. This approach ensured both extended time for fungal colonization and sufficient litter material remaining for analyses. Furthermore, this improved cross-location comparisons of fungal communities established on leaves of a given functional type because similar decomposition stages were compared, independent of the incubation period needed to reach that stage. Litter bags retrieved from the streams were placed in cool boxes at temperatures similar to stream conditions, and immediately returned to the laboratory. In the laboratory, the leaves were rinsed with tap water, and 10 leaf disks of 14.2 mm diameter were cut from 10 different leaves per mesh bag. The disks were placed in glass Petri dishes filled with 20 mL of stream water, and incubated at the average stream temperature recorded by data loggers during litter exposure in the streams. Laboratory incubations to induce fungal sporulation (Gessner *et al.* 2003) were standardized to a duration of 240 degree-hours to account for differences in temperature. After incubation, the leaf disks were removed and the conidial suspensions transferred to centrifuge tubes where 2 mL of 37 % formalin was added. Total volumes were adjusted to 30 mL using distilled water. Before conidial identification, Triton X-100 (0.5 %) was added to the suspensions, followed by mixing to ensure a uniform distribution of conidia. An aliquot of the suspensions was filtered through membrane filters (SMWP; 5 μm porosity; Millipore, Bedford, MA, USA), and the trapped conidia were stained with Trypan blue (0.1 % in 60 % lactic acid), counted and identified under the microscope at 200–400× (Bärlocher 2005). Because the remaining litter material from standard *Ailanthus*

Table 2 – Litter species of four functional types at each of five locations arranged along a latitudinal gradient

Functional type	Tropical	Mediterranean	Temperate	Boreal	Subarctic
Evergreen	*Eperua falcata* (Aubl.)	*Quercus ilex* (L.)	*Ilex aquifolium* (L.)	*Rhododendron tomentosum* (Harmaja)	*Vaccinium vitis–idaea* (L.)
Slow-decomposing, deciduous	*Vochysia densiflora* Spruce ex Warm.	*Pistacia terebinthus* (L.)	*Fagus sylvatica* (L.)	*Betula pubescens* (Ehrh)	*Populus tremula* (L.)
Fast-decomposing, deciduous	*Qualea rosea* (Aubl.)	*Fraxinus angustifolia* (Vahl)	*Salix cinerea* (L.)	*Prunus padus* (L.)	*Sorbus aucuparia* (L.)
N-fixer	*Diplotropis purpurea* (Rich.) Amshoff	*Alnus glutinosa* (L.) Gaertn.	*Alnus glutinosa* (L.) Gaertn.	*Alnus incana* (L.) Moench	*Alnus incana* (L.) Moench

litter in the tropics was insufficient to cut disks, no conidia were determined from this litter exposed in the tropical stream.

Statistical analyses

Differences in fungal community composition between litter functional types and decomposer communities (i.e., mesh sizes) within each location were tested for significance by analysis of similarity (ANOSIM), followed by non-metric multidimensional scaling (NMDS) using the Czekanowski index (Yoshioka 2008) as a measure of ecological distance. NMDS is a non-parametric analysis that allows the mapping of the samples in multidimensional space. Using an iterative algorithm, the method minimizes the difference between the measured ecological distance and the Euclidean distance between samples in the ordination space (called stress value) (Clarke 1993). Stress values decrease as the agreement between plotted and ecological distances improves and thus give an indication of the "goodness of fit". Clarke (1993) proposed that stress values lower than 0.1 indicate a good ordination, whereas stress values above 0.35–0.40 point to randomly placed samples in the ordination space, precluding meaningful interpretation. ANOSIM allows testing for differences in community composition among groups of samples by comparing the ranks of within-group *versus* between-group distances. Outputs include significance tests based on an "R statistic", which is closer to 1 when similarity is greater within than between sets of replicates, while a value of zero indicates uniform similarities between and within sets (Clarke 1993).

Following Tuomisto (2012), we used the Hill number (Hill 1973) as a measure of species diversity, and defined species evenness as the ratio between species diversity and species richness. Because we used Hill number of order 1 (^1D) (see Hill 1973), our measure of species diversity equals the exponent of Shannon's diversity index, and evenness (^1E) equals the Buzas & Gibson (1969) measure of evenness (Tuomisto 2012). Species richness (S), species diversity as Hill number (^1D), and evenness (^1E) of leaf-associated fungal communities were analyzed using ANOVA with location, litter functional type and invertebrate community (i.e., mesh size) as fixed factors (Model 1). Post-hoc comparisons were performed among levels of significant factors using Tukey's HSD test. Because some samples (including all tropical fine and medium-sized mesh bags) contained no (or too few) conidia, our design became unbalanced with missing samples and cells. Therefore, we used Type III sums of squares, which are recommended when interaction terms are included in unbalanced designs (Quinn & Keough 2002). We also performed two alternative models (Models 2 and 3) on subgroups where all missing cells had been removed to check for consistency in the significance of the tested factors (Tables S2–S4).

As the number of conidia counted varied among samples (with some samples producing few conidia, or containing too many fine particles for reliable counts), we also checked the robustness of our results to sample size variation by applying the three models above (1, 2 and 3) to a rarefied species richness index, which estimates the number of species observed within 50 randomly sampled conidia in each sample (Table S5). ^1D was log-transformed to meet ANOVA's assumptions (normality of residuals and homogeneity of variance), which were graphically checked. All statistics were performed using R.2.15 (R Development Core Team, 2012) with *vegan*, *MASS* and *car* packages for ANOSIM, NMDS and Type III ANOVA, respectively.

Results

Composition of aquatic hyphomycete communities

A total of 39 fungal taxa were identified (Table 3). Some of them were restricted to a single location (e.g., *Tricladium splendens*, *Pyramidospora casuarinae*, *Culicidospora aquatica*), others were common at multiple sites (e.g., *Articulospora tetracladia*, *Flagellospora curvula*, *Tetrachaetum elegans*; Table 3). Tropical, Mediterranean, temperate, boreal and subarctic streams had a total of 10, 22, 19, 15 and 12 species, respectively. R values ranged from 0.1 to 0.64, with ANOSIM revealing significant differences between fungal communities among leaf types in each location ($P < 0.001$; Table 4 and Fig 1), but not between mesh sizes ($R < 0.05$; $P > 0.4$; Table 4). An exception was the tropics where samples from fine and medium-sized mesh bags did not produce conidia during laboratory incubations. However, significant differences detected by ANOSIM were not always due to differences between the same functional types across streams. For example, in the Mediterranean stream, significant differences among all five litter species were observed, while in other locations only some litter functional types differed from some others. Such differences between communities on different leaf types are reflected in a two-dimensional NMDS ordination (Fig 1). NMDS stress values ranged from 10.2 % (tropical stream) to 19.8 % (subarctic stream), which was reasonably low given the large number of samples included in each analysis.

Table 3 – Minimum and maximum proportions (% averaged per leaf litter functional type) of fungal species within communities on leaf litter decomposing at five locations along a latitudinal gradient. Question marks indicate uncertainty in species identification.

Fungal species	Tropical	Mediterranean	Temperate	Boreal	Subarctic
Alatospora acuminata Ingold		16.2–50.6	0.4–3.8		61.6–90.1
Alatospora pulchella? Marvanová		0.4–3.4		0–0.5	
Anguillospora crassa Ingold		0–0.4	0–1.0	0.1–0.7	
Anguillospora filiformis Greathead		0–0.0	0–6.7	0.5–3.6	
Anguillospora furtiva? Descals			4.8–12.6		
Anguillospora gigantea Ranzoni	0–6.1				
Anguillospora longissima (Saccardo & Sydow) Ingold		0.1–1.3		1.5–24.6	
Anguillospora rosea? Descals	0–0.8				
Anguillospora curvula? Iqbal					0–0.2
Angulospora aquatica Nilsson	0–10.42				
Articulospora tetracladia Ingold	0–1.1		0.6–2.8	1.3–27.4	0.5–7.5
Clavariopsis aquatica De Wildeman		0.0–38.1	0.4–43.2		
Clavatospora longibrachiata (Ingold) Nilsson		2.3–12.4	3.0–35.4		0–0.5
Crucella subtilis Marvanová & Suberkropp		0.1–0.2	0–0.1	0.1–1.6	
Culicidospora aquatica Petersen				0–0.2	
Flagellospora fusarioides Iqbal	0–4.8				
Flagellospora curvula Ingold	40.5–92.0	9.4–27.3	4.7–45.1	9.2–89.6	4.1–19.2
Fontanospora alternibrachiata Dyko				3.5–43.0	
Heliscella stellata (Ingold & Cox) Marvanová		0.8–6.0	0–0.5		0–0.1
Heliscella stellatacula? (Kirk ex Marvanová & Nilsson) Marvanová		0.1–42.7			
Heliscus lugdunensis Saccardo & Thérry		0–0.2	0.3–51.5		0–0.2
Lemmoniera aquatica De Wildeman		0–0.3		0.2–2.6	0–3.4
Lemmoniera cornuta Ranzoni		2–5.3			
Lemmoniera terrestris Tubaki		1.4–5.6			0–0.4
Mycocentrospora angulata? (Petersen) Iqbal			0–6.5		
Pyramidospora casuarinae Nilsson	0–0.6				
Stenocladiella neglecta (Marvanová & Descals) Marvanová & Descals		2.0–8.3	0–0.2		
Taeniospora gracilis Marvanová				0–13.1	
Tetrachaetum elegans Ingold		0–2.1	6.2–44.5	0–1.0	0–0.3
Tetracladium marchalianum De Wildeman	0–1.5	0–7.6		0.2–0.4	0–0.1
Tricladium chaetocladium Ingold		0–0.8	1.6–5.5		0.7–11.6
Tricladium patulum Marvanová				0–0.1	
Tricladium splendens Ingold			0–1.3		
Tripospermum myrti (Lind) S. Hughes		0–0.5	0–0.2		
Triscelophorus acuminatus? Nawawi	0.3–55.8				
Triscelophorus monosporus Ingold	0.5–1.0				
Tumularia aquatica (Ingold) Descals & Marvanová		0–4.5	0–3.8		
Tumularia tuberculata (Gönczöl) Descals & Marvanová		0.0–12.8	0–3.3		
Varicosporium elodeae Kegel				0.0–2.2	

Table 4 – ANOSIM results of within-stream comparisons with the ANOSIM statistic (R) and significance (P) for effects of plant litter functional type and decomposer communities (i.e., mesh size). As conidia from the tropical stream were identified only from coarse-mesh bags, the effects of the decomposer community are not given for that stream

Location	Plant litter functional type		Decomposer community	
	R	P	R	P
Tropical	0.58	<0.001	–	–
Mediterranean	0.64	<0.001	<0.01	0.40
Temperate	0.54	<0.001	0.03	0.78
Boreal	0.51	<0.001	0.02	0.84
Subarctic	0.10	0.001	<0.01	0.47

Structure and diversity of aquatic hyphomycete communities

Location and litter functional type both affected species richness and diversity in all alternative models as either main or interactive effects (Tables 5 and S2–S4). The patterns were similar for both variables across locations, being highest in the temperate and Mediterranean regions (Figs 2–3), and lowest at the latitudinal extremes, while the boreal site exhibited intermediate values. Both species richness (S) and Hill diversity (^1D) were significantly higher for communities associated with slow-decomposing ($S = 8.1 \pm 3.8$; $^1D = 4.0 \pm 2.1$ SD) and nitrogen-fixer litter ($S = 8.4 \pm 3.9$ SD; $^1D = 4.1 \pm 2.7$ SD) compared to fast-decomposing ($S = 6.6 \pm 3.3$ SD; $^1D = 3.1 \pm 1.7$ SD) litter functional types (Tukey's test; both $P < 0.05$). Evergreen and the standard *Ailanthus* litter generally exhibited intermediate to lower species richness with average

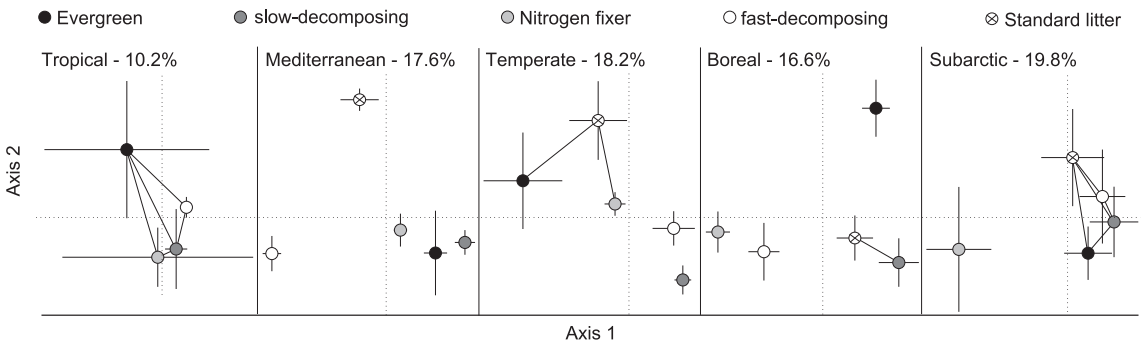

Fig 1 – NMDS ordinations of within-stream comparisons of aquatic hyphomycete communities among four litter functional types and a standard litter. Connecting lines between symbols indicate a lack of significant difference between the litter species (ANOSIM). Error bars represent ± 1 SE. Numbers refer to stress values.

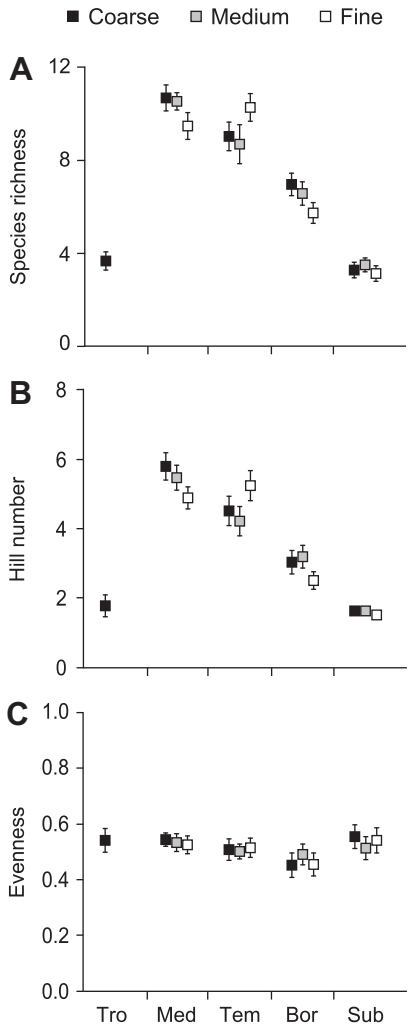

Fig 2 – Mean (A) fungal species richness, (B) species diversity (Hill number) and (C) evenness of three decomposer communities (i.e., in coarse, medium-size and fine mesh bags) at five locations along a latitudinal gradient. Error bars represent ± 1 SE.

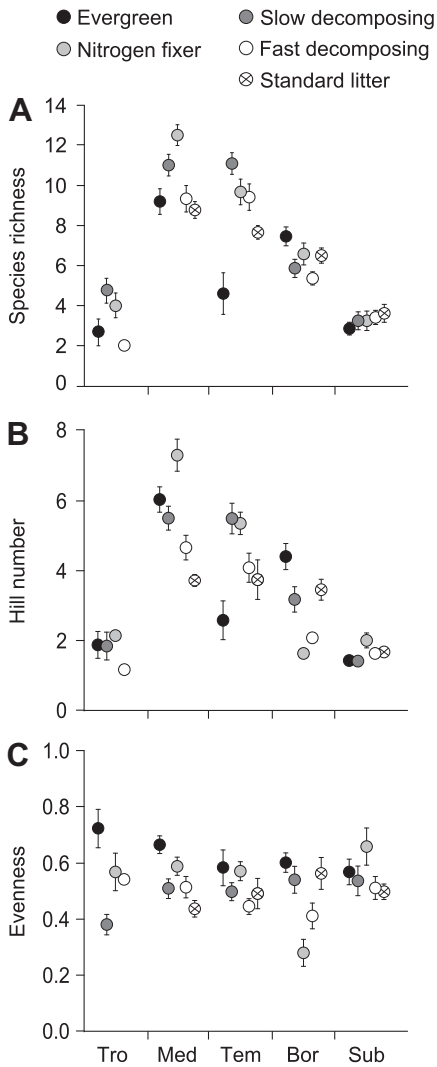

Fig 3 – Mean (A) fungal species richness, (B) species diversity (Hill number) and (C) evenness on four litter functional types (evergreen, slow-decomposing, N-fixer, fast-decomposing) and a standard litter at five locations along a latitudinal gradient. Error bars represent ± 1 SE.

Table 5 – Results of ANOVAs testing for the effects of location, plant litter functional type and decomposer community (i.e., mesh size) on species richness, species diversity (log Hill number) and Buzas & Gibson's (1969) evenness

Source of variation	*df*	Species richness		Species diversity		Evenness	
		SS	P	SS	P	SS	P
Location (L)	4	214.1	<0.001	11.6	<0.001	0.13	0.24
Litter functional type (Ft)	4	13.1	0.44	4.24	<0.001	0.66	<0.001
Decomposer community (Dc)	2	11.3	0.20	0.19	0.35	0.04	0.46
L × Ft	15	245.9	<0.001	12.8	<0.001	1.56	<0.001
L × Dc	6	11.5	0.77	0.31	0.76	0.05	0.89
Ft × Dc	8	26.1	0.48	0.18	0.98	0.11	0.78
Residuals	218	756.1		20.3		5.17	

$S = 5.8 \pm 3.2$ SD and 6.4 ± 2.6 SD, respectively. In contrast, species evenness did not vary across locations but only with litter functional type (Table 5). It was the highest on evergreen litter (0.64 ± 0.17 SD) and not statistically different between any of the other litter functional types (Tukey's test; $P < 0.05$).

A significant interaction between location and litter functional type (Table 5) indicates that differences in S and ^1D among litter functional types were not consistent across locations. For instance, ^1D on evergreen litter for the temperate stream was low compared to other litter functional types. Similarly, lower values of ^1D were found on fast-decomposing and nitrogen-fixing plant species in the boreal stream relative to other litter functional types at the respective locations (Figs 3A and B). Similarly, differences among litter types in ^1E contrasted among locations, with high and low values on nitrogen-fixer litter in the boreal and subarctic streams, respectively, compared to the other locations (Fig 3C).

Neither the invertebrate exclusion treatment (i.e., mesh size) nor its interaction with location influenced S, ^1D or ^1E ($P > 0.2$; Table 5). Finally, ANOVAs based on Models 1, 2 and 3 on all diversity metrics (including rarefied species richness) produced very similar results which led to the same conclusions (Tables S2–S5).

Discussion

The diversity of aquatic hyphomycetes in our standardized investigation at five locations across a broad latitudinal gradient did not reveal an increase with decreasing latitude as reported for many other taxonomic groups (Rosenzweig 1995; Gaston 2000). Rather, we found that diversity peaked at our mid-latitude sites (Mediterranean and temperate streams), with richness being lowest at both extremes. Although litter quality influenced fungal communities at the local scale, the highest fungal species diversity was always observed in the temperate and/or Mediterranean sites for a given litter functional type, including for a standard litter species (*A. altissima*) used across all locations. In contrast, invertebrate feeding appeared not to be an important driver of aquatic hyphomycete diversity in any of the investigated streams, as indicated by a consistent lack of variation in fungal community structure among litter enclosed in bags with three different mesh sizes. Taken together, our results strengthen the notion that aquatic hyphomycete diversity peaks at mid-latitudes (Shearer *et al.* 2007), and highlight the greater influence of litter functional type than invertebrate feeding on the diversity of aquatic hyphomycete species colonizing decomposing leaves in streams. However, this pattern is strongly influenced by the low diversity of aquatic hyphomycetes in our tropical study stream, which is unlikely to be representative for all streams in the tropics.

A combination of climate, resource quality and availability could account for the lower aquatic hyphomycete diversity observed at both extremes of our latitudinal gradient. Specifically, the low quality of most tropical litter species, and the low nutrient concentrations in stream water (Stallard 2002; Boulton 2008) could explain the low number of fungal species observed in the tropical stream. Low quality of the tropical litter is due to either high contents of refractory and inhibitory compounds or high leaf toughness (Fig S1; Table S1), reflecting plant adaptations to herbivory that persist after plant death. At high latitudes, fungal diversity might also be limited by resources and environmental characteristics, including low mean temperatures and especially the low diversity and quantity of litter inputs (Cowan & Oswood 1983). Accordingly, nutrient concentrations in stream water were the lowest at both extremities of the gradient (Table 1), which potentially limited fungal diversity and activity (Suberkropp *et al.* 2010). Future investigations involving a much larger number of streams in each of several latitudinal bands and differing in dissolved nutrient concentrations have potential to unravel the relative importances of nutrient supply and other stream characteristics related directly to latitude.

In accordance with several syntheses of aquatic hyphomycete communities (Webster & Descals 1981; Wood-Eggenschwiler & Bärlocher 1985; Bärlocher & Marvanová 2010), many of the species we found are cosmopolitan, with distributions ranging from the arctic to the tropics (e.g., *A. tetracladia*, *F. curvula*), while others are restricted to a single stream. For instance, species of the genus *Triscelophorus*, which we only observed in the tropical stream, are typically found in warm waters (Bärlocher 1992b). Growth and sporulation of aquatic hyphomycetes are affected by temperature, with some species from temperate streams exhibiting optima of mycelial growth and sporulation ranging from 10 to 25 °C (Suberkropp 1984; Chauvet & Suberkropp 1998; Dang *et al.* 2009; Geraldes *et al.* 2012), broadly consistent with their global distribution (Bärlocher & Marvanová 2010).

Seasonal changes in temperature and litter inputs could also explain the latitudinal variation in aquatic hyphomycete diversity. In particular, weak seasonal variation in the tropics narrows the annual temperature range and hence temperature-related niche space. This, together with the high litter diversity (i.e., high litter-related niche availability) at the tropical location (Table 1, Hättenschwiler *et al.* 2011) contrasts with the typical situation at higher latitudes, where litter diversity is lower, litter inputs are pulsed in the autumn, and annual temperature variation is larger (Wantzen *et al.* 2008). Interestingly, the highest aquatic hyphomycete diversity observed in the present study was in the Mediterranean stream, where the annual

temperature range was greatest of all sites and the period of litter inputs is extended due to the co-occurrence of deciduous tree species together with many evergreen species, such as *Q. ilex*, which shed leaves during spring and summer (Bellot *et al.* 1992; Bussotti *et al.* 2003). However, repeated analyses during the year (Suberkropp 1984; Gessner *et al.* 1993) would be needed to assess the importance of seasonality for variation of aquatic hyphomycete diversity across latitudes.

Within each stream, differences among litter species were observed in species richness, diversity and composition of aquatic hyphomycete communities. This finding corroborates the conclusions of Gulis (2001) and Laitung & Chauvet (2005) who observed some litter preferences (but no litter specificity) in aquatic hyphomycetes. Such differences between litter species could arise when litter properties influence the attachment, germination (Dang *et al.* 2007; Kearns & Bärlocher 2008) or growth of fungal species. As litter quality varies during the decomposition process, the structure of aquatic hyphomycete communities can also become influenced by species interactions, favouring the dominance of strong competitors in later decomposition stages. This mechanism could have led to community succession (Bärlocher 1992b) characterized by maximum aquatic hyphomycete diversity at intermediate decomposition stages (Gessner *et al.* 1993; Garnett *et al.* 2000). Because we sampled litter bags on a single occasion, we were unable to follow such community dynamics.

The within-stream differences we observed in fungal communities among litter species could also be partly due to varying decomposition stages reached by a given litter species at the time of sampling. Nevertheless, litter species of the same functional types shared some characteristics across locations that might have influenced fungal diversity consistently. Notably, nitrogen-fixing and slow-decomposing litter species often exhibited higher species richness than fast-decomposing and evergreen ones, which might be related to litter chemistry (Fig S1; Table S1) and hence to the decomposition stage reached at the time of sampling. The fast-decomposing species might have passed the intermediate decomposition stage where fungal diversity is highest, whereas the evergreen species might not have reached it by this time. This pattern holds across most locations except in the subarctic, where differences between litter species were less pronounced than elsewhere, and in the boreal where the evergreen species exhibited higher fungal species richness than would be expected under the hypothesis that succession was less advanced than on the other litter species (Fig 3A).

Although some differences among litter in bags with different mesh sizes were apparent at individual sites (e.g., lower diversity in fine mesh bags in the boreal and Mediterranean sites, but higher diversity at the temperate site), these tendencies were too weak to result in statistically significant effects. This suggests that the body-size distribution of the invertebrate communities colonizing the litter, specifically the presence or absence of medium-sized and/or large invertebrates, had little influence on fungal communities. The observed lack of conidia in fine and medium-sized mesh bags at the tropical site is unlikely to reflect invertebrate feeding, given that invertebrate abundances in the tropical stream were extremely low (A. Bruder, pers. obs.). Alternatively, even only slightly reduced water exchange in these mesh bags could have exacerbated nutrient limitation of fungal sporulation caused by the very low concentrations of dissolved nutrients in the tropical stream, and high concentrations of coloured dissolved organic carbon could have imposed an additional constraint on fungal activity in this stream (Bärlocher 1990).

Overall, the lack of invertebrate effects on aquatic hyphomycete communities corroborates findings by Howe & Suberkropp (1994), Ferreira & Graça (2006) and Chung & Suberkropp (2008) on the absence of feeding effects on aquatic hyphomycete communities. However, as in the present experiment, those studies assessed fungal communities on standardized leaf areas (leaf disks) and thus neglected indirect effects caused by competition between invertebrates and aquatic hyphomycetes, as the depletion of litter by invertebrate consumption reduces the amount of litter available for fungal colonization and could hence influence fungal communities (Bärlocher 1980). At the stream scale, Suberkropp & Wallace (1992) observed higher litter standing stocks concomitant with higher conidial production in an insecticide-treated compared to an untreated reference stream. This could reflect an indirect negative effect of litter-consuming invertebrates on aquatic hyphomycetes through leaf-litter depletion, a possible mechanism that we could not address in the present study. Finally, as our experiment was stopped when around 50 % of the fast-decomposing species remained, we might have missed any invertebrate effect occurring in later decomposition stages (Bärlocher 1980).

In conclusion, an important result of the present study using standardized procedures in five streams along a latitudinal gradient is that aquatic hyphomycete diversity might indeed peak at mid latitude as found by Shearer *et al.* (2007) in their literature analysis. In addition, it appears that the control exerted by litter quality (but not invertebrate feeding) on aquatic hyphomycete community structure could be a general pattern, since it was consistently observed at five locations on a total of 21 litter types. However, since the present study involved a single stream and a single litter species per functional type at each latitude, further investigations are needed to assess whether our preliminary conclusions hold more generally. Particularly insightful might be investigations evaluating both spatial (regional *vs.* local diversity) and temporal (e.g., seasonal changes, community dynamics during the decomposition process) variations within latitudinal bands. If the pattern found here is confirmed by such broader analyses, the mid-latitude diversity peak could have implications for stream ecosystem functioning in response to climate change. Changes in aquatic hyphomycete communities caused by climate warming could have functional ecosystem consequences (Dang *et al.* 2009) particularly in tropical and high-latitude streams where aquatic hyphomycete diversity was lowest. At present, however, projections of how climate change affects fungal diversity and translates into altered stream ecosystem functioning remain speculative.

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Supplementary data

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