



Drying shapes the ecological niche of aquatic fungi with implications on ecosystem functioning



Rebeca Arias-Real^{a,b,c,*}, Margarita Menéndez^c, Isabel Muñoz^c, Cláudia Pascoal^{a,b}

^a Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

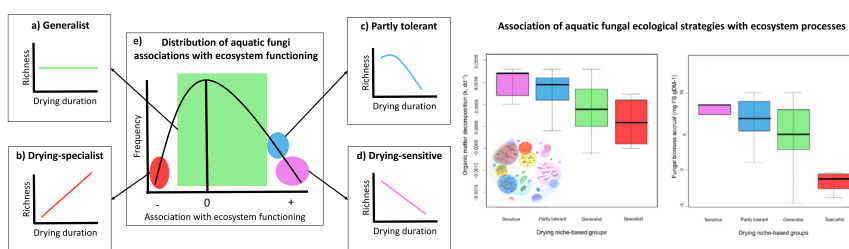
^b Institute of Science and Innovation for Bio-Sustainability (IB-S), University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

^c Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Universitat de Barcelona, Av. Diagonal, 643, 08028 Barcelona, Spain

HIGHLIGHTS

- Drying was the dominant abiotic factor shaping the composition of aquatic fungi.
- Niche-based clustering of fungi were based on specialization and affinity to drying.
- Drying sensitive taxa had the highest association with ecosystem processes.
- Generalists have emerged as successful aquatic fungal taxa in IRES.
- Drying specialists made the weakest association with ecosystem processes.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:

Aquatic hyphomycetes
Ecological niche
Fungal biomass accrual
Intermittent rivers and ephemeral streams
Organic matter decomposition
Trade-offs

ABSTRACT

Fungi are among the most abundant and diverse organisms on Earth and play pivotal roles in global carbon processing, nutrient cycling and food webs. Despite their abundant and functional importance, little is known about the patterns and mechanisms governing their community composition in intermittent rivers and ephemeral streams, which are the most common fluvial ecosystems globally. Thus far, it is known that aquatic fungi have evolved various life-history strategies and functional adaptations to cope with drying. Nevertheless, some of these adaptations have a metabolic cost and trade-offs between growth, reproduction and dispersion that may affect ecosystem functioning. Thus, understanding their ecological strategies along a gradient of drying is crucial to assess how species will respond to global change and to identify meaningful taxa to maintain ecosystem functions. By combining in situ hydrological information with a niche-based approach, we analysed the role of drying in explaining the spatial segregation of fungal species, and we determined their specialization and affinity over a gradient of drying. In addition, we estimated whether species niches are good predictors of two key ecosystem processes: organic matter decomposition and fungal biomass accrual. Overall, we found that annual drying duration and frequency were the most influential variables upon species niche differentiation across the 15 studied streams. Our cluster analysis identified four drying niche-based groups with contrasting distributions and responses over the drying gradient: drying-sensitive, partly tolerant to drying, generalist, and drying-resistant specialist. In addition, we found that species belonging to the drying specialist group showed a weak contribution to both ecosystem processes, suggesting trade-offs between drying resistance strategies and the energy invested in growth. Taken together, our results suggest that increased water scarcity may jeopardise the capacity of aquatic fungi to guarantee ecosystem functioning and to maintain biogeochemical cycles despite their ability to cope with drying.

1. Introduction

Fungi are among the most abundant and diverse organisms on Earth and are present in nearly all environments, including terrestrial, marine and freshwater environments (Hawksworth and Lücking, 2017). In

* Corresponding author at: Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Universitat de Barcelona, Av. Diagonal, 643, 08028 Barcelona, Spain.

E-mail address: rebeca.arias.real@ub.edu (R. Arias-Real).

<http://dx.doi.org/10.1016/j.scitotenv.2022.160374>

Received 21 July 2022; Received in revised form 14 November 2022; Accepted 16 November 2022

Available online 22 November 2022

0048-9697/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

freshwater environments, 3870 fungal species have been described (Calabon et al., 2022), and their biomass accounts for 95 to >99 % of the total microbial biomass on decomposing plant detritus (Grossart et al., 2019; Gulis and Suberkropp, 2003; Krauss et al., 2011). As such, fungi play pivotal roles in maintaining multiple ecosystem functions and services, including but not limited to global carbon processing, nutrient cycling and energy transfer to higher trophic levels (Arias-Real et al., 2018, 2022b; Besemer, 2015; Gessner et al., 2010; Manning et al., 2018). Despite their abundance and functional importance, surprisingly, little is known about the patterns and mechanisms governing fungal composition and diversity in watercourses experiencing recurrent drying, i.e., intermittent rivers and ephemeral streams (IRES), which are the most common fluvial ecosystems globally (Datry et al., 2017; Messenger et al., 2021). This lack of knowledge hampers our ability to predict microbial community shifts in response to environmental change and the consequences for ecosystem functioning and global biogeochemical cycles.

Aquatic fungi (aquatic hyphomycetes and aeroaquatic hyphomycetes) are an ecological group of fungi that depends on aquatic habitats at least for part of their life cycles (Grossart et al., 2019; Grossart and Rojas-Jimenez, 2016). In addition to their reproductive systems, their colonization and dispersal capacity rely on flowing water (Chauvet et al., 2016; Duarte et al., 2015; El-Elimat et al., 2021; Grossart et al., 2022; Krauss et al., 2011). Hence, the inherent dynamism of IRES – cycles with flowing and drying phases, may be challenging for them unless aquatic fungi present morphological or functional adaptations that allow them to develop their life cycles under these stressful conditions.

It has been observed that aquatic fungi are highly plastic and resistant microorganisms (Coleine et al., 2022) with physiological and functional adaptations that have emerged over evolutionary time (Baschien et al., 2006; Belliveau and Bärlocher, 2005; Naranjo-Ortiz and Gabaldón, 2019). Indeed, aquatic fungi have evolved numerous morphological and osmotic adaptations, such as hydrophobic cell walls, which are more efficient in reaching osmotic equilibrium during flow cessation and entering dormancy during drying (Canhoto et al., 2021; Gonçalves et al., 2019; Jones and Lennon, 2010; Kakumanu et al., 2013). Furthermore, previous studies showed that hyphae may cross air-filled sediment pores to access nutrients and water during drying (Cornut et al., 2014; Ghate and Sridhar, 2015; Gionchetta et al., 2019) and that the composition of fungal communities changes over drying gradients (Arias-Real et al., 2022b; Gionchetta et al., 2020b; Mora-Gómez et al., 2018). Given that aquatic fungi can present different drying strategies depending on their eco-physiology, morphology and life-history (Crowther et al., 2014; Graça et al., 2022), the effects of drying may differ depending on which species within the community are affected, with implications for ecosystem functioning.

Aquatic fungi are capable of adapting rapidly to changing environmental conditions, which causes alterations in community structure and composition (Allison and Martiny, 2008; Wallenstein and Hall, 2012). However, these compositional shifts may alter species contributions to ecosystem functioning. These results may be due to physiological trade-offs between growth, reproduction and dispersion (Graça et al., 2022). For instance, the trade-off between resource use efficiency and maximum growth rate for bacteria is well documented (Crump and Hobbie, 2005; Lipson et al., 2009). To date, explaining the relationship between fungal diversity and ecosystem function is based on two assumptions. The first is that fungal communities have functional plasticity and are able to adjust their performance (e.g., modifying their ability to use organic matter) to accommodate drying. The other is related to functional redundancy, assuming that different species with similar roles can substitute for one another with no effects on ecosystem functioning (Allison and Martiny, 2008; Gionchetta et al., 2020b). In addition, there is now unequivocal evidence that aquatic fungal identity influences freshwater ecosystem processes (Duarte et al., 2006; Handa et al., 2014; Seena et al., 2020). However, we know little about how changes in naturally-assembled fungal communities influence ecosystem functioning.

The ecological niche concept is a powerful framework to understand how organisms respond to environmental gradients (Arias-Real et al.,

2022a; Beaugrand et al., 2020; Green et al., 2008; Hutchinson, 1957). An ecological niche defines and integrates two important types of ecological information, the habitat conditions in which organisms can grow, survive and reproduce, and the role of organisms in ecosystems, i.e., their ecological function (Beaugrand et al., 2015; Sexton et al., 2017). Thus, understanding the ecological niches of aquatic fungi along a gradient of drying is crucial to assess how species will respond to global change and to identify meaningful taxa to maintain ecosystem functions.

Thus, the main objective of this study is to gain deeper insight into the ecological strategies of aquatic fungal species and their associations with ecosystem functioning over a gradient of drying. To do so, we first analysed the role of drying vs. non-hydrological abiotic factors in explaining the spatial segregation of aquatic fungal species under a gradient of drying in 15 low-order streams. Second, we characterized their ecological niches by determining their specialization and affinity over the drying gradient and its environmental descriptors by identifying groups of species showing similar niches and responses. Finally, to understand the relationship between species drying niches and their contribution to ecosystem functioning, we investigated the association of each fungal species with two key ecosystem processes (organic matter decomposition and fungal biomass accrual). In Fig. 1, we show the expected spatial distribution of fungi over the drying gradient and their associations with ecosystem functioning. We predict that (i) drying will be the primary determinant of species spatial distribution, as water availability is the major limiting factor for the occurrence and survival of aquatic fungi (Krauss et al., 2011; Manzoni et al., 2014; Schimel et al., 2007); (ii) fungal species will aggregate into four main niche-based strategies: generalist taxa able to develop their life cycles over an ample range of drying conditions (Fig. 1a), drying specialist taxa with affinity for intermittent and ephemeral watercourses (Fig. 1b); partly tolerant taxa with affinity for low-intensity drying conditions (Fig. 1c), and drying-sensitive taxa with affinity for perennial watercourses (Fig. 1d); and finally (iii) drying specialist and generalists will have lower associations with ecosystem functioning than drying-sensitive taxa and partly tolerant taxa as a result of eco-evolutionary trade-offs (e.g., metabolic trade-offs) resulting from their adaptation to recurrent drying (Fig. 1e).

2. Material and methods

2.1. Study sites

This study was conducted at 15 independent streams located in eight river basins of the Mediterranean climate with low human impact along a wide intermittent gradient (drying duration between 0 and 340 days within a year and drying frequency between 1 and 7 periods within a year) in Catalonia (NE Spain). The studied stream orders vary between three and four over an altitudinal range of 100 to 655 m.a.s.l. The primary land uses at the riparian scale were forest, scrubland, grasslands and extensive agriculture (mainly olive groves and vineyards) (CORINE Land Cover 2006 data in a buffer area of 1 km around each sampling site) (Appendix A, Table A1). Furthermore, poplar (*Populus nigra* L.), alder (*Alnus glutinosa* (L.) Gaertner) and evergreen oak (*Quercus ilex* L.O.) were the dominant riparian vegetation types.

2.2. Survey of aquatic fungi

We sampled aquatic hyphomycete conidia just after the rainy season in February 2017 to ensure that all streams were in the flowing phase. We collected samples of white freshly accumulated foam from different locations within 100 m stretches in each stream with a spoon. The foam was then transferred to sterile glass bottles (25 ml), fixed with formaldehyde (4 %), and transported to the laboratory. Once in the laboratory, 5 ml of each foam sample, with the corresponding suspensions of conidia, was filtered through 5 µm pore-size membrane filters (Cellulose Nitrate Membrane Filters, Whatman). The retained conidia were stained with 0.1 % Trypan Blue solution in lactic acid. Then, we scanned the surface of the filter under a light microscope (400×) and identified all aquatic hyphomycete

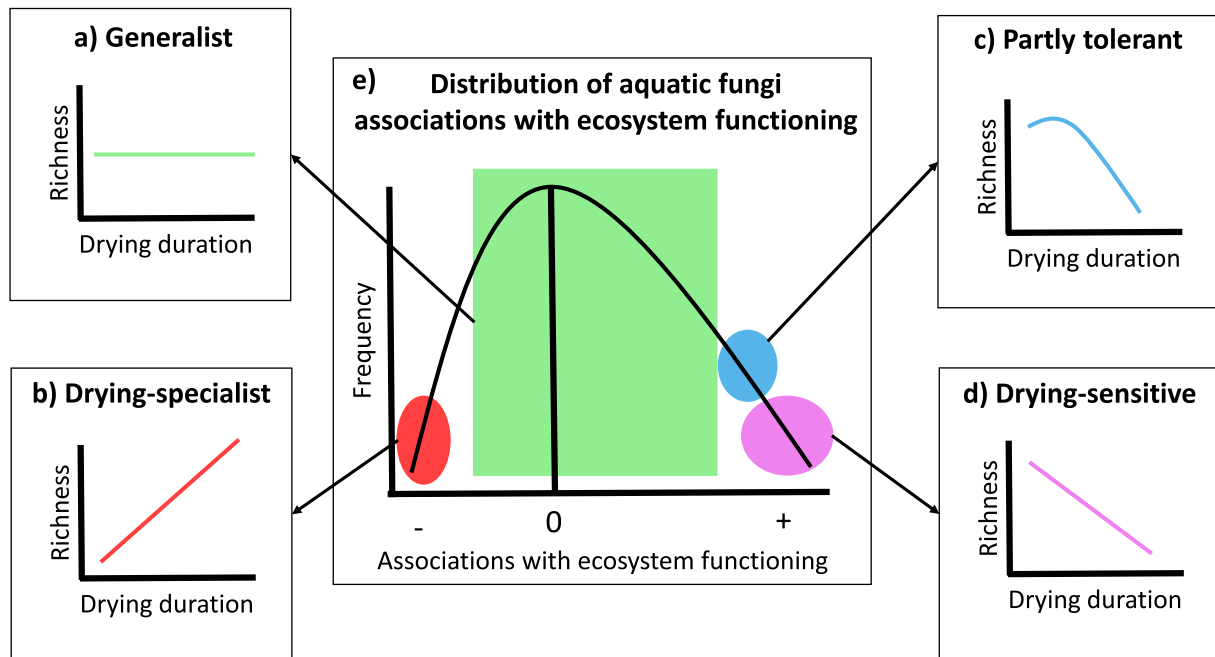


Fig. 1. Hypothetical expectations of fungal taxon richness responses of each drying niche-based group to a drying gradient (a–d) and the expected association of each drying niche-based group with ecosystem functioning (e; the curve represents the distribution frequency of individual species' and the expected association with each ecosystem process: organic matter decomposition and fungal biomass accrual).

species based on conidial morphology and dimensions until the lowest possible taxonomic level (mainly species). Aquatic hyphomycete species were documented as present/absent.

To avoid spurious results, only 38 taxa (from the total of 74 taxa), which occurred at least in two sites out of 15 (occurrence $\geq 13\%$), were considered for statistical analyses (see below).

2.3. Characterization of ecological niches and strategies of aquatic fungi

Ecological niches were calculated in a multidimensional space built upon two different aspects of the drying process (annual drying duration and frequency) and five additional abiotic descriptors that may influence fungal species occurrences (temperature, conductivity, and concentrations of soluble reactive phosphorus, dissolved inorganic nitrogen and dissolved oxygen). To calculate annual drying duration and frequency, one year before our biological sampling (February 2016), we placed temperature and water level data loggers on each streambed to measure the daily variation in streambed temperature (Arias-Real et al., 2021), which allowed us to infer water presence (Appendix B). Abiotic features were characterized up to three times (February 2016, September 2016 and February 2017) at each stream location, when surface water was present. Conductivity, water temperature, pH and dissolved oxygen were measured using a portable probe (YSI Professional Plus Multiparameter Instrument, USA). We further collected water samples to quantify the concentrations of dissolved inorganic nitrogen (DIN: N-nitrate + N-nitrite + N-ammonium) and soluble reactive phosphorus (SRP) (Appendix C).

We calculated niche specialization and affinity for each aquatic fungal taxon using the Outlying Mean Index (OMI) (Dolédec et al., 2000). OMI analysis is a multivariate coinertia analysis to describe species niches along environmental gradients where the main advantage is the lack of assumption about the shape of species response and the equal weight attributed to all sites, regardless of their species richness. We calculated niche specialization and affinity for each aquatic fungus using the ade4 R package. Niche specialization (OMI) represents the deviation between the mean habitat conditions of a species and the average habitat conditions along a flow intermittence gradient. The OMI ranges from 0 to 100, where greater OMI values represent a more specialized strategy for a

given portion of the gradient as opposed to generalist strategies (low OMI values). Niche affinity is represented by the first axis (drying axis) and second axis (non-hydrological environmental axis) of the multidimensional space (Heino and Grönroos, 2014; Tales et al., 2004) (see Results).

To identify groups of species with similar ecological niches, taxa were assigned to their drying specialization and affinity through a k-means clustering procedure. The ecological niche variables were standardized before analysis. We evaluated the statistical performance (sum of squares) and ecological meaning of a range of potential clusters, representing two to ten ecological niche-based groups of aquatic fungi. Finally, we retained the cluster splitting taxa into four drying niche-based groups, as they showed a good explanatory capacity (sum of squares = 69%) and coherent ecological grouping in the flow intermittence gradient: drying-sensitive, partly tolerant, generalist and drying-specialist taxa.

2.4. Associations of aquatic fungal identity with ecosystem processes

We quantified two key ecosystem processes in which aquatic fungi play a key role: organic matter decomposition and fungal biomass accrual. We calculated temperature-corrected decomposition rates (degree days, dd^{-1}) (Stout, 1989) from *Populus canadensis* wood sticks after 90–360 days of incubation following an exponential model (Petersen and Cummins, 1974). We determined fungal biomass accrual based on changes in the ergosterol concentration of each wood stick (Gessner, 2020) and using a conversion factor of 5.5 mg of ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). Biomass accumulation was expressed in mg of fungal biomass per gram of stick dry mass (methodological details in Appendix D).

To estimate species' association with each ecosystem process (EP), we determined mean differences in ecosystem processes between sites where the species occurred and sites where the species was absent as follows:

$$\text{Species association with an EP} = EP_{\text{presence}} - EP_{\text{absence}}$$

These values represent a proxy of species associations with ecosystem functioning under realistic field conditions. Although this correlative approach does not allow to tease apart abiotic and individual species effects on ecosystem functioning (van der Plas, 2019), it provides a

complementary perspective in comparison with manipulative, reductionist approaches by i) covering multiple fungal species from naturally-assembled communities, and ii) integrating realistic abiotic and biotic interactions affecting species occurrences and their effects on ecosystem functioning.

3. Results

3.1. Fungal ecological niches and strategies over the drying gradient

Over the drying gradient, aquatic fungi varied in their taxonomic richness (12–30 taxa). The results from the outlying mean index (OMI) showed that the first OMI axis explained 41.3 % of the total explained marginality of species distribution and was related to annual drying duration ($r_p = 0.65$) and drying frequency ($r_p = 0.64$). The second OMI axis explained 24.1 % and was related to conductivity ($r_p = -0.51$), SRP ($r_p = -0.58$) and DIN ($r_p = -0.61$). Fungal species show contrasting strategies over the drying gradient, which were evidenced through different combinations of drying specialization (OMI) and affinity (OMI Axis 1) (Table 1, Fig. 2).

Our cluster analysis identified four drying niche-based groups that showed contrasting distributions over the drying gradient (Fig. 3). The first drying niche-based group was made of drying-sensitive (i.e., perennial-flow specialists) with high sensitivity to drying stress (mean OMI: 43.82; mean tolerance: 48.73; mean OMI Axis 1: -0.97) (Table 1; Fig. 2). This drying niche-based group included five taxa showing significant departures from average drying affinity (*Lunulospora curvula*, *Clavariopsis azlanii*, *Tumularia aquatica*, *Triscelophorus acuminatus* and *Clavariopsis aquatica*) (Table 1; Fig. 2). The second drying niche-based

group (partly tolerant) included taxa with a wider distribution over the drying gradient (mean OMI: 21.2) and a certain tolerance to short drying periods (mean tolerance: 63.8; mean OMI Axis 1: -0.81) (Table 1; Fig. 2). This drying niche-based group included six taxa (*Campylospora chaetocladia*, *Cylindrocarpon* sp., *Margaritispora aquatica*, *Helliscella stellata*, *Tetracladium furcatum* and *Fusarium* sp.) (Table 1; Fig. 2). The third drying niche-based group encompassed 22 generalist taxa showing the widest distributions over the drying gradient (mean OMI: 7.77, mean tolerance: 71.56; mean OMI Axis 1: -0.18) (Table 1; Fig. 2). This drying niche-based group included terrestrial species (e.g., *Alternaria* sp.) (Table 1; Fig. 2). Finally, the fourth drying niche-based group was made of drying specialists (mean OMI: 13.16, mean tolerance: 76.32; mean OMI Axis 1: 0.56) (Table 1; Fig. 2). This drying niche-based group included *Volucrispora graminea*, *Tetracladium marchalianum*, *Mycocentrospora acerina* and *Isthmotricladia* sp. We found higher drying tolerance in generalists and drying-resistant specialists (Table 1).

3.2. Responses of aquatic fungal ecological niches to drying

Generally, aquatic fungal richness showed a decline in sensitive and partly tolerant taxa over the drying gradient, but partly tolerant taxa showed less pronounced declines (Fig. 4a). Indeed, sensitive taxa tended to disappear in streams with >100 dry days within a year, whereas partly tolerant taxa were able to survive in streams with >100 dry days within a year (Fig. 4b). Generalist taxa experienced moderate positive or negative responses, whereas drying specialist taxa showed weak or moderate

Table 1

Fungal species' ecological strategies (drying niche-based group), specialization (OMI), affinity (OMI Axis 1; annual drying duration and frequency), and associations with organic matter (OM) decomposition (k , dd^{-1}) and fungal biomass (FB) accrual (mg FB gDM^{-1}) of aquatic fungal taxa over the drying gradient. Taxa with greater association with ecosystem functioning are in bold (OM decomposition $\geq 0.0010 \text{ dd}^{-1}$; fungal biomass $\geq 5 \text{ mg FB gDM}^{-1}$). NA indicates taxa for which niche features could not be calculated because they appeared at all sites.

Taxon	Ecological strategy	Specialization (OMI)	Affinity (OMI Axis 1)	Association with OM decomposition (dd^{-1})	Association with FB (mg FB gDM^{-1})
<i>Lunulospora curvula</i>	Sensitive	33.8	-0.89	0.0007	7.22
<i>Clavariopsis azlanii</i>	Sensitive	44.0	-1.11	0.0012	8.46
<i>Tumularia aquatica</i>	Sensitive	64.2	-0.74	0.0013	14.10
<i>Triscelophorus acuminatus</i>	Sensitive	44.0	-1.11	0.0012	8.46
<i>Clavariopsis aquatica</i>	Sensitive	33.1	-1.00	0.0005	2.99
<i>Campylospora chaetocladia</i>	Partly tolerant	19.1	-0.90	0.0006	6.94
<i>Cylindrocarpon</i> sp.	Partly tolerant	22.8	-0.82	0.0010	6.51
<i>Margaritispora aquatica</i>	Partly tolerant	25.6	-1.04	0.0013	5.04
<i>Helliscella stellata</i>	Partly tolerant	25.2	-0.87	0.0011	8.79
<i>Tetracladium furcatum</i>	Partly tolerant	13.3	-0.60	0.0009	10.05
<i>Fusarium</i> sp.	Partly tolerant	21.2	-0.58	-0.0001	1.01
<i>Anguillospora crassa</i>	Generalist	4.4	-0.41	0.0000	9.37
<i>Fusarium culmorum</i>	Generalist	1.9	0.01	0.0002	6.64
<i>Heliscus submersus</i>	Generalist	5.8	-0.40	0.0011	10.06
<i>Stenoclaadiella neglecta</i>	Generalist	2.7	-0.34	0.0011	9.44
<i>Alatospora pulchella</i>	Generalist	1.8	-0.22	0.0007	9.08
<i>Lemoniera cornuta</i>	Generalist	5.7	-0.28	0.0003	0.10
<i>Tricladium angulatum</i>	Generalist	3.1	-0.15	0.0008	2.61
<i>Lemoniera terrestris</i>	Generalist	8.0	-0.31	-0.0004	4.52
<i>Lemoniera alabamensis</i>	Generalist	12.5	-0.11	0.0013	5.22
<i>Anguillospora rossea</i>	Generalist	8.7	-0.27	0.0001	3.43
<i>Articulospora tetracladia</i>	Generalist	17.7	-0.63	0.0005	7.46
<i>Filosporella annelindica</i>	Generalist	30.7	-0.09	-0.0017	-4.30
<i>Tetracladium maxiliforme</i>	Generalist	2.9	-0.12	-0.0005	3.01
<i>Tetracladium setigerum</i>	Generalist	9.0	-0.27	0.0002	3.55
<i>Heliscus lugdunensis</i>	Generalist	10.0	-0.46	0.0015	4.99
<i>Anguillospora longissima</i>	Generalist	20.9	-0.17	0.0007	3.85
<i>Alternaria</i> sp.	Generalist	0.7	-0.14	0.0007	8.34
<i>Diplocladiella scalaroides</i>	Generalist	2.8	-0.27	0.0009	4.94
<i>Anguillospora furvula</i>	Generalist	3.7	0.13	-0.0006	-3.43
<i>Lemoniera aquatica</i>	Generalist	18.0	0.50	0.0000	2.24
<i>Alatospora acuminata</i>	Generalist	0.0	0.00	NA	NA
<i>Flagellospora curvula</i>	Generalist	0.0	0.00	NA	NA
<i>Volucrispora graminea</i>	Specialist	16.2	0.50	0.0005	-0.80
<i>Tetracladium marchalianum</i>	Specialist	3.9	0.26	-0.0005	-3.63
<i>Mycocentrospora acerina</i>	Specialist	14.9	0.40	0.0008	-1.60
<i>Isthmotricladia</i>	Specialist	17.7	1.08	-0.0003	-0.39

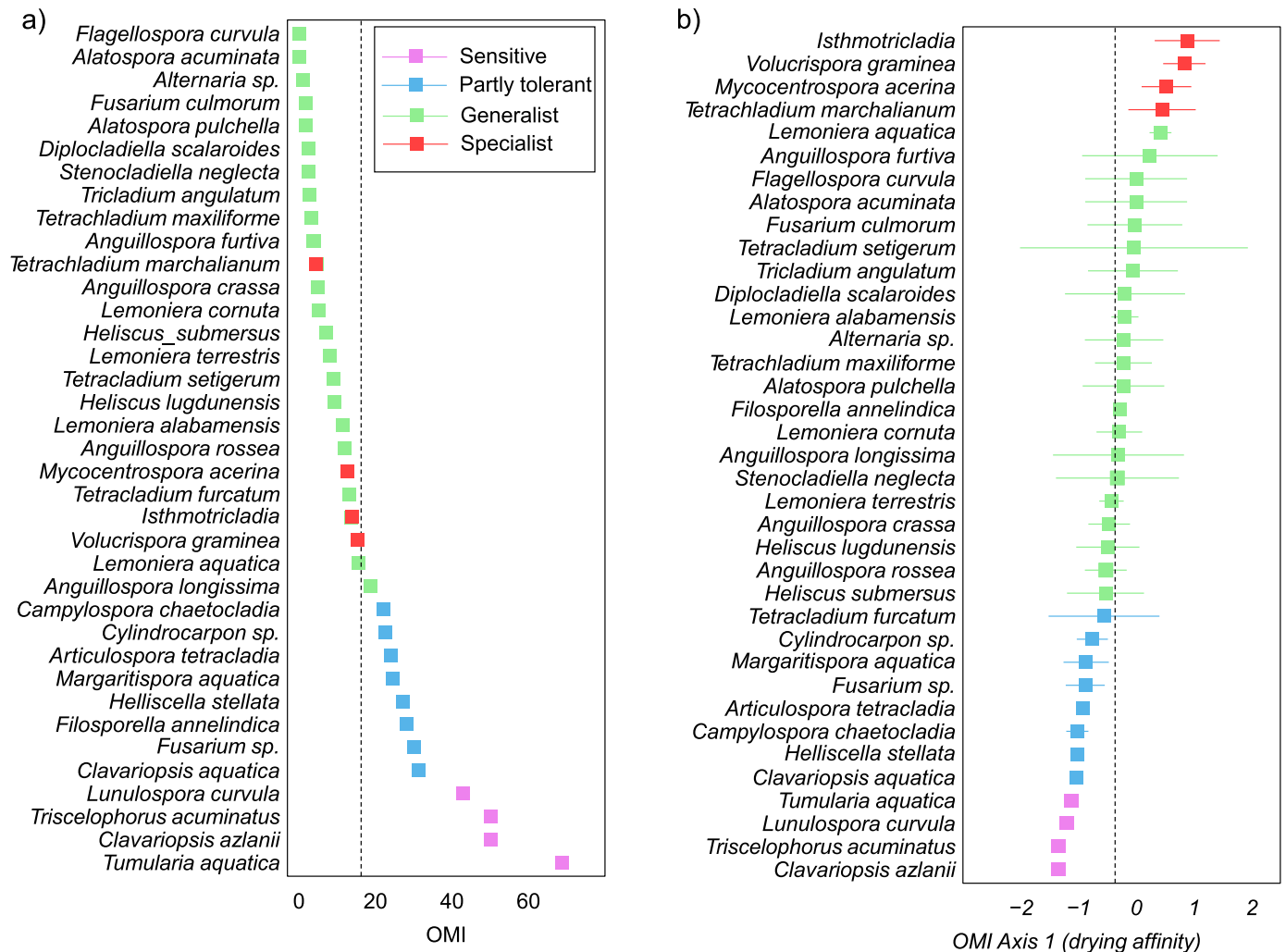


Fig. 2. Specialization (OMI; a) and affinity (OMI Axis 1; b) of aquatic fungal species over the drying gradient. The different colours represent the four drying niche-based groups. Horizontal bars (b) represent the drying niche breadth (drying tolerance).

increases over the drying gradient (Fig. 4a). Both were able to appear even in ephemeral streams with >200 dry days within a year (Fig. 4b).

3.3. Associations of fungal ecological strategies with ecosystem processes

Fungal species showed contrasting associations with organic matter decomposition and fungal biomass accrual, where most species showed intermediate values and few of them had larger positive or negative associations (Fig. 5). We observed that species that belong to drying-sensitive and partly tolerant niches had higher contributions to organic matter decomposition (mean effects: 0.0010 and 0.0008 dd^{-1} , respectively) and fungal biomass accrual (mean effects: 8.24 and 6.39 mg FB gDM^{-1} , respectively), than generalists (mean effects on decomposition: 0.0003; mean effects on FB: 4.56 mg FB gDM^{-1}) (Table 1). Drying-specialists had the lowest association with both ecosystem processes, eventually exhibiting a negative correlations with fungal biomass accrual (mean effects on decomposition: 0.0001; mean effects on FB: -1.61).

4. Discussion

Our findings confirm that drying emerges as the dominant abiotic factor regulating the composition of aquatic fungi in IRES. In parallel, our results reveal four groups of aquatic fungi showing contrasting distributions and responses over the drying gradient: drying-sensitive, partly tolerant to drying, generalist and drying-specialist. We also found that species belonging

to sensitive and partly tolerant niche-based groups had a potentially higher contribution to both ecosystem processes than generalists and drying specialists, suggesting a functional trade-off between drying-resistant strategies and the energy invested in growth and reproduction. Taken together, our results suggest that increased drying may jeopardise aquatic fungal capacity to guarantee ecosystem functioning and to maintain biogeochemical cycles despite their ability to cope with drying.

In accordance with our first hypothesis, we found that drying duration and frequency were the most influential variables upon aquatic fungal niche differentiation even when we considered the background of environmental variability. These results are aligned with previous studies showing that aquatic fungal communities experience shifts in richness and composition when exposed to drying (Arias-Real et al., 2022b; Gionchetta et al., 2020a; Schreckinger et al., 2021). Moreover, it is recognized that the occurrence and survival of aquatic fungi are controlled by environmental factors, such as oxygen availability (Medeiros et al., 2009), temperature, inorganic nutrient concentration and conductivity (Duarte et al., 2017; Gonçalves et al., 2016; Gulis et al., 2019; Larned et al., 2010; Pascoal et al., 2005), which are affected during flow reduction and drying. The fact that most aquatic fungi are highly responsive to changes in nutrient concentrations, water availability and UV radiation together with their intimate association with the substrate they colonize reinforces the idea of drying as the main driver of aquatic fungal distribution. Nonetheless, these variables, which were represented by the second OMI axes, were less influential in fungal species distributions than the drying descriptors.

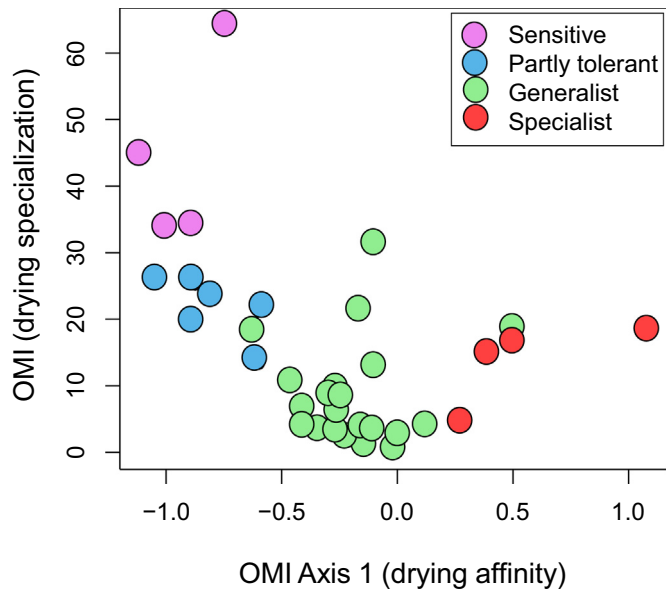


Fig. 3. Distribution of the four drying niche-based groups over gradients of drying affinity (OMI Axis 1) and specialization (OMI). Drying niche affinity is represented by the first axis of the drying space, which was positively correlated with annual drying duration and drying frequency.

In addition, the distribution of aquatic fungi depends on their dispersal and colonization capacity, which may be constrained during flow cessation and drying (Duarte et al., 2015; Gessner et al., 2010; Gulis, 2001; Read et al., 1992). In terrestrial ecosystems, dispersal limitation is more important than abiotic filtering (deterministic process) in shaping fungal community structure (Cline and Zak, 2014). Microbial dispersal can be favoured by

certain conidial traits that enhance mobility and passive transport (Evans et al., 2017). This suggests that the size and shape of conidia may be relevant for aquatic fungal distribution over the drying gradient. For instance, species with filiform spores, such as *Flagellospora curvulla* or *Angillospora longissima* (generalist niche-based group), are able to disperse in interstitial water by moving into the sediments to protect their mycelia and propagules during drying (Ghate and Sridhar, 2015). However, species with branched (*Clavariopsis aquatica* and *Triscelophorus acuminatus*), tetra-radiate (*Clavariopsis azlanii*), sigmoid (*Lunulospora curvula*), and fusiform/rhomboid compact (*Tumulularia aquatic*) morphologies have lower dispersal capacity in sediment, making them more vulnerable to drying (Cornut et al., 2014).

Our analyses found four ecological strategies that segregated over the drying gradient, matching our second hypothesis. As found for other stressors, such as salinity or pollutants, long-term exposure to recurrent drying events has favoured the development of ecological strategies that segregate niches and taxa over the drying gradient (Grossart et al., 2022; Gutiérrez-Cánovas et al., 2013). In our study, we found that some species specialized in both extremes of the gradient (drying sensitive vs. drying specialists) or develop different degrees of tolerance that made them capable to tolerate a wider range of drying conditions (partly tolerant to drying and generalists). Previous studies have demonstrated that communities can shift towards a more drying specialized community able to develop specific drying-resistant life strategies (Jones and Lennon, 2010; Shade et al., 2012). These community changes are characterized by a decrease in taxa sensitive to drying and an increase in the proportion of generalists and specialists over the drying gradient (Allison and Martiny, 2008; Gionchetta et al., 2020b; Wallenstein and Hall, 2012). For instance, in our study, Leotiomycetes were largely dominated by generalists and drying specialist niche-based group, which include several endophytes and root symbionts (Quandt and Haelewaters, 2021; Selosse et al., 2008). In fact, we observed that >35 % and 25 % of generalists and drying specialist niche-based groups, respectively, are root endophytes. This reinforces the idea that some aquatic fungi could have a dual life cycle, including a terrestrial phase as an endophyte with some dormant structures or in roots exposed

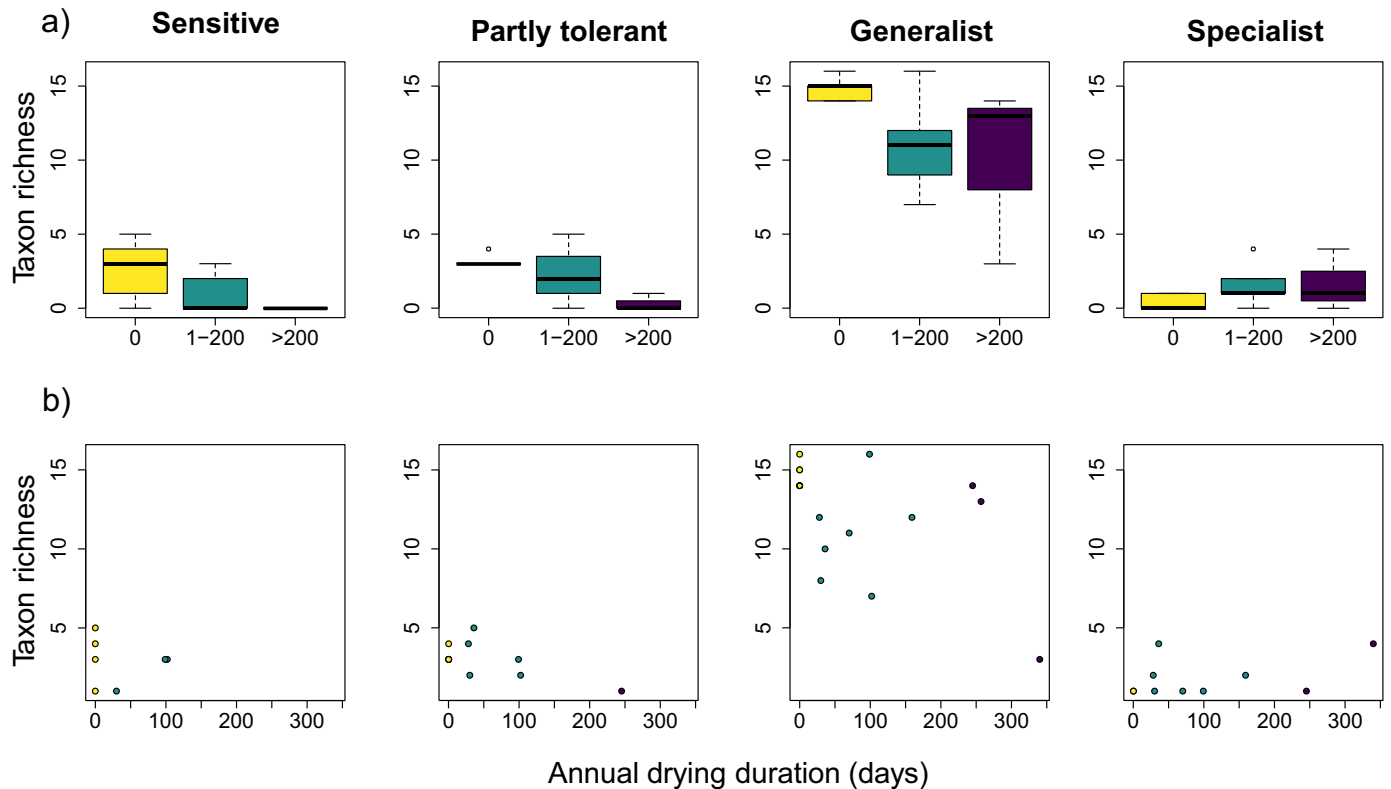


Fig. 4. Bar (a) and scatter (b) plots responses of each drying niche-based group to annual drying duration.

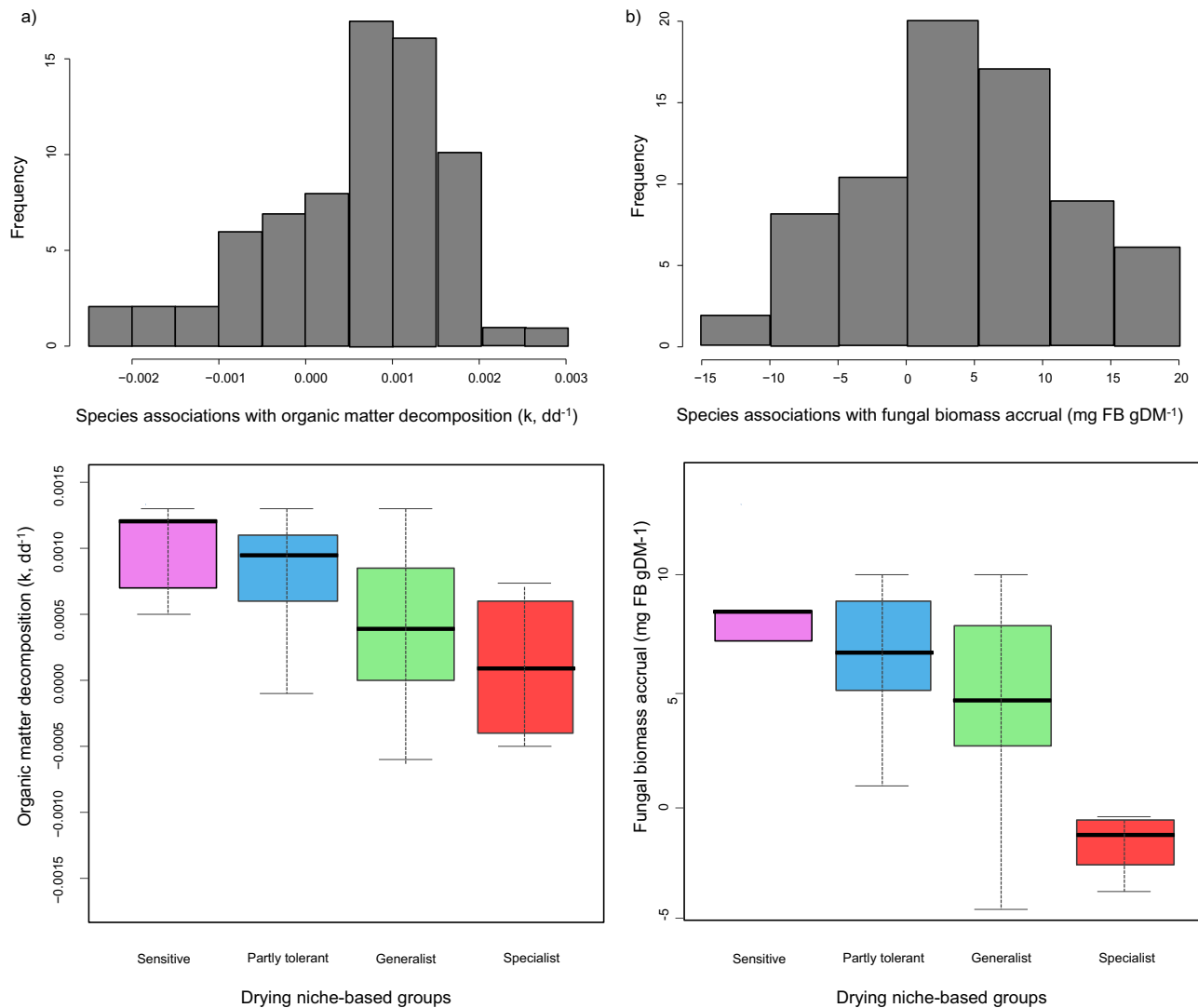


Fig. 5. Histograms and boxplots showing the frequency distribution of aquatic fungal associations with organic matter decomposition (a) and fungal biomass accrual (b).

to water, which could be a desiccation-resistance life strategy that allows them to survive in IRES (Bärlocher, 2009; Lusk, 2008; Sridhar, 2009).

Although fungi are ubiquitous and resistant (Coleine et al., 2022), our study showed that IRES are inhabited by generalists and few well-adapted (drying-specialized) fungi. Thus, the generalist niche emerged as a successful strategy in IRES as occurred with other natural stressors (Arribas et al., 2018). The dominance of generalist taxa within communities suggests that evolution had selected those traits able to cope with stressful conditions but also to be successful when flow returns. This behaviour may be explained by a combination of complementary traits that enable niche complementary and species coexistence (Naeem and Wright, 2003).

Matching our third hypothesis, we found that drying niches exhibited contrasting associations with ecosystem processes, with drying resistant taxa (partly-tolerant to drying, generalist and drying specialists) showing lower values. This can be explained because drying adaptations such as down regulation of metabolic activity or entry in dormancy involve metabolic cost (Frossard et al., 2012; Gessner et al., 2010), which can reduce species performance. Indeed, we showed that species belonging to the drying-sensitive and partly tolerant niche-based groups might include the most productive taxa, suggesting a trade-off between fungal biomass production vs. efficiency to cope with drying. On average, taxa belonging to drying-sensitive and partly tolerant niche-based groups showed the highest associations with organic matter decomposition. Thus, variation in fungal

community composition was accompanied by changes in fungal ecological strategies with possible consequences for ecosystem processes. The skewed distribution of freshwater fungal species towards positive values (Fig. 5) may reflect that both complementarity and selection effects are important to sustain ecosystem processes (Duarte et al., 2006). As such, our results complement previous research showing that fungal richness correlates positively with organic matter decomposition and fungal biomass accrual (Arias-Real et al., 2020, 2022b; Gessner et al., 2010).

In particular, extreme association values may indicate the existence of keystone species with disproportionately large effects on ecosystem functioning (Duarte et al., 2006), which might display a drying sensitive behaviour. Thus, the combination of highly performing taxa and niche complementarity in streams with permanent flow may explain the higher levels of ecosystem functioning. Our estimation of multi-species associations with two ecosystem processes provides a realistic perspective that complements insights obtained from manipulative approaches that focused on a reduced number of taxa and environmental conditions (Duarte et al., 2006; Graça et al., 2022).

However, we need to consider some limitations which are inherent to the correlative nature of our approach. For example, the estimation of associations with ecosystem functioning might be overestimated in rich communities, where complementarity effects also influence ecosystem processes. Also, our correlative approach cannot tease apart the influence of abiotic variation in species performance.

Future studies, including functional metagenomics and trait-based approaches, may enable a better predictive capacity of aquatic fungi contribution to ecosystem functioning under field conditions.

5. Conclusions

Our study contributes to a better understanding of how drying stress can alter fungal communities and their contribution to ecosystem functioning. Combined with high-resolution hydrological, our niche-based approach result can be helpful to analyse the ecological adaptation of fungi to drying and, consequently, to understand how aquatic fungi will respond to the expected increase in drying duration and frequency. Our study revealed that it is critical to understand aquatic fungal patterns across drying gradients to better understand how ecosystems respond to global change and to include aquatic fungi in global biogeochemical models.

CRedit authorship contribution statement

Rebeca Arias-Real: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Margarita Menéndez:** Conceptualization, Investigation, Methodology, Validation, Supervision, Writing – review & editing. **Isabel Muñoz:** Conceptualization, Investigation, Methodology, Resources, Funding acquisition, Validation, Supervision, Writing – review & editing. **Cláudia Pascoal:** Conceptualization, Investigation, Methodology, Validation, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We gratefully acknowledge to the field assistance of Verónica Granados and to Cayetano Gutiérrez-Cánovas for his help with the statistical analyses in R. We would like to thank Kevin Kuehn, Charlie Bond and Sergi Sabater for constructive suggestions on earlier versions of the manuscript.

Funding

This work was funded by MCIN/AEI/10.13039/501100011033 through the project RIVSTRESS (PID2020-115708RB-C21), and by project STREAMECO (PTDC/CTA-AMB/31245/2017), funded by the Portuguese Science and Technology Foundation (FCT) and the European Regional Development Fund (ERDF) through the COMPETE2020—Programa Operacional Competitividade e Internacionalização (POCI). RA-R held a post-doctoral grant “Margarita Salas” from the Spanish Ministry of Universities and the Next Generation EU - Recovery, Transformation and Resilience Plan.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.160374>.

References

Allison, S.D., Martiny, J.B.H., 2008. Resistance, resilience, and redundancy in microbial communities. *Proc. Natl. Acad. Sci.* 105, 11512–11519. <https://doi.org/10.1073/pnas.0801925105>.

- Arias-Real, R., Menéndez, M., Abril, M., Oliva, F., Muñoz, I., 2018. Quality and quantity of leaf litter: both are important for feeding preferences and growth of an aquatic shredder. *PLoS One* 13(12): e0, 1–17. <https://doi.org/10.1371/journal.pone.0208272>.
- Arias-Real, R., Muñoz, I., Gutiérrez-Cánovas, C., Granados, V., Lopez-Laseras, P., Menéndez, M., 2020. Subsurface zones in intermittent streams are hotspots of microbial decomposition during the non-flow period. *Sci. Total Environ.* 703, 135485. <https://doi.org/10.1016/j.scitotenv.2019.135485>.
- Arias-Real, R., Gutiérrez-Cánovas, C., Menéndez, M., Granados, V., Muñoz, I., 2021. Diversity mediates the responses of invertebrate density to duration and frequency of rivers' annual drying regime. *Oikos* 00, 1–13. <https://doi.org/10.1111/oik.08718>.
- Arias-Real, R., Gutiérrez-Cánovas, C., Menéndez, M., Muñoz, I., 2022a. Drying niches of aquatic macroinvertebrates identify potential biomonitoring indicators in intermittent and ephemeral streams. *Ecol. Indic.* 142, 109263. <https://doi.org/10.1016/j.ecolind.2022.109263>.
- Arias-Real, R., Gutiérrez-Cánovas, C., Muñoz, I., Pascoal, C., Menéndez, M., 2022b. Fungal biodiversity mediates the effects of drying on freshwater ecosystem functioning. *Ecosystems* 25, 780–794. <https://doi.org/10.1007/s10021-021-00683-z>.
- Arribas, P., Botella-Cruz, C.G.-C.M., Cañedo-Argüelles, M., Carbonell, J.A., Millán, A., Pallarés, S., Velasco, J., Sánchez-Fernández, D., 2018. Insect communities in saline waters consist of realised but not fundamental niche specialists. *Philos. Trans. R. Soc. B Biol. Sci. (This issue)*.
- Bärlocher, F., 2009. Reproduction and dispersal in aquatic hyphomycetes. *Mycoscience* 50, 3–8. <https://doi.org/10.1007/S10267-008-0449-X>.
- Baschien, C., Marvanová, L., Szewzyk, U., 2006. Phylogeny of selected aquatic hyphomycetes based on morphological and molecular data. *Nova Hedwigia* 83, 311–352. <https://doi.org/10.1127/0029-5035/2006/0083-0311>.
- Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., Kirby, R.R., 2015. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat. Clim. Chang.* 5, 695–701.
- Beaugrand, G., Kirby, R., Goberville, E., 2020. The mathematical influence on global patterns of biodiversity. *Ecol. Evol.* 10, 6494–6511. <https://doi.org/10.1002/ece3.6385>.
- Belliveau, M.J.-R., Bärlocher, F., 2005. Molecular evidence confirms multiple origins of aquatic hyphomycetes. *Mycol. Res.* 109, 1407–1417. <https://doi.org/10.1017/S0953756205004119>.
- Besemer, K., 2015. Biodiversity, community structure and function of biofilms in stream ecosystems. *Res. Microbiol.* 166, 774–781. <https://doi.org/10.1016/j.resmic.2015.05.006>.
- Calabon, M.S., Hyde, K.D., Jones, E.B.G., Luo, Z.-L., Dong, W., Hurdeal, V.G., Gentekaki, E., Rossi, W., Leonardi, M., Thiyagaraja, V., Lestari, A.S., Shen, H.-W., Bao, D.-F., Boonyuen, N., Zeng, M., 2022. Freshwater fungal numbers. *Fungal Divers.* 114, 3–235. <https://doi.org/10.1007/s13225-022-00503-2>.
- Canhoto, C., Bärlocher, F., Cañedo-Argüelles, M., Gómez, R., Gonçalves, A.L., 2021. In: Swan, C.M., Boyero, L., Canhoto, C. (Eds.), *Salt Modulates Plant Litter Decomposition in Stream Ecosystems BT - The Ecology of Plant Litter Decomposition in Stream Ecosystems*. Springer International Publishing, Cham, pp. 323–345. https://doi.org/10.1007/978-3-030-72854-0_15.
- Chauvet, E., Cornut, J., Sridhar, K.R., Selosse, M.A., Bärlocher, F., 2016. Beyond the water column: aquatic hyphomycetes outside their preferred habitat. *Fungal Ecol.* 19, 112–127. <https://doi.org/10.1016/j.funeco.2015.05.014>.
- Cline, L.C., Zak, D.R., 2014. Dispersal limitation structures fungal community assembly in a long-term glacial chronosequence. *Environ. Microbiol.* 16, 1538–1548. <https://doi.org/10.1111/1462-2920.12281>.
- Coleine, C., Stajich, J.E., Selbmann, L., 2022. Fungi are key players in extreme ecosystems. *Trends Ecol. Evol.* 37, 517–528. <https://doi.org/10.1016/j.tree.2022.02.002>.
- Cornut, J., Chauvet, E., Mermillod-Blondin, F., Assemat, F., Elger, A., 2014. Aquatic hyphomycete species are screened by the hyporheic zone of woodland streams. *Appl. Environ. Microbiol.* 80, 1949–1960. <https://doi.org/10.1128/AEM.03024-13>.
- Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R., Bradford, M.A., 2014. Untangling the fungal niche: the trait-based approach. *Front. Microbiol.* 5, 579. <https://doi.org/10.3389/fmicb.2014.00579>.
- Crump, B.C., Hobbie, J.E., 2005. Synchrony and seasonality in bacterioplankton communities of two temperate rivers. *Limnol. Oceanogr.* 50, 1718–1729. <https://doi.org/10.4319/lo.2005.50.6.1718>.
- Datry, T., Singer, G., Sauquet, E., Jorda-Capdevila, D., Von Schiller, D., Magand, C., Pařil, P., Miliša, M., Acuña, V., Alves, M.H.M.H., Augéard, B., Brunke, M., Cid, N., Csabai, Z., England, J., Froebrich, J., Koundouri, P., Lamouroux, N., Martí, E., Morais, M., Munné, A., Mutz, M., Vladimir, P., Previšić, A., Reynaud, A., Robinson, C., Sadler, J., Skoulikidis, N., Terrier, B., Tockner, K., Vesely, D., Zoppini, A., Von Schiller, Daniel, Magand, C., Pa, P., Miliša, M., Acuña, V., Alves, M.H.M.H., Augéard, B., Brunke, M., Cid, N., Csabai, Z., England, J., Froebrich, J., Koundouri, P., Lamouroux, N., Martí, E., Morais, M., Munné, A., Pesic, V., Previšić, A., Reynaud, A., Robinson, C., Sadler, J., Skoulikidis, N., Terrier, B., Tockner, K., Vesely, D., Zoppini, A., 2017. Science and Management of Intermittent Rivers and Ephemeral Streams (SMIRES). *Res. Ideas Outcomes* 3, e21774. <https://doi.org/10.3897/rio.3.e21774>.
- Dolédéc, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: a new method. *Ecology* 81, 2914–2927. [https://doi.org/10.1890/0012-9658\(2000\)081\[2914:NSICAA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2).
- Duarte, S., Pascoal, C., Cássio, F., Bärlocher, F., 2006. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. *Oecologia* 147, 658–666. <https://doi.org/10.1007/s00442-005-0300-4>.
- Duarte, S., Baerlocher, F., Cassio, F., 2015. Biogeography of aquatic hyphomycetes: current knowledge and future perspectives. *Fungal Ecol.* 19, 169–181. <https://doi.org/10.1016/j.funeco.2015.06.002>.
- Duarte, S., Cássio, F., Pascoal, C., 2017. Environmental drivers are more important for structuring fungal decomposer communities than the geographic distance between streams. *Limnetica* 36, 491–506. <https://doi.org/10.23818/limn.36.17>.

- El-Elimat, T., Raja, H.A., Figueroa, M., Al Sharie, A.H., Bunch, R.L., Oberlies, N.H., 2021. Freshwater fungi as a source of chemical diversity: a review. *J. Nat. Prod.* 84, 898–916. <https://doi.org/10.1021/acs.jnatprod.0c01340>.
- Evans, S., Martiny, J.B.H., Allison, S.D., 2017. Effects of dispersal and selection on stochastic assembly in microbial communities. *ISME J.* 11, 176–185. <https://doi.org/10.1038/ismej.2016.96>.
- Frossard, A., Gerull, L., Mutz, M., Gessner, M.O., 2012. Disconnect of microbial structure and function: enzyme activities and bacterial communities in nascent stream corridors. *ISME J.* 6, 680–691. <https://doi.org/10.1038/ismej.2011.134>.
- Gessner, M.O., 2020. Ergosterol as a measure of fungal biomass. *Methods to Study Litter Decomposition: A Practical Guide*. Springer Netherlands, Netherlands, pp. 231–236 https://doi.org/10.1007/1-4020-3466-0_25.
- Gessner, M.O., Chauvet, E., 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. *Appl. Environ. Microbiol.* 59, 502–507 <https://doi.org/PMC202134>.
- Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 2010. Diversity meets decomposition. *Trends Ecol. Evol.* 25, 372–380. <https://doi.org/10.1016/j.tree.2010.01.010>.
- Ghate, S.D., Sridhar, K.R., 2015. Diversity of aquatic hyphomycetes in streambed sediments of temporary streamlets of Southwest India. *Fungal Ecol.* 14, 53–61. <https://doi.org/10.1016/j.funeco.2014.11.005>.
- Gionchetta, G., Oliva, F., Menéndez, M., Lopez, P., Romani, A.M., 2019. Key role of streambed moisture and flash storms for microbial resistance and resilience to long-term drought. *Freshw. Biol.* 64, 306–322. <https://doi.org/10.1111/fwb.13218>.
- Gionchetta, G., Artigas, J., Arias-Real, R., Oliva, F., Romani, A.M., 2020a. Multi-model assessment of hydrological and environmental impacts on streambed microbes in Mediterranean catchments. *Environ. Microbiol.* 22, 2213–2229. <https://doi.org/10.1111/1462-2920.14990>.
- Gionchetta, G., Oliva, F., Romani, A.M., Bañeras, L., 2020b. Hydrological variations shape diversity and functional responses of streambed microbes. *Sci. Total Environ.* 714, 136838. <https://doi.org/10.1016/j.scitotenv.2020.136838>.
- Gonçalves, A.L., Lirio, A.V., Graça, M.A.S., Canhoto, C., 2016. Fungal species diversity affects leaf decomposition after drought. *Int. Rev. Hydrobiol.* 101, 78–86. <https://doi.org/10.1002/iroh.201501817>.
- Gonçalves, A.L., Simões, S., Bärlocher, F., Canhoto, C., 2019. Leaf litter microbial decomposition in salinized streams under intermittency. *Sci. Total Environ.* 653, 1204–1212. <https://doi.org/10.1016/j.scitotenv.2018.11.050>.
- Graça, D., Fernandes, I., Cássio, F., Pascoal, C., 2022. Eco-physiological responses of aquatic fungi to three global change stressors highlight the importance of intraspecific trait variability. *Microb. Ecol.* <https://doi.org/10.1007/s00248-022-02007-7>.
- Green, J.L., Bohannon, B.J.M., Whitaker, R.J., 2008. *Microbial biogeography: from taxonomy to traits*. *Science (80-)* 320, 1039–1043.
- Grossart, H.-P., Rojas-Jimenez, K., 2016. Aquatic fungi: targeting the forgotten in microbial ecology. *Curr. Opin. Microbiol.* 31, 140–145. <https://doi.org/10.1016/j.mib.2016.03.016>.
- Grossart, H.-P., Van den Wyngaert, S., Kagami, M., Wurzbacher, C., Cunliffe, M., Rojas-Jimenez, K., 2019. Fungi in aquatic ecosystems. *Nat. Rev. Microbiol.* 17, 339–354. <https://doi.org/10.1038/s41579-019-0175-8>.
- Grossart, H.-P., Hassan, E.A., Masigol, H., Arias-Andres, M., Rojas-Jimenez, K., 2022. In: Mehner, T., Tockner, K.B.T.-E. of I.W. (Eds.), *Inland Water Fungi in the Anthropocene: Current and Future Perspectives*, Second Ed Elsevier, Oxford, pp. 667–684. <https://doi.org/10.1016/B978-0-12-819166-8.00025-6>.
- Gulis, V., 2001. Are there any substrate preferences in aquatic hyphomycetes? *Mycol. Res.* 105, 1088–1093. [https://doi.org/10.1016/S0953-7562\(08\)61971-1](https://doi.org/10.1016/S0953-7562(08)61971-1).
- Gulis, V., Suberkropp, K., 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshw. Biol.* 48, 123–134. <https://doi.org/10.1046/j.1365-2427.2003.00985.x>.
- Gulis, V., Su, R., Kuehn, K.A., 2019. *Fungal decomposers in freshwater environments. The Structure and Function of Aquatic Microbial Communities*. Springer, pp. 121–155.
- Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P., Ormerod, S.J., 2013. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Glob. Ecol. Biogeogr.* 22, 796–805. <https://doi.org/10.1111/geb.12060>.
- Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu, S., Schmid, B., van Ruijven, J., Vos, V.C.A., Hättenschwiler, S., 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509, 218–221. <https://doi.org/10.1038/nature13247>.
- Hawksworth, D.L., Lücking, R., 2017. *Fungal Diversity Revisited: 2.2 to 3.8 Million Species. The Fungal Kingdom*. Wiley Online Books. <https://doi.org/10.1128/9781555819583.ch4>.
- Heino, J., Grönroos, M., 2014. Untangling the relationships among regional occupancy, species traits, and niche characteristics in stream invertebrates. *Ecol. Evol.* 4, 1931–1942.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*. Cold Spring Harbor Laboratory Press, pp. 415–427.
- Jones, S.E., Lennon, J.T., 2010. Dormancy contributes to the maintenance of microbial diversity. *Proc. Natl. Acad. Sci.* 107, 5881–5886. <https://doi.org/10.1073/pnas.0912765107>.
- Kakumanu, M.L., Cantrell, C.L., Williams, M.A., 2013. Microbial community response to varying magnitudes of desiccation in soil: a test of the osmolyte accumulation hypothesis. *Soil Biol. Biochem.* 57, 644–653. <https://doi.org/10.1016/j.soilbio.2012.08.014>.
- Krauss, G.J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., Bärlocher, F., 2011. Fungi in freshwaters: ecology, physiology and biochemical potential. *FEMS Microbiol. Rev.* 35, 620–651. <https://doi.org/10.1111/j.1574-6976.2011.00266.x>.
- Larned, S.T., Datry, T., Arscott, D.B., Tockner, K., 2010. Emerging concepts in temporary-river ecology. *Freshw. Biol.* 55, 717–738. <https://doi.org/10.1111/j.1365-2427.2009.02322.x>.
- Lipson, D.A., Monson, R.K., Schmidt, S.K., Weintraub, M.N., 2009. The trade-off between growth rate and yield in microbial communities and the consequences for under-snow soil respiration in a high elevation coniferous forest. *Biogeochemistry* 95, 23–35. <https://doi.org/10.1007/s10533-008-9252-1>.
- Lusk, C., 2008. Constraints on the evolution and geographical range of Pinus. *New Phytol.* 178, 1–3. <https://doi.org/10.1111/j.1469-8137.2008.02371.x>.
- Manning, D.W.P., Rosemond, A.D., Gulis, V., Benstead, J.P., Kominoski, J.S., 2018. Nutrients and temperature additively increase stream microbial respiration. *Glob. Chang. Biol.* 24, e233–e247. <https://doi.org/10.1111/gcb.13906>.
- Manzoni, S., Schaeffer, S.M., Katul, G., Porporato, A., Schimel, J.P., 2014. A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils. *Soil Biol. Biochem.* 73, 69–83.
- Medeiros, A.O., Pascoal, C., Graça, M.A.S., 2009. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshw. Biol.* 54, 142–149. <https://doi.org/10.1111/j.1365-2427.2008.02101.x>.
- Messenger, M.L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., Datry, T., 2021. Global prevalence of non-perennial rivers and streams. *Nature* 594, 391–397. <https://doi.org/10.1038/s41586-021-03565-5>.
- Mora-Gómez, J., Duarte, S., Cássio, F., Pascoal, C., Romani, A.M., 2018. Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. *Sci. Total Environ.* 621, 486–496. <https://doi.org/10.1016/j.scitotenv.2017.11.055>.
- Naem, S., Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.* 6, 567–579.
- Naranjo-Ortiz, M.A., Gabaldón, T., 2019. Fungal evolution: diversity, taxonomy and phylogeny of the Fungi. *Biol. Rev.* 94, 2101–2137. <https://doi.org/10.1111/brv.12550>.
- Pascoal, C., Marvanová, L., Cássio, F., 2005. Aquatic hyphomycete diversity in streams of Northwest Portugal. *Fungal Divers.* 19, 109–128.
- Petersen, R., Cummins, K., 1974. Leaf processing in a woodland stream. *Freshw. Biol.* 4, 343–368. <https://doi.org/10.1111/j.1365-2427.1974.tb00103.x>.
- Quandt, C.A., Haelewaters, D., 2021. Phylogenetic advances in Leotiomyces, an understudied clade of taxonomically and ecologically diverse fungi. *Encyclopedia of Mycology*. Elsevier.
- Read, S.J., Moss, S.T., Jones, E.B.G., 1992. In: Bärlocher, F. (Ed.), *Attachment and Germination of Conidia BT - The Ecology of Aquatic Hyphomycetes*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 135–151 https://doi.org/10.1007/978-3-642-76855-2_7.
- Schimel, J., Balsler, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88, 1386–1394.
- Schreckinger, J., Mutz, M., Mendoza-Lera, C., Frossard, A., 2021. Attributes of drying define the structure and functioning of microbial communities in temperate riverbed sediment. *Front. Microbiol.* 12, 676615. <https://doi.org/10.3389/fmicb.2021.676615>.
- Seena, S., Casotti, C., Cornut, J., 2020. Inter- and intraspecific functional variability of aquatic fungal decomposers and freshwater ecosystem processes. *Sci. Total Environ.* 707, 135570. <https://doi.org/10.1016/j.scitotenv.2019.135570>.
- Selosse, M.-A., Vohnik, M., Chauvet, E., 2008. Out of the rivers: are some aquatic hyphomycetes plant endophytes? *New Phytol.* 178, 3–7. <https://doi.org/10.1111/j.1469-8137.2008.02390.x>.
- Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R., Slatyer, R.A., 2017. Evolution of ecological niche breadth. *Annu. Rev. Ecol. Syst.* 48, 1–24.
- Shade, A., Peter, H., Allison, S., Baho, D., Berga, M., Buergmann, H., Huber, D., Langenheder, S., Lennon, J., Martiny, J., Matulich, K., Schmidt, T., Handelsman, J., 2012. Fundamentals of microbial community resistance and resilience. *Front. Microbiol.* 3, 417. <https://doi.org/10.3389/fmicb.2012.00417>.
- Sridhar, K.R., 2009. Fungi in the tree canopy—an appraisal. In: Rai, M., Bridge, P. (Eds.), *Appl. Mycology*. CAB International, UK, pp. 73–91 <https://doi.org/10.13140/2.1.3537.1521>.
- Stout, R.J., 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. *Can. J. Fish. Aquat. Sci.* 46, 1097–1106. <https://doi.org/10.1139/f89-142>.
- Tales, E., Keith, P., Oberdorff, T., 2004. Density-range size relationships in French riverine fishes. *Oecologia* 138, 360–370. <https://doi.org/10.1007/s00442-003-1430-1>.
- van der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.* 94, brv.12499. <https://doi.org/10.1111/brv.12499>.
- Wallenstein, M.D., Hall, E.K., 2012. A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning. *Biogeochemistry* 109, 35–47. <https://doi.org/10.1007/s10533-011-9641-8>.