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Biodiversity of leaf litter fungi in streams along a latitudinal gradient

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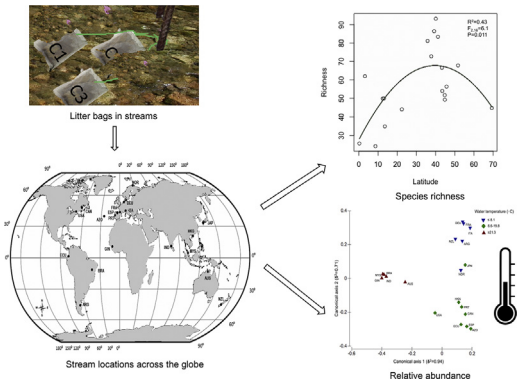
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HIGHLIGHTS

- Large-scale patterns of fungal diversity in freshwaters are unknown.
- Our study is based on fungi colonized on plant litter in 19 globally distributed streams.
- Hump-shaped distribution of fungal richness along the absolute latitude was seen.
- Community composition of fungi was grouped according to thermal preferences.

GRAPHICAL ABSTRACT



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ABSTRACT

Global patterns of biodiversity have emerged for soil microorganisms, plants and animals, and the extraordinary significance of microbial functions in ecosystems is also well established. Virtually unknown, however, are large-scale patterns of microbial diversity in freshwaters, although these aquatic ecosystems are hotspots of biodiversity and biogeochemical processes. Here we report on the first large-scale study of biodiversity of leaf-litter fungi in streams along a latitudinal gradient unravelled by Illumina sequencing. The study is based on fungal communities colonizing standardized plant litter in 19 globally distributed stream locations between 69°N and 44°S. Fungal richness suggests a hump-shaped distribution along the latitudinal gradient. Strikingly, community composition of fungi was more clearly related to thermal preferences than to biogeography. Our results suggest that identifying differences in key environmental drivers, such as temperature, among taxa and ecosystem types is critical to unravel the global patterns of aquatic fungal diversity.

1. Introduction

The role of freshwater ecosystems as components of the global carbon cycle is being increasingly acknowledged (Perkins et al., 2012; Martínez et al., 2014). Streams are hotspots of CO_2 emission (Perkins et al., 2012; Battin et al., 2009) as they receive organic carbon of terrestrial origin and its in-stream decomposition releases CO_2 to the atmosphere. The underlying processes, including the decomposition of riparian plant litter, are strongly driven by the activities of fungi (Cornut et al., 2010; Duarte et al., 2015, 2016; Seena et al., 2017), although other microbes and invertebrates can also play a role (Hieber and Gessner, 2002). Importantly, decomposition rates of litter in streams can be affected by fungal diversity, either directly or through trophic effects (Lecerf et al., 2005; Srivastava et al., 2009; Jabiol et al., 2013a). Therefore, it is essential to understand the global distribution and diversity patterns of aquatic fungi, to allow predicting ecosystem responses to global change (Violle et al., 2014).

There has been considerable debate as to whether microbes follow similar global distribution patterns as plants and animals (Fuhrman et al., 2008; Fierer et al., 2011; Azovsky and Mazei, 2013; Tedersoo et al., 2014). Issues include the questions whether microbes follow a latitudinal diversity gradient characterized by increasing richness from the poles to the tropics (Hillebrand, 2004; Mittelbach et al., 2007; Fuhrman et al., 2008; Andam et al., 2016), and to what extent biogeographic history structures present-day species distributions. The importance of plate tectonics in governing the global distribution of plants and animals is well established (Briggs, 1995; Holden, 2012; C.B. Cox et al., 2016), with many taxa following either the Laurasian or Gondwanan distribution patterns (Holden, 2012). In contrast, one of the most enduring tenets in microbial ecology is Baas-Becking's hypothesis, initially proposed primarily for bacteria, that "*everything is everywhere, but the environment selects*" (Bass-Becking, 1934; De Wit and Bouvier, 2006). Extending this to eukaryotes, Fenchel (1993) suggested that smaller organisms tend to have wider or more even cosmopolitan distribution, a higher efficiency of dispersal, a lower rate of allopatric speciation and lower rates of local and global extinction than do larger organisms. Foissner (1999) proposed the 'moderate endemicity model' of microbial biogeography for free-living protists, which suggests that a substantial portion of these taxa have a restricted distribution, i.e., they are not cosmopolitan despite suitable habitats at many locations.

Importantly, however, even a global reach of microbial propagules does not preclude latitudinal patterns of microbial diversity and participation in ecosystem processes: distance from poles may be an important proxy for various ecological drivers such as precipitation and temperature. For example, soil fungal communities clearly differ among bioregions, even though soil extracellular activities are highly convergent (Talbot et al., 2014). This suggests that dispersal limitation or climatic patterns could be primary drivers determining fungal communities in soils. Taylor et al. (2006) concluded that certain well-characterized fungal complexes (*Neurospora*, *Saccharomyces*, *Schizophyllum*, *Lentinula*) have a true biogeography with phylogentically distinct groups in different regions. On the other hand, *Aspergillus fumigatus* has maintained a globally homogeneous population, possibly due to recent expansion of its preferred environment.

The richness of soil fungi generally decreases towards the poles (Tedersoo et al., 2014), and fungi with strong dispersal abilities

dominate at high latitudes (F. Cox et al., 2016). By contrast, the species richness of aquatic hyphomycetes, a polyphyletic group of stream fungi that assume dominant roles in litter decomposition, was found to peak at mid-latitudes and to be lowest towards the extremes of the latitudinal gradient on the northern hemisphere in a study comparing five locations at latitudes ranging from the subarctic to the tropics (Jabiol et al., 2013b). A survey of published studies confirmed that aquatic hyphomycete species diversity peaks in temperate streams, and high community similarities were found between geographically distant locations in comparable climatic zones (Duarte et al., 2016). However, given the limited scope of previous investigations and their reliance on spore morphotypes, the presence of globally congruent patterns of stream fungal diversity remains uncertain.

The objective of the present study was to determine fungal diversity and community composition based on molecular analyses of communities associated with decomposing leaf litter. The global-scale study stretched over a 113° latitudinal gradient of 19 stream locations on five continents. Given that latitude is widely recognized as a broad climate surrogate (Parmesan and Yohe, 2003; Jetz et al., 2008; Boyero et al., 2011a; Jabiol et al., 2013b), we tested the hypothesis that fungal richness decreases with latitude, similar to the pattern described for most plants and animals (Hillebrand, 2004; Kinlock et al., 2018). Furthermore, we investigated whether the global distribution of specific fungal taxa follows the well-established biogeographic realms, eight of which are generally recognized to be based on distributional patterns of terrestrial species resulting from the isolation of populations by continental drift (Olson et al., 2001).

2. Materials and methods

2.1. Stream sites and field work

A total of 19 streams were chosen for a coordinated multi-site experiment. The streams were distributed across both hemispheres with locations extending from 69° N to 44° S (Table 1, Fig. 1). Mean annual air temperature (°C) and rainfall (mm) data were obtained from climate-data.org (http://en.climate-data.org/; accessed February 2016) and AIC (Autoridad Interjurisdiccional de Cuencas de los Ríos Limay, Neuquén y Negro, Bureau of Water Resources Management, Argentina; http://www.aic.gov.ar/aic/default.aspx#v; accessed February 2016). The following conditions of the study sites were chosen:

Table 1
Geographical locations and environmental characteristics of the 19 stream sites on five continents.

Location	Latitude	Longitude	Altitude (m)	Annual mean air temperature (°C)	Annual mean rainfall (mm)
Norway (NOR)	69°18′N	20°25′E	77	0.9	542
Germany (DEU)	51°42′N	10°23′E	528	8.0	734
Canada (CAN)	45°43′N	64°09′W	88	5.2	1215
Italy (ITA)	44°45′N	7°17′E	406	12.4	769
France (FRA)	43°28′N	2°13′E	548	13.2	739
Spain (ESP)	43°18′N	3°15′W	134	14.1	1174
Portugal (PRT)	40°5′N	8°14′W	276	15.8	958
United States of America (USA)	39°14′N	76°44′W	75	12.6	1091
Azores (AZO)	37°44′N	25°28′W	300	17.4	988
Japan (JPN)	35°49′N	138°31′E	1076	11.2	1296
Hong Kong (HKN)	22°25′N	114°10′E	197	22.8	2080
India (IND)	12°28′N	75°35′E	173	26.8	4273
Guinea (GIN)	8°38′N	9°30′W	571	24.0	2750
Malaysia (MYS)	3°10′N	101°46′E	167	27.1	2492
Ecuador (ECU)	0°14′S	78°0′W	3061	9.6	1204
Brazil (BRA)	12°57′S	39°26′W	285	22.9	960
Australia (AUS)	13°6′S	130°47′E	129	27.4	1694
Argentina (ARG)	41°14′S	71°16′W	1204	8.8	1500
New Zealand (NZL)	44°49′S	170°30′E	285	10.6	527

experimental streams were low order (1–3 according to Strahler, 1957), had a depth < 50 cm and width < 5 m, were characterized by coarse substrate, generally by cobbles, and lacked major anthropogenic impacts and invasive tree species. Stream physico-chemical characteristics, including concentrations of dissolved nutrients (nitrogen [N] and phosphorus [P]), were determined (APHA, 1995) when the leaf litter was deployed and retrieved.

Alnus glutinosa (L.) Gaertn. (black alder; Betulaceae) leaves were collected at a single site on the banks of the Mondego River at Lages, Coimbra, Portugal (40°11′21″N, 8°25′30 W″). Alder was chosen because the genus is widespread in the Holarctic and also occurs in the Neotropics (Boyero et al., 2011a) and because it has high-quality leaves (e.g. Hladyz et al., 2009; Fernandes et al., 2014). Although alder trees do not occur in some of the study regions, their soft texture and high nitrogen concentrations do not impose any colonization impediment to microbial communities (Fernandes et al., 2014; Chauvet et al., 2016) and the leaves are also readily consumed by tropical detritivores (Graça et al., 2001). Moreover, the species has been previously used as a standard litter in large-scale decomposition studies (e.g. Boyero et al., 2011a; Woodward et al., 2012).

Kits containing air-dried alder leaves (three replicates, each containing 2 g of leaves), fine-mesh (0.5 mm) nylon bags, DNAgard® (Biomatrica, San Diego, CA, USA) and protocols were shipped from Coimbra, Portugal, to the other 18 locations distributed across the globe. DNAgard® was used to collect, ship and store leaf discs at ambient temperature. Ten leaf discs (12 mm diameter) were cut from randomly selected alder leaves before shipping. DNA was extracted and pooled and composition of the initial (control) microbial community was determined by Illumina MiSeq sequencing. Leaves were not sterilized before colonization to avoid changes in litter chemistry (Howard and Frankland, 1974); microbes initially present on the litter have little influence on fungal colonization dynamics (Bärlocher and Kendrick, 1974), since stream fungi are rapid colonizers that quickly outcompete terrestrial taxa (Nikolcheva et al., 2005; Frossard et al., 2013).

Strictly standardized litter colonization experiments were conducted in the 19 study streams during the dry season in tropical and during autumn in temperate and subarctic streams. At each site, litter bags were deployed in riffle areas rich in oxygen (Table 2), at water depths of <30 cm. Experiments were terminated when an estimated 40–50% of the initial litter mass was lost, as inferred from previous decomposition studies (Boyero et al., 2011a, 2015). The exact colonization period at each site is given in Table S1. Three litter bags were retrieved and 10 leaf discs (12 mm diameter) were cut per bag with a sterile cork borer, immediately placed in 3 sterile screw-cap tubes containing 1 ml of DNAgard® solution and sent to the laboratory at the University of Coimbra, Portugal, for DNA extraction.

2.2. DNA extraction, Miseq sequencing and bioinformatics analysis

From each replicate set of 10 leaf discs, microbial DNA was extracted with the PowerSoil® DNA isolation kit (MoBio laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The concentration of extracted DNA (>20 ng/μl) was confirmed with a NanoDrop 2000c spectrophotometer (Wilmington, DE, USA) before storing the DNA at −20 °C. The DNA of all replicate samples from each site was pooled and then amplified for sequencing at RTLGenomics (Lubbock, TX, USA) in a two-step process. The forward primer was made with the (5′-3′) Illumina i5 sequencing primer (TCGTCGGCAGCGTCAGATG TGTATAAGAGACAG) and the ITS3F primer (GCATCGATGAAGAACG CAGC) (White et al., 1990). The reverse primer was generated with the (5′-3′) Illumina i7 sequencing primer (GTCTCGTGGGCTCGGAGAT GTGTATAAGAGACAG) and the ITS4R primer (TCCTCCGCTTATTGAT ATGC) (White et al., 1990). Amplifications were done in 25 μl reactions with the Qiagen HotStar Taq master mix (Qiagen Inc., Valencia, CA, USA), 1 μl of each 5 μM primer, and 1 μl of DNA template. Reactions were executed on ABI Veriti thermocyclers (Applied Biosytems,

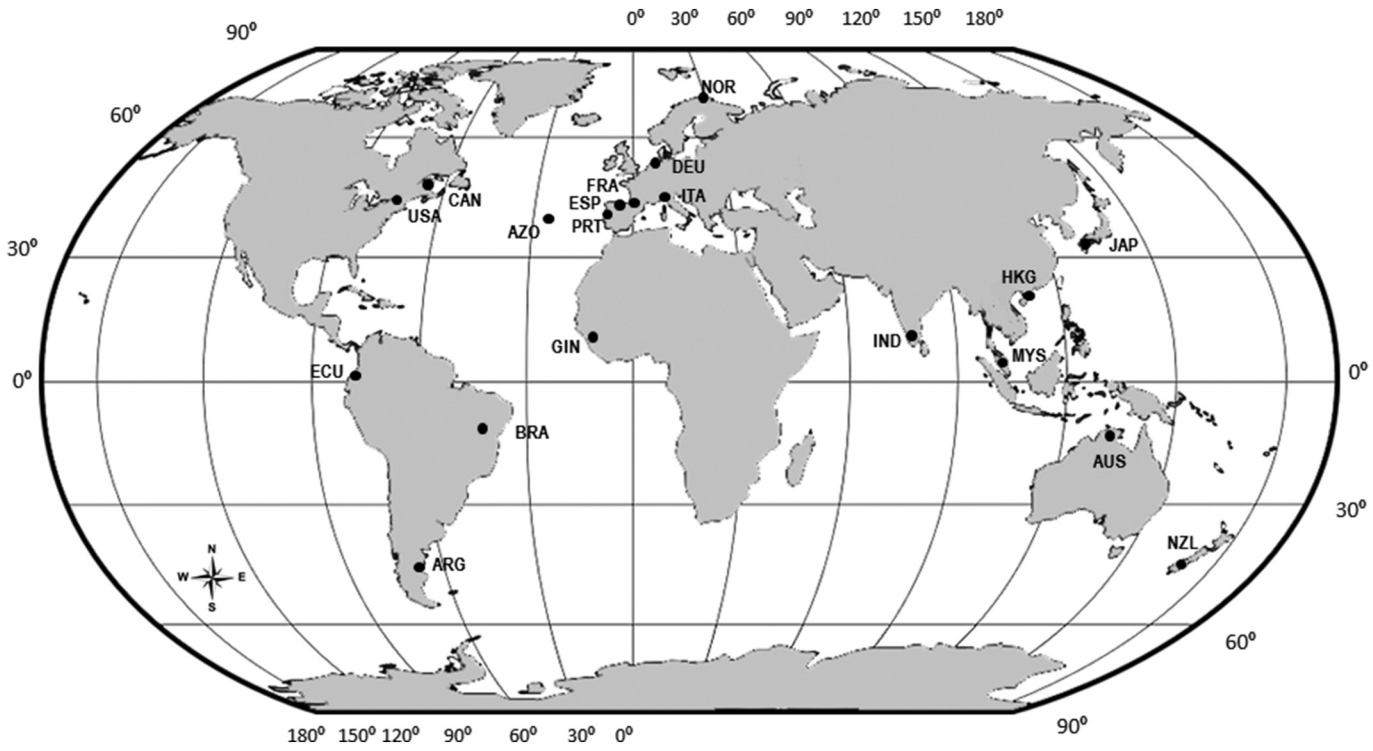


Fig. 1. Distribution of the 19 stream sites across the globe. Norway (NOR), Germany (DEU), Canada (CAN), Italy (ITA), France (FRA), Spain (ESP), Portugal (PRT), United States of America (USA), Azores (AZO), Japan (JPN), Hong Kong (HKN), India (IND), Guinea (GIN) Malaysia (MYS), Ecuador (ECU), Brazil (BRA), Australia (AUS), Argentina (ARG), New Zealand (NZL).

Carlsbad, CA, USA) under the following PCR conditions: 95 °C for 5 min, 25 cycles of 94 °C for 30 s, 54 °C for 40 s, 72 °C for 1 min, followed by one cycle of 72 °C for 10 min and 4 °C hold.

Products from the first stage amplification were subjected to a second round of amplification with similar PCR conditions except that only 10 cycles were run. The Illumina Nextera PCR primers for the second PCR runs were AATGATACGGCGACCACCGAGATCTACAC[i5index]TCGTCGGCAGCGTC (forward) and CAAGCAGAAGACGGCATACGAGAT[i7index]GTCTCGTGGGCTCGG (reverse). Amplification products were visualized with eGels (Life Technologies, Grand Island, NY, USA) and then pooled at equimolar concentrations. Size selection of each pool was done in two rounds of SPRI select (BeckmanCoulter, Indianapolis, IN, USA) in a 0.7 ratio for both rounds. The pooled amplification products were run on a Fragment Analyzer, quantified on a Qubit 2.0 fluorometer (Life Technologies, Grand Island, NY, USA), then loaded on an Illumina MiSeq (Illumina, Inc., San Diego, CA, USA) 2 × 300 flow cell (10pM) and finally sequenced to minimum 10,000 reads for an entire sample with a minimum of 7500 reads per sample.

Quality trimming was performed on the fastq using the SolexaQA++ dynamictrim utility (version 3; Cox et al., 2010) with a minimum threshold of 25. If length of a read dropped below 50 bp after quality trimming, it was removed. The retained forward and reverse reads of the dataset were merged by using FLASH (version 1.211; Magoč and Salzberg, 2011). A dereplication step followed to remove duplicate reads using VSEARCH software (version3; Rognes et al., 2016). Chimeras were removed by using Mothur (version1.39.5; Schloss et al., 2009) with the unified system for DNA-based fungal species (UNITE) and international nucleotide sequence database collaboration (INSDC)

Table 2
Average physico-chemical characteristics and nutrient concentrations of the 19 streams across the globe.

Location*	Water temperature (°C)	Conductivity ($\mu S \cdot cm^{-1}$)	Dissolved oxygen ($mg \cdot L^{-1}$)	pH	Nitrate-N ($mg \cdot L^{-1}$)	Phosphate-P ($mg \cdot L^{-1}$)
NOR	3.1	65.9	13.2	8.4	0.074	0.001
DEU	6.9	59.5	11.5	7.4	0.805	0.004
CAN	10.8	45.3	10.0	6.8	0.080	0.010
ITA	3.8	143.0	9.9	8.4	0.300	0.040
FRA	8.1	86.4	10.3	6.8	1.058	0.040
ESP	8.6	92.4	11.6	7.7	0.219	0.005
PRT	14.7	47.8	9.7	7.0	0.062	0.002
USA	9.5	96.2	10.2	6.9	0.095	0.001
AZO	15.2	141.2	8.5	7.3	0.050	0.011
JPN	9.7	57.0	9.9	7.0	0.286	0.014
HKN	19.8	40.5	8.1	6.8	0.137	0.015
IND	23.7	257.0	7.2	7.3	1.150	0.005
MYS	26.2	25.6	10.74	6.7	0.650	0.001
GIN	22.3	31.0	8.7	7.6	0.880	0.073
ECU	10.2	82.9	8.5	8.2	0.004	0.010
BRA	21.3	39.9	8.2	5.0	0.670	0.040
AUS	25.0	9.2	8.0	6.0	0.018	0.002
ARG	4.0	110.9	10.8	7.3	0.112	0.005
NZL	6.3	79.7	12.8	7.8	0.094	0.032

* For full country names and geographical locations see Table 1.

for fungal ITS databases (version released on 28-06-2017) used as a reference (Koljalg et al., 2013). The resulting operational taxonomic units (OTUs) were clustered by using Swarm (version 2.2.2; Mahé et al., 2014). The longest sequence from each OTU was selected as representative of that OTU. Singletons were removed from the analyses and assignment of taxonomy was performed with a BLAST of the OTU representatives against the UNITE+INSDC fungal ITS databases (version released on 28-06-2017; https://unite.ut.ee). Robust assignments to the fungal kingdom were made for the sequences with an expected (E) value < e−50 and a sequence similarity >75%. Moreover, query sequences with an *E*-value between e−08 and e−50 with sequence similarity >75% were manually checked against the 100 best-matching sequences for accurate assignment (Li et al., 2016). Raw sequences from the alder leaves before exposure in the stream and after retrieval of the leaves were deposited in the National Center for Biotechnology Information (NCBI) database (Sequence Read Archives; SRA) under accession numbers SRP072752 and SRP100503, respectively.

2.3. Data analysis

We used linear regression models (Zuur et al., 2007) to assess the relationship between physico-chemical characteristics of the streams and latitude. Rarefaction curves showing the number of sequences versus the number of fungal OTUs in all locations were computed to check whether OTUs were close to saturation. The OTUs of the initial community were then removed from the OTUs of the samples for further analyses and rarefaction curves were generated. The relative abundances of the OTUs and rarefied OTU richness were calculated using the R (version 3.5; R Core Team, 2018) package *vegan* (version 2.5-2; Oksanen et al., 2018).

The relationship between rarefied OTU richness and latitude, other physico-chemical and environmental parameters were determined by linear regression; a quadratic term was added to the model if data suggested a nonlinear relationship. All regressions were performed using R (version 3.5; R Core Team, 2018). All data were checked for normality and homoscedasticity; when necessary, a natural log transformation was applied to meet these assumptions. Barplots of fungal OTUs were generated based on average relative abundances. A Bray–Curtis similarity matrix (Bray and Curtis, 1957) was calculated based on the log-transformed relative abundance data. Patterns in fungal community structure across stream locations were displayed using Canonical Analysis of Principal Coordinates (CAP; Anderson and Willis, 2003) based on relative abundances of OTUs. Permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008) was used to test for differences between sample clouds separated by two CAP axes. Unrestricted permutation of the raw data (9999 permutations) was used for PERMANOVA. PERMANOVA and CAP analyses were performed using PRIMER 6 (Primer-E Ltd., Plymouth, UK; Clarke and Gorley, 2006). A Venn diagram was generated with Venny 2.1 (Oliveros, 2015) to determine the percentage of shared OTUs between the sample clouds separated along the two CAP axes.

3. Results

3.1. Physico-chemical stream characteristics

Mean stream water temperature during the study (3.1–26.2 °C), mean annual air temperature (0.9–27.4 °C), and mean annual rainfall (527–4273 mm) at the 19 sites (Tables 1, 2) were all negatively related to absolute latitude (Fig. 2a–c). Only a high-altitude (3061 m asl) site near the equator in Ecuador emerged as an outlier of this general latitudinal trend (Table 1; Fig. 2a–c). There were no latitudinal patterns in mean pH, conductivity or concentrations of phosphate or nitrate ($p = 0.73–0.14$ and $R^2 = 0.01–0.12$). The concentrations of dissolved oxygen were positively related to latitude (Fig. 2d).

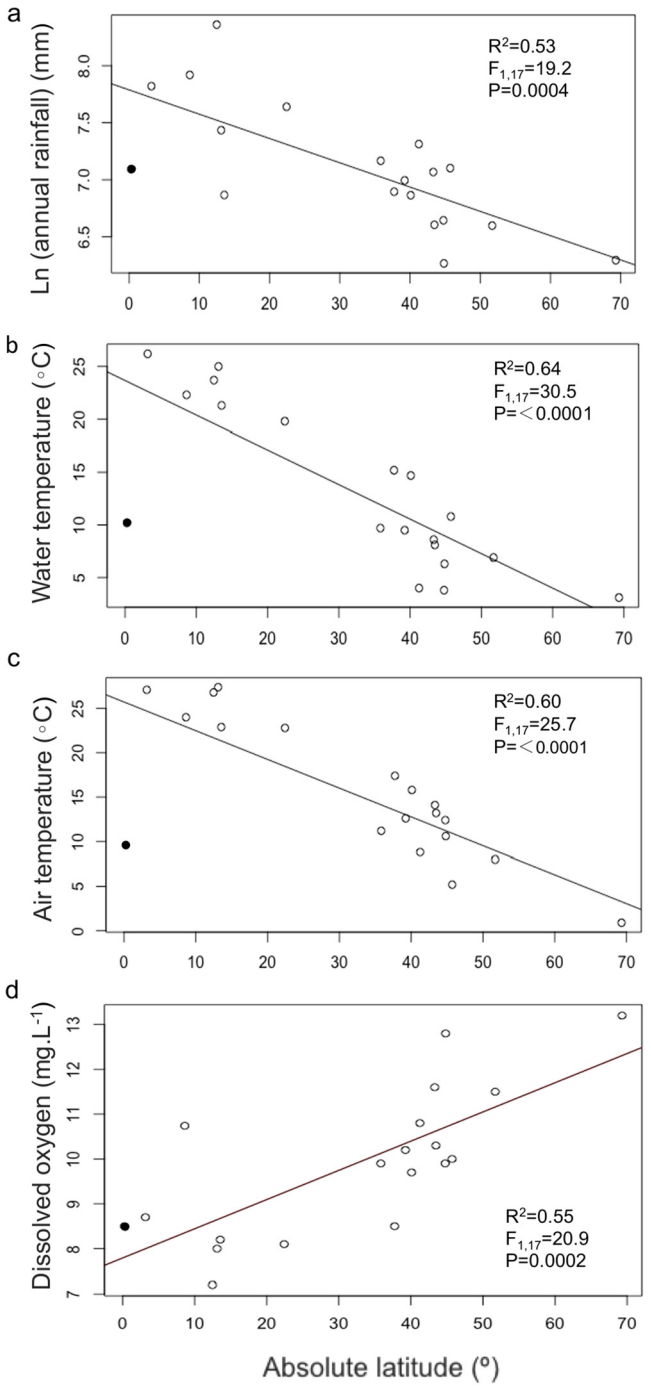


Fig. 2. Linear regressions (n = 19; ● Ecuador, ○ other locations) of the relationships between absolute latitude of stream sites and the natural logarithm of mean annual rainfall (a), mean stream water temperature (b), mean annual air temperature (c) and mean dissolved oxygen (d).

3.2. Illumina MiSeq sequencing

Illumina MiSeq sequencing of colonized alder leaves initially yielded 1,093,416 reads. These were reduced to 859,892 after filtering for quality and length. Joining the forward and reverse reads reduced the number to a total of 229,194 reads, of which 44,138 remained after dereplication and 42,618 after removing chimeras (Table S2). All 'no hits' and OTUs belonging to the kingdom Plantae (14.6%) were also removed. Finally, removal of OTUs of the initial community from the samples yielded 1311 OTUs (Table S3).

3.3. Relative abundance of aquatic fungi

Fungal OTUs were assigned primarily to the phylum Ascomycota (79.7%), followed by Mucoromycota (16.8%), Basidiomycota (0.4%) and Chytridiomycota (0.2%). The remaining 10.6% of the fungal OTUs were unidentified. The relative abundances of fungal classes varied among locations: streams with water temperature ≥8.6 °C (except in Japan) contained mainly Eurotiomycetes and Mucormycetes (Azores, Brazil, Canada, Ecuador, Hong Kong, Malaysia, Portugal, Spain, USA), Saccharomycetes (India, Guinea), or Sordariomycetes and unknown fungi (Australia) and the streams with temperature ≤8.1 and Japan consisted mainly of Leotiomycetes, Dothideomycetes and Rhizophydiomycetes (Fig. 3).

3.4. Fungal richness

The rarefaction curve of the initial community was very different from those of the streams (Fig. S1a). Rarefaction curves of the streams had clearly distinct and separate trajectories, suggesting that they realistically represented inherent diversity patterns (Fig. S1b). After removing the OTUs of the initial community and singletons from the OTUs of the samples, the rarefaction curve approached asymptotes (Fig. S2a). Rarefaction curves of the rarefied OTUs are depicted in Fig. S2b. Rarefied OTU richness was lowest at latitudinal extremes, peaked at mid-latitude regions (Fig. 4, Table S4), and was insensitive to altitude, water physicochemical and other environmental characteristics of the streams sites (Table S4). The species richness in Ecuador (25.6) was almost the same as in Guinea (24.2) at 8.6° latitude of (Fig. 4), whereas the species richness in Malaysia at a latitude of 3.2° was exceptionally high (61.9).

3.5. Endemism and ubiquity

In total, the relative abundance of OTUs that were unique to single locations and identified as exclusive endemics were 29%, showing moderate endemism. The relative abundance of these endemic fungal taxa did not follow any well-defined geographical trend (Fig. S3, Table S5). The relative abundance of endemic OTUs was highest in Ecuador and Hong Kong (97%) closely followed by Malaysia (72%), Portugal (55%) and Japan (54%). Australia and Guinea did not have any exclusive endemics. The average relative abundance of the endemic OTUs was highest in the Neotropic realm (55%), followed by the Indo-Malayan (40%), Palaearctic (35%), Australasian (21%) and Nearctic realms (19%). The Afrotropic realm did not have any endemic OTUs (Table S6). In total, the relative abundance of aquatic hyphomycetes (i.e. Ingoldian fungi) was 17%; however, in France (48.0%), Germany (47.5%) and Italy (46.8%) almost half of all fungi were aquatic hyphomycetes. The aquatic hyphomycete *Lemonniera aquatica* was the most widespread species, occurring in 8 of the 19 locations (Table S7).

3.6. Relationship with water temperature

The fungal communities were separated into three distinct groups based on stream temperature ranges observed during the study (≤8.1 °C, 8.6–19.8 °C and ≥21.3 °C). The only exception was Japan, which was included in the coolest group (Fig. 5). The overall classification accuracy rate based on these three temperature groups was 83.3%, 87.5% and 80.0%, respectively. Both the first ($\delta^2 = 0.94$) and the second ($\delta^2 = 0.80$) squared canonical correlations were large. The first canonical axis separated the communities of the tropical streams (≥21.3 °C) from those of the other two groups, and the second axis separated the communities in streams experiencing temperatures of 8.6–19.8 °C from the others. PERMANOVA established that the relationship with stream water temperature was significant ($F_{2,18} = 2.19$, $P = 0.0001$). The percentage of OTUs that exclusively belonged to the temperature groups ≤8.1 °C, 8.6–19.8 °C and ≥21.3 °C was 19.8, 47.6 and 18.8%, respectively. Streams with water temperatures ≤8.1 °C and between 8.6 and 19.8 °C shared 3.2% of the OTUs, whereas streams with temperatures ≤8.1 °C and ≥21.3 °C, and 8.6–19.8 °C and ≥21.3 °C shared 2.4% and 6.9% of the OTUs, respectively (Fig. 6).

4. Discussion

A decrease in species richness with latitude is the best studied and most widely documented pattern of the distribution of life on earth, particularly in plants and animals (Peay et al., 2016). Many environmental factors, including temperature and rainfall, change systematically with latitude, and may therefore be primary drivers of global diversity patterns. A key discovery of our global study is that fungal taxon richness diverges from the conventional macroecological pattern, showing a clear decline towards the equator. It appears to form a hump-shaped relationship with latitude, with a peak in temperate streams at mid-latitudes (Fig. 4).

A high-altitude (3061 m asl) site near the equator (0.25°) in Ecuador emerged as an outlier in the general latitudinal trend reflecting air temperature, water temperature, dissolved oxygen concentration and annual rainfall; the fungal species richness in Ecuador was almost the same as in Guinea at 8.63°. Malaysia (3.2° latitude) exhibited a very high species richness (61.9) when compared to Ecuador (25.6) and

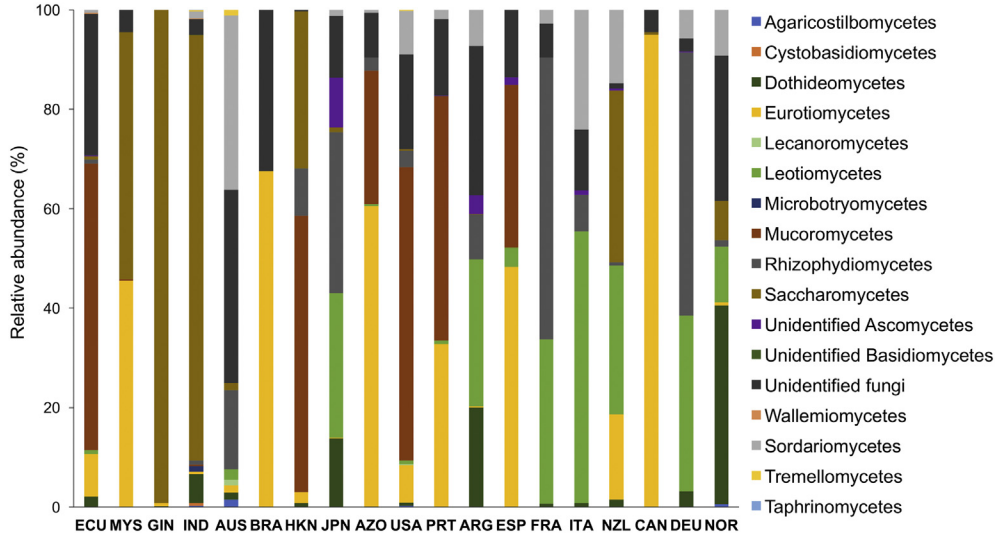


Fig. 3. Relative abundances of fungal operational taxonomic units (OTUs). For locations of stream sites see Fig. 1. The countries are arranged in increasing order of absolute latitude.

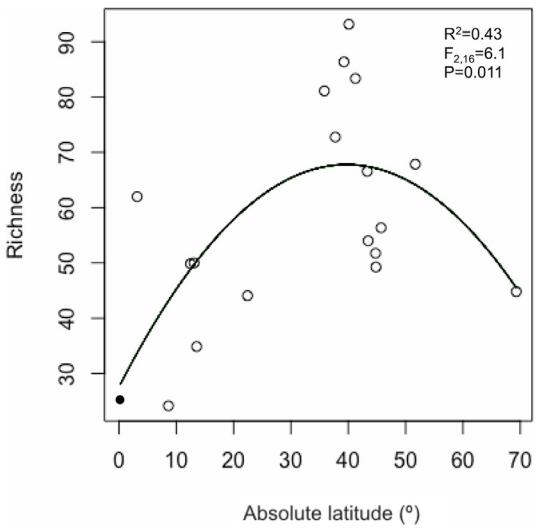


Fig. 4. Quadratic regression (n = 19; ● Ecuador, ○ other locations) between absolute latitude and fungal OTU richness.

Guinea (24.2), but was closer to the species richness (49.9) in India (12.5° latitude). Malaysia has been identified as a global hotspot of plant species richness and endemism, in part due to its high diversity in habitat types and soil characteristics (Sodhi et al., 2004). Over 10,000 species of flowering plants occur in Malaysia, including 2830 tree species in Peninsular Malaysia (Bidin and Latiff, 1995). Among the tree species, 155 of Dipterocarpaceae (the dominant forest trees) have been recorded from Peninsular Malaysia, and 267 dipterocarps have been recorded from Borneo (Brearley et al., 2016). The high habitat, soil and plant diversity and variability in leaf litter characteristics with respect to nutrients, secondary compounds and toughness, could be conducive to supporting a high diversity of fungal decomposers in streams.

Our study included only a single location above latitude 60, which limits the power of inference for subarctic sites. However, declining diversity at higher latitudes was also suggested in two previous reviews based on morphotypes and conidium production of aquatic hyphomycetes (Wood-Eggenschwiler and Bärlocher, 1985; Duarte et al., 2016), both of which included several subarctic streams (e.g., Müller-Haeckel and Marvanová, 1977). Since aquatic hyphomycetes are an important component of fungal communities in streams, this pattern of low diversity at high-latitudes may also hold for stream fungi in general.

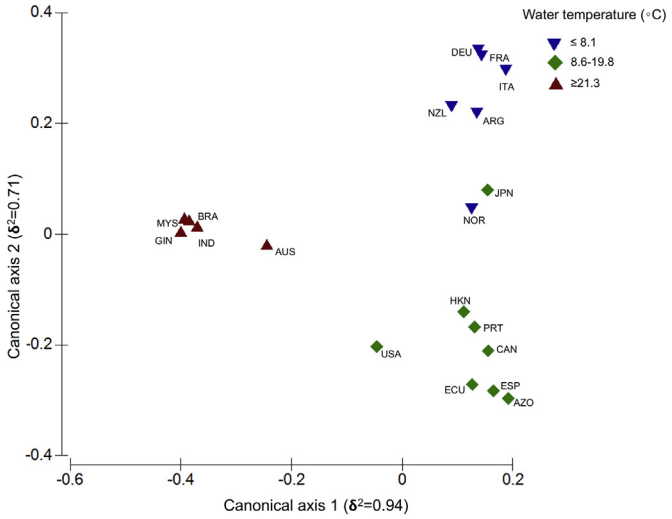


Fig. 5. Canonical analysis of principal coordinate (CAP) ordinations of the relative abundances of fungal OTUs. Locations are colour coded according to mean water temperature. Mean stream water temperature bands were ≤8.1 °C, 8.6–19.8 °C and ≥21.3 °C. For locations of stream sites see Fig. 1.

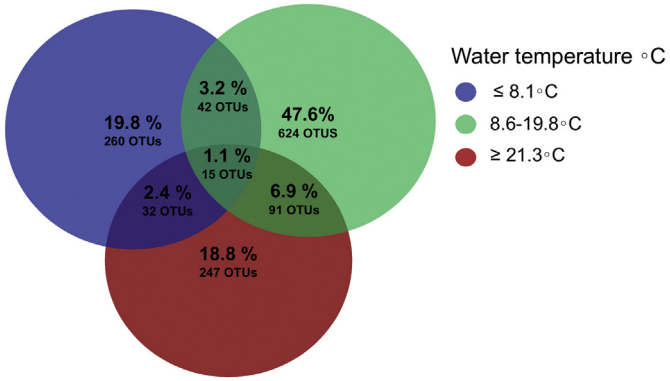


Fig. 6. Venn diagram showing the percentage of unique and shared OTUs between the three stream water temperature groups. Mean stream water temperature bands were ≤8.1 °C, 8.6–19.8 °C and ≥21.3 °C.

The apparent diversity peak we observed in temperate streams could be due to greater niche differentiation along the temperature axis, associated with a wider range and more pronounced seasonal fluctuations (Allan and Castillo, 2007; Shearer et al., 2007; Jabiol et al., 2013b). The resulting hump-shaped pattern of stream fungal diversity strikingly deviates from that of a global study on soil fungal diversity (Tedersoo et al., 2014), which demonstrated macroecological patterns similar to those of other organisms. Distance from equator had the strongest effect on richness of soil fungi, with the diversity of most fungal groups peaking in the tropics, although ectomycorrhizal fungi and certain fungal classes were most diverse in temperate or boreal ecosystems. Which mechanisms could account for this discrepancy in large-scale diversity patters of fungi in streams and soils? Environmental conditions and fungal communities in these ecosystems differ in many fundamental ways (Vinson and Hawkins, 2003; Allan and Castillo, 2007; Gessner et al., 2010; Bärlocher and Boddy, 2016), implying that global diversity patterns of different taxa in different habitats need not match, as was also found for litter-consuming detritivores in streams (Boyero et al., 2011b).

A key difference lies in the effects of precipitation: in terrestrial conditions, where fungal diversity strongly correlates with mean annual precipitation (Tedersoo et al., 2014). The effect of water availability may be straightforward and direct by a lack of moisture inhibiting fungal activity or indirect by affecting the level of primary productivity (Hawkins et al., 2003; Hawkins and Diniz-Filho, 2004). In contrast, since all the streams in our study were permanent, water scarcity was unlikely to have had a direct influence. Fungal diversity may nevertheless be affected by hydrological disturbances such as floods (which may displace fungi and their substrates) and droughts (which may dry stream beds, or, deplete oxygen and concentrate substrates and nutrients in the remaining pools; Allan and Castillo, 2007; Larned et al., 2010).

An important result of our study is the finding that litter-associated fungi in streams tend to occur in thermal bands, independent of biogeographic realms. The three fungal clusters we identified from different locations corresponded to distinct ranges of water temperature, indicating that temperature is key in determining the occurrence and composition of litter-associated fungi in streams across the globe. This pattern reflects differences in the preferred thermal ranges of aquatic hyphomycete species established in laboratory studies for growth (Suberkropp, 1984), reproduction (Chauvet and Suberkropp, 1998) and activity (Ferreira and Chauvet, 2011; for a review, see Canhoto et al., 2016). Thus, given the importance of fungi in litter decomposition in streams (Cornut et al., 2010; Duarte et al., 2015, 2016), large-scale variation and temperature shifts due to climate change are likely to

influence not only the composition of fungal communities but also rates of carbon and nutrient cycling (Dang et al., 2009; Martínez et al., 2014).

The reason for the dominance of aquatic hyphomycetes in temperate regions (Table S7), and their relative scarcity in tropical regions, is unknown. In part, this outcome could be an artefact, due to differences in research efforts and resulting in more limited knowledge of aquatic hyphomycetes in warmer climates. In addition, aquatic hypomycetes, even those of tropical origin, are relatively sensitive to elevated temperatures (Singh and Musa, 1977; Bärlocher and Boddy, 2016).

Our study suggests that stream fungi associated with decomposing leaf litter appear to follow the 'moderate to pronounced endemicity model' of microbial biogeography initially proposed for small eukaryotes (Foissner, 1999), meaning that few species are truly cosmopolitan. However, this conclusion needs further backing by collections from a wider range of streams before generalisations about global distribution patterns can be confidently made. Therefore, future research needs to include comparisons of a much larger number of distinct locations under similar climates and at similar latitudes to substantiate whether community similarity across regions is typically temperature-driven, as our results suggest.

Published evidence indicates that the biogeography of freshwater fungi classified as aquatic hyphomycetes is species-specific (Duarte et al., 2012), and that, as reported here, community composition in geographically distant locations within comparable climatic zones can be similar (Duarte et al., 2016). A caveat to such generalisations about biogeographic diversity patterns is the fact that fungi undergo distinct successions during litter decomposition (Suberkropp, 1984; Gessner et al., 1993). Even within a stream, leaves collected at different decomposition stages or in different seasons may harbour different fungal communities. However, our choice to characterize fungal communities at a defined stage of litter decomposition (i.e. 40–50% of initial litter mass remaining), when aquatic hyphomycete communities have well established on decomposing leaves (Gessner et al., 1993), suggests that consideration of successional changes of fungal communities on decomposing litter is unlikely to shift the general geographic pattern observed in our comparative analysis across multiple globally distributed sites.

The fungal communities in our globally distributed streams were invariably dominated by Ascomycota, as has also been observed in soils (Schneider et al., 2012). However, fast-growing moulds such as *Penicillium* and *Mucor*, yeasts and chytrids were the most abundant fungi in streams where water temperature was ≥8.6C (Fig. 3). The one exception was a stream in Japan which was dominated by aquatic hyphomycetes (63%; Table S7) located at higher altitude (1076 m) than the other locations (75 to 300 m) within that same water temperature range (Table 1). This may reflect that altitude in addition to latitude plays a significant role in structuring fungal communities in streams (Chauvet, 1991; Shearer et al., 2015), as it also does in sediments (Wu et al., 2013) and soils (Siles et al., 2017).

Our results point to an overwhelming influence of water temperature on the overall diversity distribution of litter-associated fungi in streams and also a strong influence on fungal community composition. This lends some support to the hypothesis by Bass-Becking (1934), though there is no evidence that the regions we identified were determined by continental drift. When looking at aquatic hyphomycetes as an important subset of stream fungi, it becomes clear that the ability to widely disperse and colonize geographically distant streams varies widely and is species-specific.

Global warming is likely to induce shifts in microbial communities colonizing decomposing litter in streams, particularly in communities dominated by species adapted to cool environments (Christiansen et al., 2017) or in those that currently experience minimal temperature fluctuations, such as streams near the equator (Perez et al., 2016). A corollary of such community shifts that may involve the loss of key species is that expression patterns of enzymes essential in litter decomposition may lead to cascading adverse effects on food webs, alter biogeochemical cycles (Christiansen et al., 2017) and compromise ecosystem services and human well-being (Chapin III et al., 2000; Sandifer et al., 2015).

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Conflict of interest

The authors declare that they have no conflict of interest, whether of a financial or other nature.

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