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Seasonal variations of aquatic hyphomycete communities in a temperate, a Mediterranean and a tropical stream

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SUMMARY

Aquatic hyphomycete diversity and community composition varies with temperature in space and time. The distribution of species is influenced by temperature along latitudinal gradients, and species richness increases from tropical to temperate latitudes. This pattern is thought to result from an adaptation to cold water, as well as from the highest seasonal temperature fluctuation in temperate streams. Seasonal temperature variations actually influence the occurrence of species in temperate streams. However, much less is known about the seasonal variability of tropical aquatic hyphomycete communities, and no study to date compared this variability across latitudes. In this study, we sampled aquatic hyphomycete communities in 3 streams located under different climates (temperate, Mediterranean and tropical), every month during one year. According to our predictions, we found the highest seasonal variability of aquatic hyphomycete communities in the Mediterranean stream, where temperature fluctuations were also the strongest. However, and despite a high and relatively constant temperature, aquatic hyphomycete communities in the tropical stream exhibited significant seasonal variations as well as the highest species richness. This result contrasts with previous results and highlights the need for further comprehensive studies on aquatic hyphomycete biogeography.

INTRODUCTION

Aquatic hyphomycetes are a polyphyletic group of fungi (Belliveau and Bärlocher 2005) that play a key role in stream ecosystems (Gessner and Chauvet 1994). They decompose plant litter from surrounding terrestrial ecosystems and are a pivotal link between this resource and higher trophic levels, such as stream invertebrates (Bärlocher and Kendrick 1973). They are found in streams located at every latitude, from the tropics to the Arctic (Duarte et al. 2016). Latitude has a well-established effect on the species composition of aquatic hyphomycete communities (Duarte et al. 2016, Seena et al. 2019). Some species are cosmopolitan and can be found at any point along the latitudinal gradient. Others are restricted to narrower ranges of climatic conditions (Wood-Eggenschwiler and Bärlocher 1985). Latitude may also influence the number of species, as first suggested by Shearer et al. (2006), who collected literature data and reported a higher number of species in temperate than in tropical aquatic ecosystems. However, this pattern was interpreted as a potential bias in the sampling effort, since most studies that addressed aquatic hyphomycete diversity had been carried out in the temperate streams of the Northern hemisphere. Later, several experimental data supported this pattern. Using a morphological approach, Jabiol et al. (2013) compared conidial assemblages from leaf-associated aquatic hyphomycetes in 5 streams located from the subarctic to the tropics. They found the highest species richness in the Mediterranean and temperate streams, while tropical, boreal, and subarctic streams exhibited lower diversity. Using Illumina sequencing, Seena et al. (2019) performed a large-scale assessment of leaf-associated fungi in 19 streams distributed around the globe. Again, they confirmed a higher number of taxa (Operational Taxon Unit) of aquatic fungi under the intermediate latitudes. Finally, Barreto et al. (2023) also determined from conidia morphology that leaf-associated aquatic hyphomycete diversity decreases along a latitudinal temperature gradient, from subtropical to tropical Latin America.

This diversity pattern contradicts the common view that biodiversity is the highest at low latitudes (Pianka 1966, Rozensweig 1995). The reasons for this pattern remain poorly understood, and several hypotheses have been suggested. First, this could result from a better adaptation of aquatic hyphomycetes to low temperature (Graça et al. 2016). Several aquatic hyphomycete species actually exhibit a growth optimum at a relatively low temperature (e.g., 15-20°C; Suberkropp 1984, Chauvet and Suberkropp 1998), even though tropical species obviously tolerate higher temperature levels (Sridhar and Bärlocher 1993; Rajashekhar and Kaveriappa 2000). Another hypothesis is related to the temporal heterogeneity due to the seasonal variability of temperature and leaf litter inputs (Shearer et al. 2006, Graça et al. 2016). Under a temperate climate, annual temperature variation is high (cold in winter and hot in summer), and leaf litter inputs are typically pulsed during autumn. To the contrary, tropical streams are exposed to a relatively constant temperature over the year, and often to a more variable and protracted litter subsidy (Wantzen et al. 2008). Consequently, there could be more opportunities for niche differentiation in temperate streams, which would exhibit a higher pool of species (i.e., including a mix of winter/summer species) while tropical communities would be dominated by a few competitive species.

The latter hypothesis is supported by the seasonal variation of aquatic hyphomycete community composition in temperate streams (Suberkropp 1984, Thomas et al. 1992, Fabre 1998, Chauvet 1991), which could be – at least in part – related to the thermal preferences of species (Suberkropp 1984). In comparison, very little is known about the seasonal variability of aquatic hyphomycete communities in tropical streams (see Khallil et al. 1993, Sales et al. 2014), which should be less pronounced than in temperate streams due to relatively constant temperature. To our knowledge, no study to date has been dedicated to comparing the seasonal fluctuations of aquatic hyphomycete communities across latitudes. Here we collected foam samples every month during 1 year in 3 streams located under different climatic areas: one tropical stream in the French West Indies (Bras David, Guadeloupe), one Mediterranean stream (Massane, Eastern Pyrénées), and one temperate stream (Valserine, Jura). According to previous findings, we expected to observe a negative effect of temperature on aquatic hyphomycete species richness and a significant effect of temperature on community composition. Consequently, the highest species richness (α diversity) is expected in the temperate stream because of the low average temperature. Moreover, high seasonal variation of temperature in the Mediterranean stream could contribute to high seasonal fluctuation (β diversity) and overall species richness (γ diversity) despite potentially low α diversity in summer due to high temperature. To the contrary, high and relatively constant temperature in the tropical stream should limit species richness (α and γ diversity) and seasonal variation (β diversity) of aquatic hyphomycete community composition.

MATERIALS AND METHODS

Study sites

The streams are located in Guadeloupe (Bras David, Guadeloupe National Park), in the Pyrénées Orientales (Massane, Massane National Reserve), and the Jura (Valserine, Haut-Jura Regional Park). Sampling was done monthly in each stream during 1 year (Table 1). On each stream, temperature, discharge, physical and chemical (conductivity and pH) data were monitored or collected from existing surveys all over the sampling period. At the tropical site, temperature, discharge, physical and chemical monitoring were performed close to the sampling area (ca. 400 m downstream) by the Observatoire de l'eau et de l'érosion aux Antilles (Obsera) (https://www.ipgp.fr/observation/obsera/, last accessed 05/11/2025). In the Mediterranean site, temperature and physical and chemical data were recorded in situ using data loggers (HOBO UA-001-64, Bourne, MA, USA) and a Hanna Instruments (HI9829) probe. Discharge data were obtained from a station located 10 km downstream on the Hydroportail online database (https://www.hydro.eaufrance.fr/, last accessed 05/11/2025). Finally, all parameters in the temperate stream were monitored 12 km downstream of the sampling site. They were recorded using a data logger (temperature) and from the Hydroportail (discharge) and Naïades databases (https://naiades.eaufrance.fr/, last accessed 05/11/2025). Consequently, temperature, water physico-chemical properties, and discharge data do not necessarily reflect the environmental conditions at the study site with accuracy but remain useful to compare streams and assess the temperature seasonal variability.

Table 1. Location, sampling dates and physical and chemical parameters (pH and conductivity) in the 3 study streams.

Stream	Climate	Coordinates	Altitude (m)	pH	Cond. (µS cm^{-1})	Discharge (min-max-average) (m^3 s^{-1})	Sampling period
Bras David	Tropical	16°10'29'' N 61°41'39'' W	223	7.10	80.00	0.49 – 49.88 – 2.00	11/2023 – 10/2024
Massane	Mediterranean	42°29'05'' N 03°01'50'' E	690	7.16	84.08	0.00 – 5.76 – 0.09	12/2023 – 11/2024
Valserine	Temperate	46°21'59'' N 05°59'35'' E	980	8.22	393.10	0.10 – 18.1 – 2.54	01/2024 – 12/2024

Sampling and conidia identification

Two foam samples were collected each month in the streams using a spoon, transferred to a 2 mL tube and fixed with FAA (ethanol 70 %: acetic acid: formalin 37 % (16 :3 :1)). Samples were then filtered on nitrocelullose membranes (5 µm porosity) and stained with Trypan blue (5 % in 60 % lactic acid). Filters were finally put on a microscopic slide and scanned under the microscope at × 200 magnification. Two hundred conidia were counted and identified in one sample per month and stream. When fewer than 200 conidia occurred in the first sample, the second sample was processed in the same way, and the results were pooled together. Conidia were identified at the species level when possible, using Chauvet (1990), Gulis et al. (2020), Santos-Flores and Betancourt-Lopez (1997), and Fiuza et al. (2017), or classified into morphospecies. Species nomenclature complies with the Index Fungorum (https://indexfungorum.org/) and the French taxonomic reference TAXREF (Gargominy et al. 2022).

Data analysis

To analyse community composition, a Non-Metric Multidimensional Scaling (NMDS) was performed for each stream using Bray-Curtis ecological distances after a Hellinger transformation of abundance data, and excluding rare species (i.e., less than 3 conidia in total). Hierarchical classifications were computed for each stream to identify clusters of samples, and permutational analyses of variance (PERMANOVA) allowed to assess the significance of water temperature on community composition. The Dufrene-Legendre indicator species analysis

(Dufrene and Legendre 1997) was finally used to identify species that were significantly associated with a cluster.

Since all samples did not contain the same amounts of conidia, we used a rarefied species richness as a measure of α diversity to compare the number of species among streams and months. This rarefied species richness corresponds to an estimation of the number of species found if 90 conidia had been counted in each sample. The 90 threshold is the lowest value that allows including all samples in the analysis. A standard error was computed for each value of rarefied species richness. β diversity was defined for each stream as the dispersion of samples (i.e., months) around the centroid of each stream. Finally, we considered the total (pooled over the year) number of species per stream as a measure of γ diversity. Correlations between rarefied species richness and physico-chemical parameters was analysed using Pearson correlations. All analyses were performed using R 4.0.3 (R core team 2020) with the package vegan (Oksanen et al. 2020)

RESULTS

Water temperature

The annual temperature variations are the highest in the Mediterranean stream (Fig. 1), where temperature was at its lowest on the 8th February (maximum daily temperature 2.09 °C) and reached 25.12 °C in summer (1st August). In the temperate stream, overall temperature is lower and slightly less variable between summer, when maximum daily temperature reached 18.05 °C (12th August), and winter, when maximum daily temperature as low as 3.05 °C occurred (1st January). Finally, the tropical stream exhibits a much more constant and warm temperature all around the year, with maximum daily temperature ranging from 21.62°C (9th February) to 26.67°C (12th June).

Variations of community composition

In total, 98 morpho-species were found (Fig. 2, Supplementary File S1), and 66 were identified to the species level. Species occurrence data were deposited in the public French INPN database (ww.inpn.mnhn.fr/) which periodically synchronises with the GBIF database (www.gbif.org). The 3 streams clearly harboured distinct aquatic hyphomycete communities. Four species were cosmopolitan and were encountered in the 3 streams (*Anguillospora crassa*, *Flagellospora curvula*, *Alatospora acuminata*, and *Tetracladium marchalianum*). Besides these 4 species, the temperate and Mediterranean streams had 12 species in common, and consequently shared ca. 1/3 of their species pool. Similarity with the tropical stream was lower. It had only 6 species in common with the temperate stream, and 9 with the Mediterranean stream.

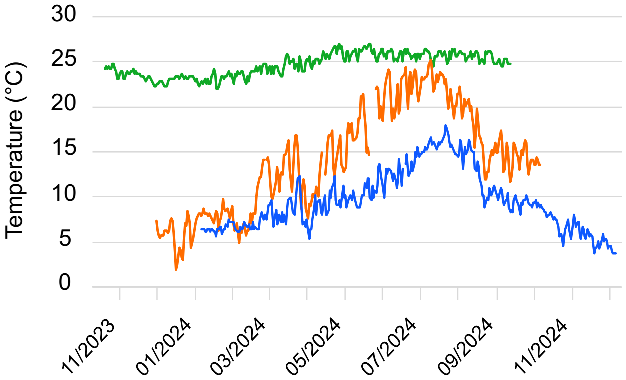

Figure 1. Temporal variation of stream water temperature in the tropical (green), Mediterranean (red) and temperate (blue) streams during the sampling period.

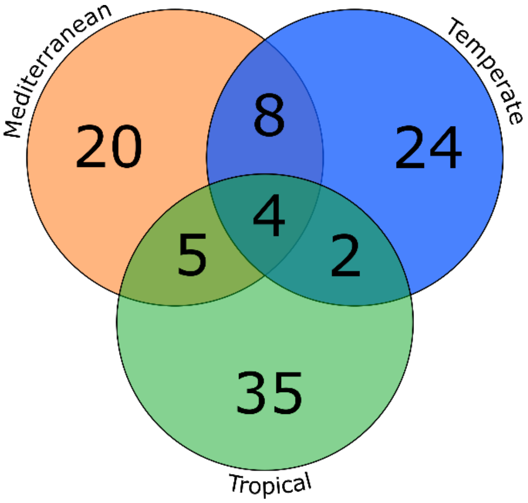

Figure 2. Venn diagram illustrating the number of shared vs. unique species in each stream.

The species composition of aquatic hyphomycete communities also varied within streams, i.e. among seasons. In the tropical stream, distinct communities occurred between the dry (July to October) and the wet (November to June) seasons (Fig. 3). Most species occurred year-round, but some exhibited seasonal patterns: *Phalangispora constricta* and *Campylospora filicladia* were more common during the wet season, while *Campylospora chaetocladia*, *Tricladium* sp. and *Lunulospora curvula* were more abundant during the dry season (Fig. 3). In the Mediterranean stream, the cluster analysis distinguished between 'summer' (May to October) and 'winter' (November to April) communities. Species that were found in higher relative density during summer included *Triscelophorus acuminatus*, *Anguillospora crassa* and *Clavariopsis aquatica*. Species that were more common during winter were *Lemonniera terrestris*, *Heliscella stellata*, and *Taeniospora gracilis*, though they were not identified as significant indicator species. Finally, and contrary to the two other streams, three clusters were identified on the temperate stream. One matches winter samples (November to April), another one late spring/early summer (May to July), and the last one late summer/early autumn (August to October). Winter samples were dominated by *Alatospora acuminata*, which was found year-round but with much higher relative densities during winter. Some species were found in late summer (*Lemonniera aquatica*) or spring (*Erynia conica*, *Tricladium curvisporium*) while others were more abundant from May to October (e.g., *Tetracladium marchalianum*). In the Mediterranean and temperate streams but not in the tropical stream, these seasonal shifts of species composition were statistically related to temperature variations (Fig. 3).

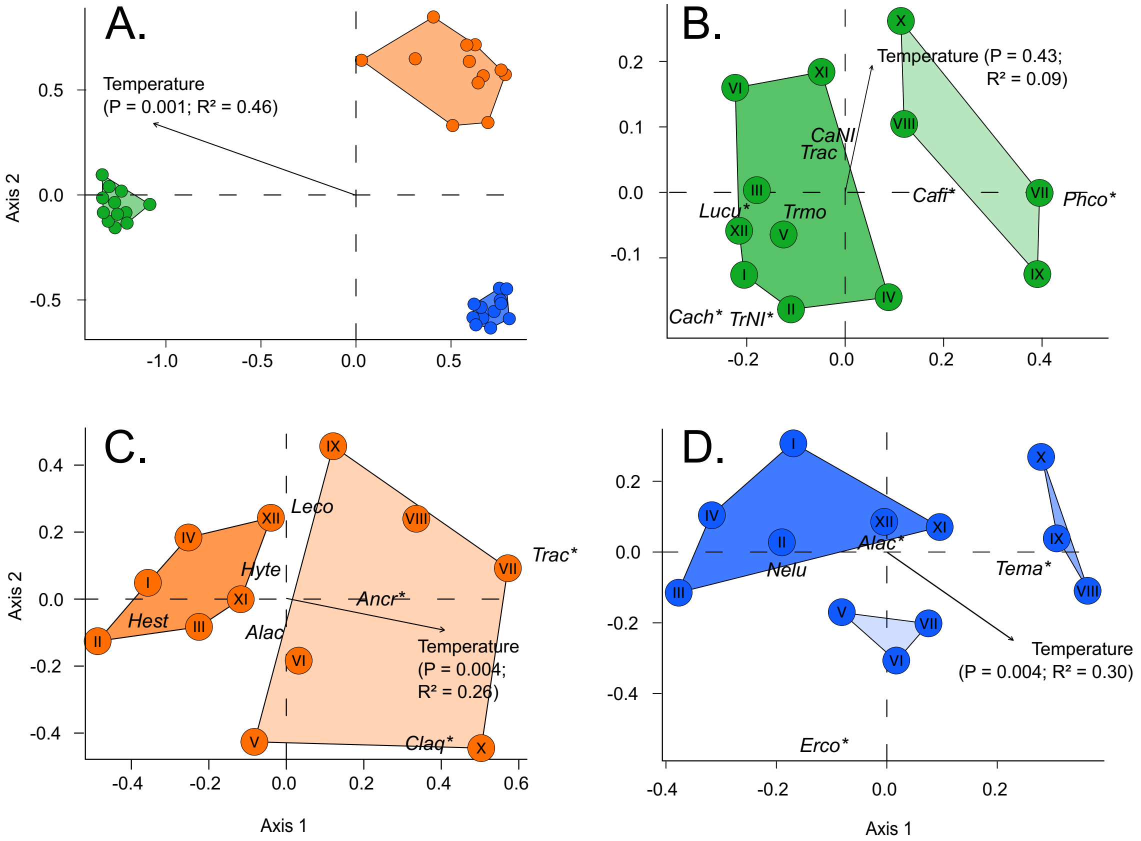

Figure 3. Non-Metric Multidimensional Scaling of aquatic hyphomycete communities. In A all streams were included in the analyses, and B-D are analyses within each stream. Green: tropical, Red: Mediterranean and Blue: temperate. In B-D, the samples are identified with roman numbers corresponding to months (I-XII). The arrow is the projection of temperature, and P and R^2 indicate the results of PERMANOVA. Convex hulls group the samples belonging to the same clusters according to hierarchical analyses. In B-D, the coordinates of both dominant (relative density > 5 %) and significant indicator species (*) are provided. Correspondence between abbreviations and full species names are given in the Supplementary File S1.

Variations of species richness

Rarefied species richness (α diversity) was significantly higher but also more variable from month to month in the tropical stream (12.28 ± 3.20 SD) compared with the Mediterranean (10.16 ± 1.67 SD) and the temperate (9.31 ± 1.09 SD) streams, where it was lower and much less variable. Total species pool (γ diversity) was also the highest in the tropical stream (46 species), while the temperate (38 species) and Mediterranean (37 species) streams exhibited a lower species richness. Finally, β diversity, as assessed from the dispersion of samples around the centroid of each stream, was the highest in the Mediterranean stream and the lowest in the temperate stream (Table 2).

Table 2. Aquatic hyphomycete diversity metrics in each stream.

	Average rarefied species richness and 95 % CI	**Seasonal variability (dispersion of sample around the centroid)**	**Total number of species**
	(α diversity)	**(β diversity)**	**(γ diversity)**
Tropical	12.28 [11.00 – 13.56]	0.238	46
Mediterranean	10.16 [8.88 – 11.44]	0.298	37
Temperate	9.31 [8.03 – 10.59]	0.215	38

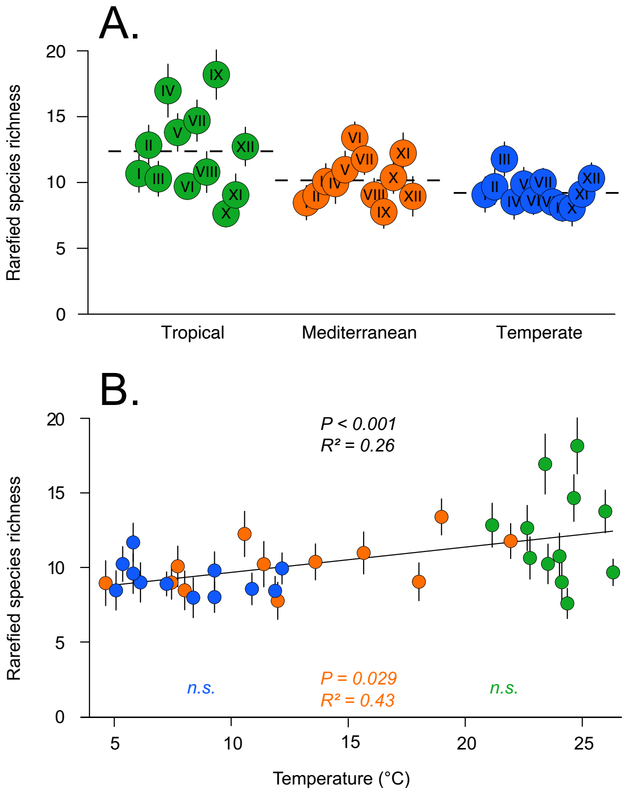

Figure 4. Rarefied species richness A – grouped by stream and B – along the temperature gradient. In A, dashed lines are stream average and dots are identified with the month in roman number (I-XII). In B, the line is the regression of the global analysis (including all streams). P values and R^2 are the results of Pearson correlations including all streams (black) or computed within streams. Green: tropical, red: Mediterranean and blue: temperate. Errors bars are the standard errors associated with computing the rarefaction.

Overall, a positive effect of stream water temperature on α species richness was observed, but was clearly due to differences between stations (i.e., higher species richness in the warmest tropical stream). Within streams, this temperature effect was significant in the Mediterranean stream only (Fig. 4), where rarefied species richness varied between 7.8 and 13.4 species. It was the lowest in February and September, and exhibited 2 peaks: in June (13.4) and November (12.2). In the temperate stream, no effect of temperature was found on α diversity. The number of species was relatively constant year-round, from 8.0 to 10.0, except for a peak in March (11.8 species). In the tropical stream, a high variability occurred from month to month. Rarefied species richness varied from 7.6 (October) to 18.2 (September) with no obvious seasonal pattern.

DISCUSSION

The species composition of aquatic hyphomycete communities clearly varies across space and time. One likely driver of these variations is temperature, which determines the presence or abundance of a species according to its thermal preferences (Duarte et al. 2016; Seena et al. 2019). Consequently, even though some cosmopolitan species are known, many are restricted to a narrow latitudinal band (Wood-Eggenschwiler and Bärlocher; Duarte et al. 2016; Seena et al. 2019). In our study, a few cosmopolitan species were found, but the tropical stream mostly exhibited tropical species (Santos-Flores and

Bétancourt-Lopez 1996) and lacked most species that are common to higher latitudes. Conversely, the temperate stream harbored species that are well known from high latitudes, and the Mediterranean stream was somewhat intermediate, sharing around a half and a fourth of its species with the temperate and the tropical stream, respectively. At the local scale, temperature was also important in determining the succession of species over the year, as previously suggested by Suberkropp (1984).

Alatospora acuminata illustrates a species for which the relative density varied in space and time according to temperature (Supplementary File S2). It is a cosmopolitan species but reaches its optimum under cold conditions. It often ranges among the dominant species from temperate (e.g. Fabre 1998) to subarctic (Müller-Haëckel and Marvanova, Jabiol et al. 2013) streams of the Northern hemisphere, but was also previously reported in tropical areas (e.g. Bärlocher et al. 2010). Its distribution is consistent with its thermal preferences, since temperatures higher than 20°C (i.e., lower than stream water temperature under the tropics) tend to inhibit its growth (Suberkropp 1984). In our study, its density increased with latitude from the tropical to the temperate stream. In the latter, it was even found at its highest densities during winter when the temperature is the lowest. To the contrary, conidia belonging to the genus *Triscelophorus* (*T. monosporus* and *T. acuminatus*) are found in higher density in warmer conditions. They dominated the tropical stream and are known to occur in the warmest stations of temperate regions (i.e., lowland or summer samples; Chauvet 1991). In our study, it was also found in the Mediterranean stream (not in the temperate stream), but only during summer and early autumn.

Previous results described a peak of aquatic hyphomycete diversity at intermediate latitudes (Jabiol et al. 2013, Seena et al. 2019, Barreto et al. 2022), which was thought to reflect a negative influence of excessive temperature under the tropics. This was clearly not the case in our study. The warm tropical stream harbored the highest species richness, and the colder temperate stream the lowest. This discrepancy with existing data is intriguing, and identifying its causes is clearly out of the range of our study. Though one important difference between this and previous studies is that we described aquatic hyphomycete communities from foam samples, when previous studies mostly relied on fungal communities associated with decomposing leaf litter, either by counting conidia produced from leaf baits (Jabiol et al. 2013, Barreto et al. 2022) and metabarcoding (Seena et al. 2019). It is well known that using different sampling techniques can lead to dissimilar results (Shearer and Webster, 1985). Foam samples are less standardized but often harbor more species than conidia assemblages obtained from leaf-baits (Wood-Eggenschwiler and Bärlocher 1983, Pascoal et al. 2005). This higher species richness in foam than in litter samples was even more pronounced for surveys that were conducted in tropical streams (Iqbal 1994, Maddodi et al. 2008). This suggests that stream-scale aquatic hyphomycete species richness could be underestimated in the tropics when relying only on communities associated with one (or a few) litter species (Jabiol et al. 2024). Another explanation is that our temperate stream exhibited a higher pH than the 2 others, which can inhibit aquatic hyphomycete species richness (Wood-Eggenschwiler and Bärlocher 1983, Bärlocher 1987). Additional studies, including a broader range of environmental conditions at each latitude, would be needed to confirm these results.

As expected, the seasonal variability (β diversity) was the highest in the Mediterranean stream, where annual temperature fluctuations are the strongest. In this stream, species richness also varied between seasons, with, again, a peak of species richness at high temperature (i.e., during summer). However, another peak occurred in November, which suggests that temperature is not the only factor at play. Moreover, in the other streams, temperature was not always a significant predictor of species composition or richness. Instead, other environmental factors were probably involved in the variations of species composition between seasons. Stream turbulence and flow velocity can stimulate the liberation of conidia in stream water (Webster and Towfik 1972, Sanders and Webster 1980, Bärlocher et al. 2011), increase the number of conidia in the water column, and increase the probability of rare species. This mechanism could explain the low conidia diversity during late summer in the Mediterranean stream. It may also allow the immersion and conidia production by fungi that grow on the river banks and usually do not contribute to the pool of conidia in the water column. For instance, the wet season samples in the tropical stream contained higher densities of *Phalangispora constricta*, a species that is known to be able to sporulate in a terrestrial environment (Nawawi and

Webster 1982) and is likely adapted to an aero-aquatic life cycle. Finally, turbulence also interferes with the production of foam, its quality, and persistence over time. Thus, depending on flow conditions, a foam sample collected at a given place could have accumulated a species assemblage that is relevant to different spatial (different distances upstream) or temporal (depending on the time persistence of the foam) scales.

Another factor that varies across seasons and latitudes is the timing of leaf litter subsidies. In temperate streams, the highest density of conidia assemblages in stream water occurs in autumn, when stream leaf litter availability is the highest (Suberkropp 1997, Bärlocher 2000). This coincides with the peak of diversity we observed during November in the Mediterranean stream. However, no diversity peak or community shift was observed at the beginning of autumn in the temperate stream. One possible explanation could be that the autumn peak does not occur in places where evergreen tree species dominate, such as in Australian streams dominated by eucalypt trees (Thomas et al. 1989) or in our temperate stream (Valserine), where coniferous trees dominate the upstream part of the catchment. Another possibility is that foam samples are not the best approach to detect shifts in species richness when it covaries with conidia density. Since foam samples are not quantitative, the only way to homogenize the sampling effort across samples is by standardizing the number of conidia. Thus, in conditions where a few species dominate with massive conidia production (i.e., after litterfall at early decomposition stages; Gessner et al. 1993), the detection probability of rare species decreases, and species richness is underestimated. Interestingly, the indicator species of spring samples in the temperate stream (*Erynia conica*) is not a leaf decomposer but a fungal entomopathogen (Descals and Webster 1984). As a consequence, its seasonal occurrence does not follow the availability of leaf litter subsidies but is synchronous with the emergence of stream invertebrates.

Temperature, water flow, and litter availability are tightly intertwined: litter fall often occurs at periods of abrupt changes in weather conditions, such as temperature (autumn) or precipitation (dry/wet season). In temperate and Mediterranean streams, low flow conditions mostly occur during summer when the temperature is high, then counteract a potential stimulation of hyphomycete activity by temperature. Finally, high discharge can alter the distribution and availability of litter in the stream and influence aquatic hyphomycete conidia density (Gönczöl and Revay 2004). Consequently, disentangling these effects on the seasonality of aquatic hyphomycete communities remains a matter of conjecture. Further surveys are needed, and should obviously include a larger set of streams to encompass the natural variability of environmental conditions within each climatic area, including variable chemical conditions such as pH and conductivity. As discussed above, future studies should also use several complementary techniques of sampling simultaneously, since not all provide the same picture of the community. Combining ecological, morphological, and molecular approaches seems particularly relevant to the biogeography of aquatic hyphomycetes. Finally, sigmoid species (such as *Flagellospora curvula* and *Anguillospora crassa* that were common to the 3 studied streams) are not always easy or possible to identify morphologically. Based on available ITS rDNA barcodes, Franco-Duarte et al. (2022) found that *Anguillospora crassa* actually belonged to two distinct groups, and reported likely misidentifications for several sigmoid species (*Amniculicola longisima*, *Flagellospora curvula*, *Anguillospora furtiva*). Combining molecular and morphological tools would thus allow confirming if conidia that are morphologically similar across latitudes actually belong to the same species.

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AUTHOR CONTRIBUTIONS

JJ designed the study, identified conidia, analyzed the data, and wrote the manuscript. All authors contributed to the sampling and provided feedback on the writing of the manuscript.

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