

Article

Drying Shapes Aquatic Fungal Community Assembly by Reducing Functional Diversity

Rebeca Arias-Real ^{1,2,3,*} , Pilar Hurtado ^{4,5,6}, Giulia Gionchetta ⁷ and Cayetano Gutiérrez-Cánovas ⁶ 

¹ Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

² Institute of Science and Innovation for Bio-Sustainability (IB-S), University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

³ Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Universitat de Barcelona, Av. Diagonal, 08028 Barcelona, Spain

⁴ Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/de José Gutiérrez Abascal, 2, 28006 Madrid, Spain

⁵ Dipartimento di Farmacia, Università di Genova, viale Cembrano, 4, 16148 Genova, Italy

⁶ Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, C/Tulipán s/n, 28933 Mostoles, Spain

⁷ Department of Surface Waters—Research and Management, Eawag, Swiss Federal Institute of Aquatic Science and Technology, 6047 Kastanienbaum, Switzerland

* Correspondence: rebeca.arias.real@ub.edu or rebeca.arias.real@gmail.com

Abstract: Aquatic fungi are highly diverse organisms that play a critical role in global biogeochemical cycles. Yet it remains unclear which assembly processes determine their co-occurrence and assembly patterns over gradients of drying intensity, which is a common stressor in fluvial networks. Although aquatic fungi possess drying-specific adaptations, little is known about how functional similarity influences co-occurrence probability and which functional traits are sorted by drying. Using field data from 15 streams, we investigated how co-occurrence patterns and assembly processes responded to drying intensity. To do so, we determined fungal co-occurrence patterns, functional traits that best explain species co-occurrence likelihood, and community assembly mechanisms explaining changes in functional diversity over the drying gradient. Our results identified 24 species pairs with positive co-occurrence probabilities and 16 species pairs with negative associations. The co-occurrence probability was correlated with species differences in conidia shape and fungal endophytic capacity. Functional diversity reduction over the drying gradient is generally associated with non-random abiotic filtering. However, the assembly processes changed over the drying gradient, with random assembly prevailing at low drying intensity and abiotic filtering gaining more importance as drying intensifies. Collectively, our results can help anticipate the impacts of global change on fungal communities and ecosystem functioning.

Keywords: aquatic hyphomycetes; co-occurrence patterns; drying events; flow intermittence; functional diversity; functional traits



Citation: Arias-Real, R.; Hurtado, P.; Gionchetta, G.; Gutiérrez-Cánovas, C. Drying Shapes Aquatic Fungal Community Assembly by Reducing Functional Diversity. *Diversity* **2023**, *15*, 289. <https://doi.org/10.3390/d15020289>

Academic Editors: Spiros Papakostas and Nikolaos Monokrousos

Received: 29 November 2022

Revised: 10 February 2023

Accepted: 14 February 2023

Published: 16 February 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Aquatic hyphomycetes are one of the most diverse groups of aquatic fungi that influence multiple freshwater ecosystem functions [1–3]. In particular, these microorganisms process large amounts of terrestrial and aquatic detritus (i.e., leaf litter, leaves, needles, twigs, and branches of terrestrial plants) [1], becoming essential players in carbon processing [4–6], nutrient cycling [7], and energy transfer to higher trophic levels [8,9]. Among freshwater habitats, aquatic fungi are primarily found in streams and rivers [2,10] because their reproductive systems and dispersal capacities rely on flowing water [11–13]. Fluvial ecosystems are now exposed to increasing duration and frequency of drying events due to climate change and overexploitation of freshwater resources [14,15], thus posing a risk to aquatic hyphomycete biodiversity and their functional contribution. Therefore,

understanding the ecological mechanisms that shape fungal communities in response to drying is required to anticipate and mitigate biodiversity loss and functional changes in freshwater ecosystems.

Currently, more than half of the global draining networks present watercourses that dry out at some point during the year [16], and their spatial extent is expected to increase because of water scarcity and climate change [17,18]. Thus, intermittent rivers and ephemeral streams (IRES) offer an unparalleled opportunity to explore changes in functional diversity and community assembly mechanisms over drying gradients. Studies based on functional traits provide new research avenues to understand how drying events affect aquatic fungal communities by revealing their mechanisms to cope with drying [19,20]. For instance, trait sorting is expected to explain compositional changes during dry–wet cycles [21,22], favoring species with drying-resistant features. Specifically, some aquatic fungi have a short life cycle that enhances reproductive capacity [23] and has specialized strategies for resistance against desiccation stress [24]. An additional challenge to survive in drying watercourses is to protect and disperse mycelia and propagules [5,25,26]. To date, it is known that aquatic fungi can cope with drying conditions as endophytes in roots exposed to water and within riparian vegetation (e.g., on leaves and in tree holes) [13,26–29]. Furthermore, their hyphae may cross air-filled sediment pores to access nutrients and water during drying [30], with the potential to survive on the streambed sediment or hyporheic zone. Drying-mediated shifts in functional trait composition can modify biotic interactions and species co-occurrence patterns, thus affecting community assembly and ecosystem functioning [31]. However, little is known about which fungal traits are sorted by drying events and which assembly processes determine changes in fungal communities over the drying gradient.

Aquatic fungi are commensal microorganisms that establish rich communities and can show positive, negative, or neutral co-occurrence patterns between species [19,32]. These co-occurrence patterns simultaneously reflect the interactions between organisms (i.e., biotic interactions that depend on the identity and life strategies of organisms) and environmental effects (i.e., abiotic or environmental filtering) [33]. Specifically, co-occurrence patterns may reveal the extent to which groups of organisms share habitat preferences [32] and the extent of interspecific interactions (i.e., interactions occur when the presence/absence of a species has some influence on the occurrence of another). In addition, other factors, such as organism dispersal and colonization capacities, can influence co-occurrence patterns [34,35]. Such patterns are expected to change over abiotic stress gradients (e.g., the stress gradient hypothesis) [36,37]. Community assembly processes reflect two opposing forces that occur simultaneously, which stabilize communities and maintain diversity and ecosystem functioning [33,38]. First, functionally similar species can be constrained when they show a strong overlap in resources, leading to competitive exclusion [39]. This limiting similarity mechanism tends to reduce competition by diversifying niches, resulting in higher functional diversity than expected by chance [40]. Second, species can be more functionally similar than expected by chance when abiotic filtering constrains the range of successful functional trait profiles in a community [41]. However, evidence of fungal species interactions and assembly processes are based on manipulative experiments in which fungal diversity and abiotic variations are artificially reduced [20,42,43]. Consequently, the degree to which drying affects the assembly processes of fungal communities in IRES and the associated alterations in their taxonomic and functional diversities remain unclear. Thus, realistic studies exploring the co-occurrence patterns and assembly processes of naturally assembled communities along drying gradients are crucial for predicting the consequences of flow reductions in freshwater ecosystems.

Using aquatic fungal communities collected from 15 streams, we investigated how co-occurrence patterns and assembly processes changed across a wide gradient of annual drying, ranging from 0 to 340 dry days. The specific objectives of this study were (1) to characterize the co-occurrence patterns of aquatic fungi over the drying gradient by determining the number of species pairs with positive, negative, and neutral co-occurrence

patterns; (2) to assess which functional traits best correlate with species co-occurrence probabilities; and (3) to explore which assembly processes (limiting similarity and abiotic filtering) explain changes in functional diversity along the drying gradient. Overall, we hypothesized that traits conferring resistance to desiccation would mediate fungal species assembly patterns, which are expected to shift from the prevalence of limiting similarity or random assembly to strong abiotic filtering as drying intensifies.

2. Materials and Methods

2.1. Sampling Sites and Study Area

The sampling sites included 15 low-order and independent streams located in eight main river basins in the Catalonia region (NE Spain, Table S1). The selected sites covered a drying gradient, whereby the annual drying duration ranged from 0 to 340 days and a frequency of drying up between one and eight times per year. Primary local land uses include forest, scrubland, grasslands, and extensive agriculture (i.e., olive groves and vineyards), which characterize the study area (CORINE Land Cover 2006, buffer ~1 km). The climate of the region is typically Mediterranean with dry and warm summers, and precipitation occurs mainly during the spring and autumn. Fieldwork was conducted from February 2016 to February 2017 (see details in Section 2.2).

2.2. Hydrological and Drying Stress Characterization

The hydrological conditions of each sampling location were based on the daily variation in the streambed temperature and water level of the sampled spots. To estimate the annual hydrology of the study sites (i.e., from February 2016 to February 2017) one year prior to the sampling campaign, we placed temperature and water level data loggers at each sampling site (ACR SmartButton Logger, MicroDAQ, Concord, NH, USA; Solinst Levellogger Gold Model 3001, Solinst, Georgetown, ON, Canada). Data loggers recorded at hourly intervals for one year. Once the temperature data were retrieved, we performed a fifth-order moving average to smoothen the daily differences. We standardized each value with a fixed value per month, using data from field observations, data from meteorological stations (Servei Meteorològic de Catalunya; <http://www.meteocat.es>, accessed on 10 December 2022) near each site, and water level data from levelloggers. We corrected the occasional similarity between streambed temperature and air temperature during autumn and spring using precipitation data from meteorological stations. Once the data loggers were retrieved, we calculated the annual drying duration as the total number of zero-flow days within a year [44].

2.3. Aquatic Fungi Assemblages and Fungal Traits

Conidia of aquatic fungi (i.e., aquatic hyphomycetes) were sampled immediately after the rainy season in February 2017 to ensure that all streams were in the flowing phase. We collected fungal conidia samples with a sterile spoon from freshly accumulated white foams within 100 m stretches in each stream. Foams concentrate aquatic fungal spores, offering a cost-effective opportunity to characterize the structure and diversity of aquatic fungi [45]. Foams were then transferred to sterile glass bottles and fixed with formaldehyde (4%). Once in the laboratory, 5 mL of each foam sample was filtered through 5 µm pore-size membrane filters (Cellulose Nitrate Membrane Filters, Whatman), and stained with a 0.1% Trypan Blue solution in lactic acid. The surface of the filter was then scanned under a light microscope (400x) and whenever possible, aquatic fungi were identified at the species level based on their conidial morphology and dimensions. Aquatic fungal species were recorded as presence–absence data.

To characterize their functional traits, based on published literature, we compiled a database including six traits related to resistance to drying (Table 1). In particular, we selected the primary lifestyle, decay substrate, habitat, preference for tree-holes availability, endophyte capacity, and conidia shape, which included 20 trait categories for the 71 species found across the gradient (Table 1) [27,30,46–49].

Table 1. Functional traits selected, including trait categories and their expected relationship with drying based on published literature. Positive or negative relationships with drying are indicated by the “+” or “−” symbols, respectively.

Trait	Category	Relationship	Drying Effect	References
Primary lifestyle	Litter saprotrophic	−	Drying causes early leaf abscission affecting their basal resource	[50–52]
	Wood saprotrophic	+		
	Plant pathogenic	+		
	Mycoparasite	+		
Decay substrate	Litter	−	Drying favors non-aquatic fungi	[52,53]
	Root	+		
	Wood	+		
Habitat	Aquatic	−	Tree-holes offer an alternative aquatic habitat during drying	[28,54,55]
	Non-aquatic	+		
Tree-holes	Yes	+	Capacity to inhabit plant roots or leaves provides independence from drying	[26,27,56,57]
	No	−		
Endophyte capacity	Yes	+	Conidia/spore shape determines fungal dispersal ability within streambed sediments, which allows them to survive during the dry phase and become physiologically active in the wet phase	[13,26,29,30]
	No	−		
Conidia shape	Branched	−		
	Tetrate	−		
	Filiform	+		
	Sigmoid	−		
	Compact	−		
	Clove-shaped	−		
Spore shape	Asciospores	+		

2.4. Data Analysis

We calculated co-occurrence patterns along the drying gradient based on the presence/absence records of aquatic fungi for each site, using the *cooccur* R package and function. This function uses a probabilistic model to estimate the likelihood of each species pair occurring less or more often than expected, assuming independent species distribution [58,59]. In this analysis, we identified positive associations when the observed frequency of co-occurrence was significantly higher than expected, negative associations when the observed frequency was significantly lower than expected, and random associations when their probability was not significant from the model [58]. To infer the mechanisms driving positive and negative co-occurrence, fungal species were classified into four groups (drying sensitive, partly tolerant, specialist, and generalist) using a k-means clustering procedure based on their niche specialization and affinity [60]. These variables were obtained using an Outlier Mean Index (OMI) analysis. OMI analysis describes species niches along environmental gradients, assuming equal weights at all sites, regardless of their species richness [61].

To explore the functional dissimilarity across fungal species, we used principal coordinate analysis (PCoA) based on a fuzzy-coded adapted Gower dissimilarity matrix [62] derived from the six fungal traits. We retained the first seven functional axes because they explained 82.1% of the Gower dissimilarity matrix, ensuring an appropriate representation of this 7-dimensional space [63].

To evaluate which fungal traits influenced the co-occurrence probability, we applied Mantel-tests (*vegan* R package) [64]. We first correlated the probability of occurrence of each pair of fungal species with their functional dissimilarity based on each of the six functional traits. To do so, we calculated a matrix of species-by-species functional dissimilarities for each trait using the fuzzy-coded adapted Gower index [62]. A positive association between the probability of species occurrence and their functional dissimilarity indicates that species with lower functional similarities tend to co-occur more frequently, which is congruent with the limiting similarity mechanism.

To analyze whether the community assembly processes (limiting similarity vs. abiotic filtering) changed over the drying gradient, we calculated a functional diversity metric (functional richness) and performed null models. Functional richness was calculated as the hypervolume filled by each community in the 7-dimensional trait space (PCoA). Functional richness increases in the presence of extreme trait combinations, which is a proxy for trait range. These analyses were conducted at two scales: communities ($n = 15$) and community aggregations, considering three meaningful segments over the drying gradient [65]: permanent-flow watercourses (annual dry days = 0, $n = 5$), intermittent streams (annual dry days ranging from 1–200, $n = 7$), and ephemeral streams (annual dry days > 200, $n = 3$). These thresholds have proven useful in distinguishing the main ecological strategies of animal and microbial communities over the drying gradient [60–65]. In addition, these two scales were used to understand the main community assembly process in response to drying (community) and whether this mechanism is maintained at the three main segments of the gradient (community aggregations). Then, based on the 7-dimension functional trait space, we quantified the functional richness [66] of the 15 communities and their three aggregations over the drying gradient (permanent-flow, intermittent streams, and ephemeral streams). Finally, to determine whether the assembly processes changed over the drying gradient, we first compared the observed functional richness of the three aggregations with those obtained for 999 randomly assembled communities. Second, we compared the drying effects (estimated as Spearman's correlation coefficients) between the observed and randomized functional richness of the 15 communities. This procedure allowed us to understand whether drying reduced the functional diversity more than expected by chance over the entire gradient (abiotic filtering). For each of the 999 randomizations, we randomly reassigned functional traits to each species (maintaining constant community richness and species occurrence) and calculated the functional richness. We examined the statistical significance of the null model by determining the standardized effect sizes (SES) and the proportion of randomized values that were below or above the observed values at $\alpha = 0.05$. Positive and significant p -values may indicate limiting similarity (more functional diversity than expected by chance), whereas negative and significant p -values may reflect abiotic filtering (less functional diversity than expected by chance).

3. Results

The studied streams covered a wide drying gradient, from permanent rivers (i.e., absence of zero-flow days within a year) to ephemeral streams (with a maximum of 340 zero-flow days and eight zero-flow periods within a year). The mean drying duration was 91.1 zero-flow days, and the mean drying frequency was 2.1 zero-flow periods. A total of 71 fungal species were found in the 15 sampled streams and their occurrence patterns varied among sites, revealing a maximum occurrence of 30 species in a permanent stream and a minimum of 12 species in the most ephemeral stream. Among the 71 fungal species, *Alatospora acuminata* and *Flagellospora curvula* occurred at all the sites.

3.1. Co-occurrence Patterns of Aquatic Fungi

The co-occurrence analysis included 810 species pairs (out of 2485) that co-occurred in at least two sites. Non-random co-occurrence patterns covered 5.2% of the total, and were present in 42 pairs of species pairs. Among them, 3.1% of species pairs showed significant positive associations (i.e., more co-occurrences than expected, assuming an independent species distribution), whereas 2.1% depicted a significant negative association (i.e., fewer co-occurrences than expected, assuming an independent species distribution) (Figure 1). The majority of species pairs showed random co-occurrence patterns (94.8%).

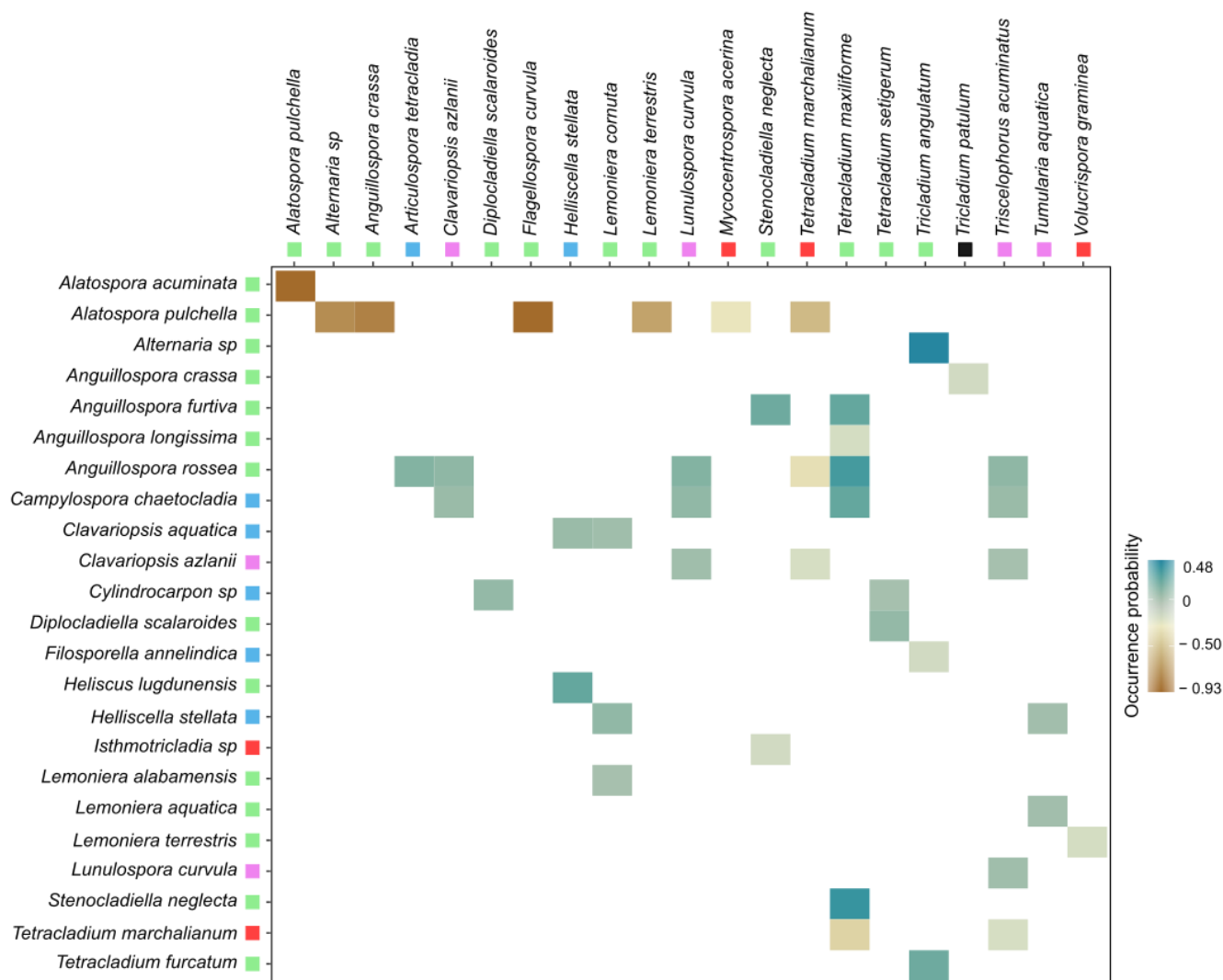


Figure 1. Heatmap showing significant co-occurrence probabilities among pairs of aquatic fungal species across the drying gradient. Colored squares next to species names represent their drying preferences and specializations: drying sensitive (pink), partly tolerant (blue), specialist (red), and generalist (green) [60]. Note that the black square indicates no information regarding the drying preference and specialization.

The species showed contrasting co-occurrence patterns depending on their drying niches (Figure 1). Whereas positive co-occurrences dominated in pairs, including either sensitive or partly tolerant species, drying specialists only displayed negative co-occurrence patterns. In contrast, generalists showed intermediate patterns with similar proportions of positive (8) and negative (7) co-occurrences. Sensitive species showed positive co-occurrences patterns with other drying-sensitive (3), partly tolerant (5), and generalist species (3). The sensitive species showing the most positive co-occurrence was *Lunulospora curvula* (4). Sensitive species showed negative co-occurrence patterns in only two cases, and both were associated with drying specialist species. Species that were partly tolerant to drying showed positive co-occurrence patterns in combination with drying-sensitive (5) and generalist species (6). *Campylospora chaetocladia* and *Helliscella stellata* were partly tolerant species with more positive co-occurrences (four each). Drying specialists showed negative co-occurrence patterns, mainly in association with generalists (4). The drying specialist *Tetraccladium marchalianum* most frequently shows negative co-occurrence with other species (5). Among generalists, *Tetraccladium maxilliforme* showed the most positive co-

occurrences (4), whereas *Alatospora pulchella* showed the most negative co-occurrences (7). All negative co-occurrence patterns for species pairs with similar drying niches occurred among generalists. Examples include the pairs formed by *A. pulchella* and *A. acuminata*, and *A. pulchella* and *Anguillospora crassa*.

3.2. Functional Dissimilarity and Co-occurrence Patterns across Fungal Species

Fungal species were ordered in a functional space of seven dimensions that explained 82.1% of the original variance (Figure 2, see Table S2 for further details). The first axis explained 24.0% of the variance and was positively correlated with litter saprotrophic lifestyle ($r = 0.54$) and negatively correlated with plant pathogenic lifestyle and endophyte capacity ($r = -0.60$ and $r = -0.88$, respectively). Axis 2 explained 15.2% of the variance and was positively correlated with plant pathogenic lifestyle ($r = 0.50$) and negatively correlated with a litter saprotrophic one ($r = -0.75$). Axis 3 explained 12.0% of the variance and was positively correlated with branched conidian shape ($r = 0.67$), whereas axis 4 explained 11.7% of the variance and was positively correlated with non-aquatic habitat ($r = 0.82$). Axis 5, explaining 7.7% of the variance, was negatively correlated with tree-holes ($r = -0.71$) and axis 6 explained 6.17% of the variance, being positively correlated with wood saprotrophic lifestyle ($r = 0.58$). Axis 7, which explained 5.3% of the variance, was positively correlated with the conidian tetraradiate shape ($r = 0.79$).

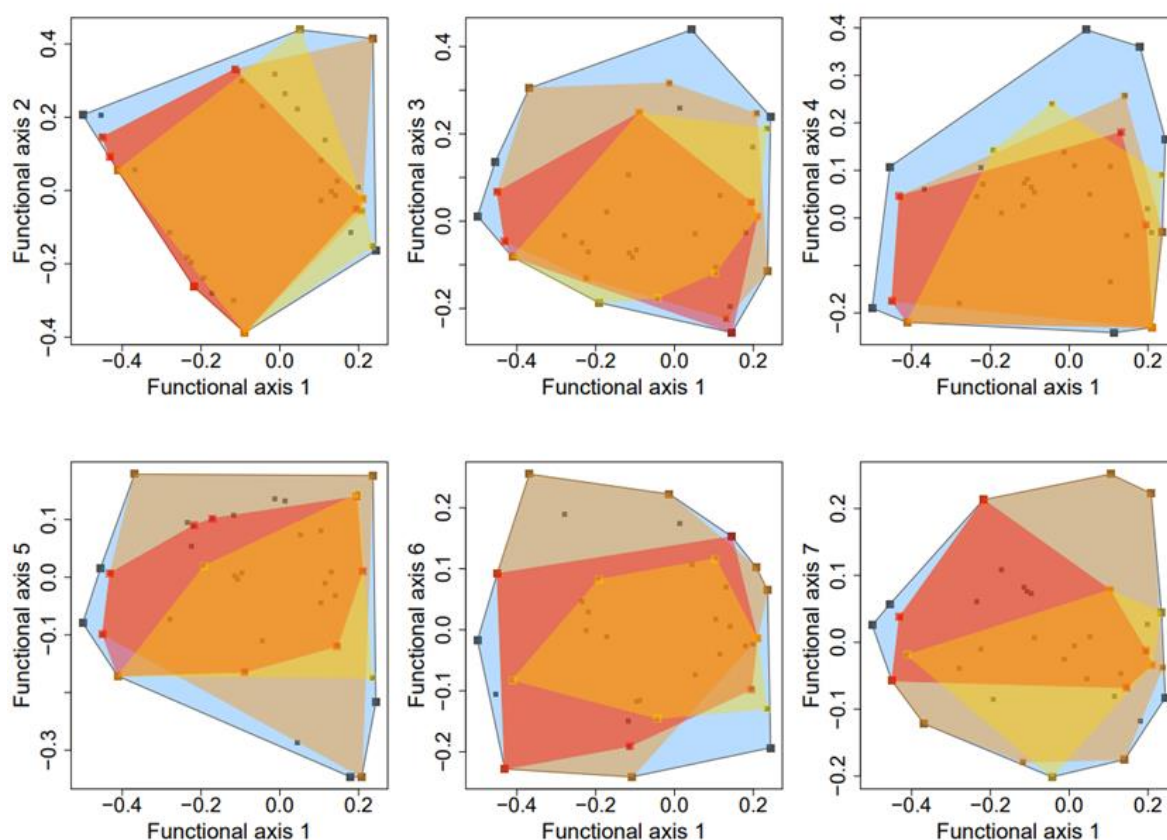


Figure 2. The PCoA ordination describes the functional space (blue) of the 71 aquatic fungal species and illustrates the reduction in functional diversity across the increased drying conditions from locations with permanent flow (light red polygon) to those with intermittent (dark red polygon) and ephemeral (yellow polygon) flow.

Increased drying conditions reduced functional diversity in such a way that fungal communities located in habitats with permanent flow occupied a wider functional space than communities inhabiting intermittent rivers and ephemeral streams (Figure 2).

Among all six fungal traits, species functional dissimilarities based on conidia shape (Mantel $r = 0.13$, $p = 0.004$) and fungal endophytic capacity (Mantel $r = 0.07$, $p = 0.033$) significantly influenced co-occurrence patterns (Table S2). As such, those species pairs with lower similarity in terms of conidia shape and endophytic capacity tended to co-occur more frequently across the drying gradient.

3.3. Functional Diversity and Community Assembly across the Drying Gradient

Null models showed that communities occurring in permanent watercourses (annual dry days = 0) had more functional richness than expected by chance ($SES = 1.79$, $p = 0.010$), whereas communities occurring at ephemeral sites (annual dry days >200) had less functional richness than expected by chance ($SES = -1.67$, $p = 0.045$). Communities inhabiting intermittent streams (annual dry days between one and 200) showed functional values indistinguishable from null expectations ($SES = -0.73$, $p = 0.237$) (Figure 3).

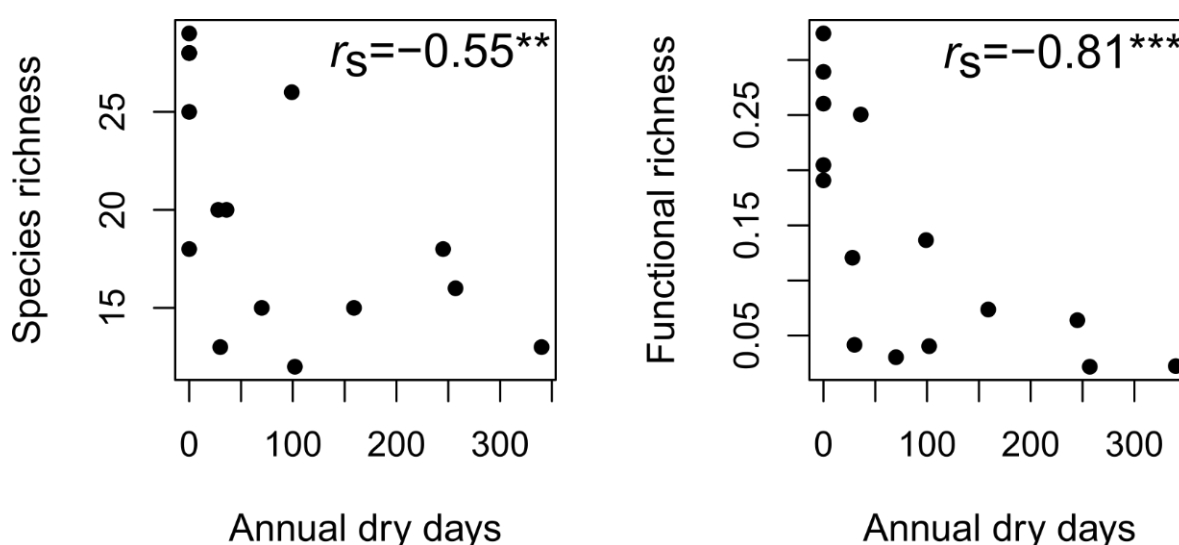


Figure 3. Plots showing the responses of aquatic fungal species functional richness (right panel) and taxonomic richness (left panel) to annual drying duration (annual dry days). Spearman correlation (r_s) and significance are also shown (**: p -value < 0.05, ***: p -value < 0.01). Functional richness and species showed a positive and significant correlation ($r_s = 0.76$; p -value: 0.001).

Drying caused a stronger decline in functional richness ($r_s = -0.81$, $p < 0.001$) than in species richness ($r_s = -0.55$, $p < 0.006$) (Figure 3). Over this drying gradient, functional richness declined more than expected by chance ($SES = -1.94$, $p = 0.007$).

4. Discussion

Our results demonstrated that drying stress shapes the co-occurrence and assembly processes of aquatic fungi. We found that only a fraction of fungal co-occurrence was non-random and that conidia shape and endophytic capacities explain the probability of species co-occurrence. In addition, our null model results indicate that drying intensity controls species co-existence by switching assembly processes over the drying gradient. Thus, competition-avoiding strategies limit species similarity in permanent-flow communities resulting in a functional diversification, whereas stress-avoiding processes under intense abiotic filtering cause a drastic loss of functional diversity. Collectively, our findings can help to better understand the effects of drying on aquatic communities and the consequences for ecosystem functioning.

4.1. Fungal Co-occurrence Patterns over the Drying Gradient

We found that the co-occurrence patterns of fungal species were strongly influenced by their drying preferences and specialization. Positive interactions were more common for

fungus species occurring at low drying intensities, as more habitats were likely to be present as well as less competitive exclusion; therefore, taxonomic and functional diversity were maximized. Although species inhabiting diverse environments are expected to compete more strongly for resources [33,40], our results showed stronger support for facilitative interactions for sensitive and partly tolerant species [67,68]. To avoid competition, fungal species might have promoted the spatiotemporal segregation of their niches by focusing on different organic substrates [69,70]. Such microhabitat partitioning could give rise to strong complementarity and foster organic matter cycling, biomass production, and energy transfer to higher trophic levels of the ecosystem level [5,8,43]. In contrast, negative interactions among generalists may reflect potential competitive interactions [60]. Some studies have found that generalist species tend to be more competitive than specialists, thus giving rise to competitive exclusion [71]. The fact that drying specialists only displayed negative interactions with drying-sensitive and generalist taxa could also be explained by species segregation due to different habitat preferences [72]. The persistence of natural stressors over geological time fosters species specialization for short portions of the stress gradient [73,74], promoting community differences explained by species turnover [5,75]. From an eco-evolutionary perspective, thriving in stressful environments provides advantages, such as reduced competition, but also requires specific adaptations and increased energy consumption to cope with stress [76,77]. Specifically, drying has a negative effect on the performance of aquatic fungi [3,78,79], affecting their reproductive capacity [13] and survival, depending on the availability of organic substrates [26].

Differences in conidia shape and endophytic capacity were the best predictors of co-occurrence probability among fungal species pairs. This result reinforces the role of functional traits mediating species co-occurrence along stress gradients [35,80,81]. Specifically, these traits seem to provide drying resistance by conferring advantages in such stressful environments, thus potentially allowing them to thrive under abiotic filtering mechanisms that shape community assembly. In this context, some conidia shapes, such as filiform spores, may be passively transported into sediments during dry periods [12,82–84], which represents a major challenge for aquatic fungi dispersal during flow cessation. On the other hand, endophytic capacity explained species co-occurrences to some extent, supporting the hypothesis that certain aquatic fungi could have a dual life cycle as a desiccation-resistance life strategy in IRES [13,28]. It is well known that aquatic fungi have evolved different life-history strategies in response to drying as a result of specialized physiological and life-history traits. In this way, a dual life cycle and functional adaptations such as hydrophobic cell walls have emerged as potentially successful strategies to cope with drying [24,85,86].

4.2. Assembly Processes of Fungal Communities over the Drying Gradient

Our results showed a clear shift in community assembly patterns over the drying gradient. Specifically, limiting similarity patterns gave rise to over-dispersed trait profiles in permanent-flow streams, whereas abiotic filtering limited the trait range in most ephemeral streams (>200 dry days). These contrasting assembly processes seem to mirror a strong change in the dominant forces shaping community assembly, consistent with the Stress Gradient Hypothesis [36,37]. Under benign conditions, competition for resource acquisition is the main challenge for species and niche diversification can be a successful strategy for stabilizing communities and avoiding competition [33,38]. When stress intensifies, biotic interactions tend to weaken and abiotic stress becomes the major filter [87,88]. Drying stress can act on either individual traits or trait combinations [89,90] resulting in increased functional similarity among species, which reduces functional diversity.

We also found that drying caused a functional trait decline greater than expected by chance and that species loss seemed to disproportionately reduce functional richness. These patterns indicate that the most functionally unique species of aquatic fungi are rapidly extirpated by drying [91], resulting in functional homogenization of the communities under stressful drying conditions. Because of their dependence on extreme trait values, functional richness reductions are ideal for identifying the loss of functionally unique species [66]. In

addition, these results suggest reduced functional redundancy of aquatic fungi, which may tend to show contrasting trait profiles to avoid competition. Other studies exploring the relationship between taxonomic and functional diversity in microbes also found reduced functional redundancy [92,93], but this is far from a universal rule [94]. Our results are also relevant to understanding the functional consequences of biodiversity loss in a climate change context, where drying events are more intense and frequent. Loss of functional diversity can partly explain the reductions in organic matter decomposition, biomass production, and reproductive capacity in fungal communities exposed to drying [22,95]. Both manipulative and observational studies have found that niche complementarity effects across fungal species play a critical role in enhancing ecosystem functioning [5,43]. In addition, reduced functional redundancy can be related to stronger functional sensitivity to biodiversity loss [96].

Taken together, our findings show that species co-occurrences and assembly processes are strongly influenced by drying intensity and that functional traits mediate their responses to drying. We also found that drying caused a reduction in functional diversity, explained by non-random trait sorting, which can compromise stream functioning as drying events become more intense and frequent as climate change intensifies. This study can help to better understand the responses of communities and ecosystem functioning to drying stress in the context of widespread increases in flow reduction and intermittency across fluvial networks.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d15020289/s1>, Table S1: Geographical and basin characterization of the studied sites; Table S2: Pearson correlation coefficients between functional space PCoA axes and original trait categories.

Author Contributions: Conceptualization, R.A.-R., P.H. and C.G.-C.; methodology, R.A.-R. and C.G.-C.; validation, R.A.-R., P.H., G.G. and C.G.-C.; formal analysis, R.A.-R., P.H. and C.G.-C.; investigation, R.A.-R., P.H., G.G. and C.G.-C.; data curation, R.A.-R. and G.G.; writing—original draft preparation, R.A.-R.; writing—review and editing, R.A.-R., P.H., G.G. and C.G.-C.; visualization, R.A.-R., P.H., G.G. and C.G.-C.; supervision, C.G.-C. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by MCIN/AEI/10.13039/501100011033 through the project RIVSTRESS (PID2020-115708RB-C21). R.A.-R. held a post-doctoral grant “Margarita Salas” from the Spanish Ministry of Universities and the Next Generation EU-Recovery, Transformation and Resilience Plan. P.H. held a post-doctoral grant “Margarita Salas” from the Spanish Ministry of Universities and the Next Generation EU-Recovery, Transformation and Resilience Plan and a ‘Juan de la Cierva-Formación’ contract (Spanish Ministry of Science and Innovation, FJC2020-045923-I). C.G.-C. was supported by a Junior Leader Fellowship contract (LCF/BQ/PR22/11920005) funded by “la Caixa” Foundation (ID 100010434).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data will be made available on request.

Acknowledgments: We gratefully acknowledge the field assistance and fungal identification provided by Margarita Menéndez and Isabel Muñoz.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Gessner, M.O.; Swan, C.M.; Dang, C.K.; McKie, B.G.; Bardgett, R.D.; Wall, D.H.; Hättenschwiler, S. Diversity meets decomposition. *Trends Ecol. Evol.* **2010**, *25*, 372–380. [[CrossRef](#)] [[PubMed](#)]
2. Grossart, H.-P.; Van den Wyngaert, S.; Kagami, M.; Wurzbacher, C.; Cunliffe, M.; Rojas-Jimenez, K. Fungi in aquatic ecosystems. *Nat. Rev. Microbiol.* **2019**, *17*, 339–354. [[CrossRef](#)] [[PubMed](#)]
3. Canhoto, C.; Gonçalves, A.L.; Bärlocher, F. Biology and ecological functions of aquatic hyphomycetes in a warming climate. *Fungal Ecol.* **2016**, *19*, 201–218. [[CrossRef](#)]

4. Krauss, G.J.; Solé, M.; Krauss, G.; Schlosser, D.; Wesenberg, D.; Bärlocher, F. Fungi in freshwaters: Ecology, physiology and biochemical potential. *FEMS Microbiol. Rev.* **2011**, *35*, 620–651. [[CrossRef](#)] [[PubMed](#)]
5. Arias-Real, R.; Gutiérrez-Cánovas, C.; Muñoz, I.; Pascoal, C.; Menéndez, M. Fungal biodiversity mediates the effects of drying on freshwater ecosystem functioning. *Ecosystems* **2022**, *25*, 780–794. [[CrossRef](#)]
6. Manning, D.W.P.; Rosemond, A.D.; Gulis, V.; Benstead, J.P.; Kominoski, J.S. Nutrients and temperature additively increase stream microbial respiration. *Glob. Change Biol.* **2018**, *24*, e233–e247. [[CrossRef](#)]
7. Kuehn, K.A. Lentic and lotic habitats as templates for fungal communities: Traits, adaptations, and their significance to litter decomposition within freshwater ecosystems. *Fungal Ecol.* **2016**, *19*, 135–154. [[CrossRef](#)]
8. Arias-Real, R.; Menéndez, M.; Abril, M.; Oliva, F.; Muñoz, I. Quality and quantity of leaf litter: Both are important for feeding preferences and growth of an aquatic shredder. *PLoS ONE* **2018**, *13*, e0208272. [[CrossRef](#)]
9. Gonçalves, A.L.; Chauvet, E.; Bärlocher, F.; Graça, M.A.S.; Canhoto, C. Top-down and bottom-up control of litter decomposers in streams. *Freshw. Biol.* **2014**, *59*, 2172–2182. [[CrossRef](#)]
10. Grossart, H.-P.; Rojas-Jimenez, K. Aquatic fungi: Targeting the forgotten in microbial ecology. *Curr. Opin. Microbiol.* **2016**, *31*, 140–145. [[CrossRef](#)]
11. Grossart, H.-P.; Hassan, E.A.; Masigol, H.; Arias-Andres, M.; Rojas-Jimenez, K. Inland water fungi in the anthropocene: Current and future perspectives. In *Encyclopedia of Inland Waters*, 2nd ed.; Mehner, T., Tockner, K., Eds.; Elsevier: Amsterdam, The Netherlands, 2022; Volume 4, pp. 667–684. [[CrossRef](#)]
12. Duarte, S.; Bärlocher, F.; Cassio, F. Biogeography of aquatic hyphomycetes: Current knowledge and future perspectives. *Fungal Ecol.* **2015**, *19*, 169–181. [[CrossRef](#)]
13. Bärlocher, F. Reproduction and dispersal in aquatic hyphomycetes. *Mycoscience* **2009**, *50*, 3–8. [[CrossRef](#)]
14. Skoulikidis, N.T.; Sabater, S.; Datry, T.; Morais, M.M.; Buffagni, A.; Dörflinger, G.; Zogaris, S.; del Mar Sánchez-Montoya, M.; Bonada, N.; Kalogianni, E.; et al. Non-perennial Mediterranean rivers in Europe: Status, pressures, and challenges for research and management. *Sci. Total Environ.* **2017**, *577*, 1–18. [[CrossRef](#)] [[PubMed](#)]
15. Gutiérrez-Cánovas, C.; Arias-Real, R.; Bruno, D.; Cabrerizo, M.J.; González-Olalla, J.M.; Picazo, F.; Romero, F.; Sánchez-Fernández, D.; Pallarés, S. Multiple-stressors effects on Iberian freshwaters: A review of current knowledge and future research priorities. *Limnetica* **2022**, *41*, 245–268. [[CrossRef](#)]
16. Messenger, M.L.; Lehner, B.; Cockburn, C.; Lamouroux, N.; Pella, H.; Snelder, T.; Tockner, K.; Trautmann, T.; Watt, C.; Datry, T. Global prevalence of non-perennial rivers and streams. *Nature* **2021**, *594*, 391–397. [[CrossRef](#)]
17. Scheider, A.; Jost, A.; Coulon, C.; Silvestre, M.; Théry, S.; Ducharme, A. Global-scale river network extraction based on high-resolution topography and constrained by lithology, climate, slope, and observed drainage density. *Geophys. Res. Lett.* **2017**, *44*, 2773–2781. [[CrossRef](#)]
18. Döll, P.; Schmied, H.M. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environ. Res. Lett.* **2012**, *7*, 014037. [[CrossRef](#)]
19. Maynard, D.S.; Bradford, M.A.; Covey, K.R.; Lindner, D.; Glaeser, J.; Talbert, D.A.; Tinker, P.J.; Walker, D.M.; Crowther, T.W. Consistent trade-offs in fungal trait expression across broad spatial scales. *Nat. Microbiol.* **2019**, *4*, 846–853. [[CrossRef](#)]
20. Crowther, T.W.; Maynard, D.S.; Crowther, T.R.; Peccia, J.; Smith, J.R.; Bradford, M.A. Untangling the fungal niche: The trait-based approach. *Front. Microbiol.* **2014**, *5*, 579. [[CrossRef](#)]
21. Battin, T.J.; Besemer, K.; Bengtsson, M.M.; Romani, A.M.; Packmann, A.I. The ecology and biogeochemistry of stream biofilms. *Nat. Rev. Microbiol.* **2016**, *14*, 251–263. [[CrossRef](#)]
22. Duarte, S.; Mora-Gómez, J.; Romani, A.M. Responses of microbial decomposers to drought in streams may depend on the environmental context. *Environ. Microbiol. Rep.* **2017**, *9*, 756–765. [[CrossRef](#)] [[PubMed](#)]
23. Gionchetta, G.; Oliva, F.; Menéndez, M.; Lopez, P.; Anna, L. Key role of streambed moisture and flash storms for microbial resistance and resilience to long-term drought. *Freshw. Biol.* **2019**, *64*, 306–322. [[CrossRef](#)]
24. Coleine, C.; Stajich, J.E.; Selbmann, L. Fungi are key players in extreme ecosystems. *Trends Ecol. Evol.* **2022**, *37*, 517–528. [[CrossRef](#)] [[PubMed](#)]
25. Gionchetta, G.; Artigas, J.; Arias-Real, R.; Oliva, F.; Romani, A.M. Multi-model assessment of hydrological and environmental impacts on streambed microbes in Mediterranean catchments. *Environ. Microbiol.* **2020**, *22*, 2213–2229. [[CrossRef](#)] [[PubMed](#)]
26. Chauvet, E.; Cornut, J.; Sridhar, K.R.; Selosse, M.A.; Bärlocher, F. Beyond the water column: Aquatic hyphomycetes outside their preferred habitat. *Fungal Ecol.* **2016**, *19*, 112–127. [[CrossRef](#)]
27. Selosse, M.-A.; Vohnik, M.; Chauvet, E. Out of the rivers: Are some aquatic hyphomycetes plant endophytes? *New Phytol.* **2008**, *178*, 3–7. [[CrossRef](#)]
28. Sridhar, K.R. Fungi in the tree canopy—An appraisal. In *Applies Mycology*; Rai, M., Bridge, P., Eds.; CAB International: London, UK, 2009; pp. 73–91. [[CrossRef](#)]
29. Ghatge, S.D.; Sridhar, K.R. Diversity of aquatic hyphomycetes in streambed sediments of temporary streamlets of Southwest India. *Fungal Ecol.* **2015**, *14*, 53–61. [[CrossRef](#)]
30. Cornut, J.; Chauvet, E.; Mermillod-Blondin, F.; Assemet, F.; Elger, A. Aquatic Hyphomycete Species Are Screened by the Hyporheic Zone of Woodland Streams. *Appl. Environ. Microbiol.* **2014**, *80*, 1949–1960. [[CrossRef](#)]
31. Concostrina-Zubiri, L.; Prieto, M.; Hurtado, P.; Escudero, A.; Martínez, I. Functional diversity regulates the effects of habitat degradation on biocrust phylogenetic and taxonomic diversities. *Ecol. Appl.* **2022**, *32*, e2599. [[CrossRef](#)]

32. Horner-Devine, M.C.; Silver, J.M.; Leibold, M.A.; Bohannan, B.J.M.; Colwell, R.K.; Fuhrman, J.A.; Green, J.L.; Kuske, C.R.; Martiny, J.B.; Muyzer, G.; et al. A Comparison of taxon co-occurrence patterns from macro- and microorganisms. *Ecology* **2007**, *88*, 1345–1353. [CrossRef]
33. Kraft, N.J.B.; Adler, P.B.; Godoy, O.; James, E.C.; Fuller, S.; Levine, J.M. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* **2015**, *29*, 592–599. [CrossRef]
34. Li, Y.; Shipley, B. Community divergence and convergence along experimental gradients of stress and disturbance. *Ecology* **2018**, *99*, 775–781. [CrossRef]
35. Gutiérrez-Cánovas, C.; Sánchez-Fernández, D.; Cañedo-Argüelles, M.; Millán, A.; Velasco, J.; Acosta, R.; Fortuño, P.; Otero, N.; Soler, A.; Bonada, N. Do all roads lead to Rome? Exploring community trajectories in response to anthropogenic salinization and dilution of rivers. *Phil. Trans. R. Soc. B* **2019**, *374*, 20180009. [CrossRef]
36. Maestre, F.T.; Callaway, R.M.; Valladares, F.; Lortie, C.J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **2009**, *97*, 199–205. [CrossRef]
37. Hammarlund, S.P.; Harcombe, W.R. Refining the stress gradient hypothesis in a microbial community. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 15760–15762. [CrossRef] [PubMed]
38. Mayfield, M.M.; Levine, J.M. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* **2010**, *13*, 1085–1093. [CrossRef] [PubMed]
39. Violle, C.; Nemergut, D.R.; Pu, Z.; Jiang, L. Phylogenetic limiting similarity and competitive exclusion. *Ecol. Lett.* **2011**, *14*, 782–787. [CrossRef]
40. Chesson, P. Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.* **2000**, *31*, 343–366. [CrossRef]
41. Cornwell, W.K.; Schilke, D.W.; Ackerly, D.D. A trait-based test for habitat filtering: Convex hull volume. *Ecology* **2006**, *87*, 1465–1471. [CrossRef]
42. Graça, D.; Fernandes, I.; Cássio, F.; Pascoal, C. Eco-physiological responses of aquatic fungi to three global change stressors highlight the importance of intraspecific trait variability. *Microb. Ecol.* **2022**. [CrossRef]
43. Duarte, S.; Pascoal, C.; Cássio, F.; Bärlocher, F. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. *Oecologia* **2006**, *147*, 658–666. [CrossRef]
44. Arias-Real, R.; Gutiérrez-Cánovas, C.; Menéndez, M.; Granados, V.; Muñoz, I. Diversity mediates the responses of invertebrate density to duration and frequency of rivers' annual drying regime. *Oikos* **2021**, *130*, 2148–2160. [CrossRef]
45. Graça, M.A.S.; Bärlocher, F.; Gessner, M.O. *Methods to Study Litter Decomposition: A Practical Guide*; Springer: Berlin, Germany, 2005. [CrossRef]
46. Sati, S.C.; Pathak, R. New root endophytic water borne conidial fungi from Kumaun Himalaya. *Curr. Bot.* **2017**, *8*, 12–16. [CrossRef]
47. Thakur, S.B. Survival of Some Aquatic Hyphomycetes under Dry Conditions. *Mycologia* **1977**, *69*, 843–845. [CrossRef]
48. Sati, S.C.; Belwal, M. Aquatic hyphomycetes as endophytes of riparian plant roots. *Mycologia* **2005**, *97*, 45–49. [CrossRef] [PubMed]
49. Gulis, V.; Marvanová, L.; Descals, E. An Illustrated Key to the Common Temperate Species of Aquatic Hyphomycetes BT. In *Methods to Study Litter Decomposition: A Practical Guide*; Graça, M.A.S., Bärlocher, F., Gessner, M.O., Eds.; Springer: Dordrecht, The Netherlands, 2005; pp. 153–167. [CrossRef]
50. Sanpera-Calbet, I.; Ylla, I.; Romaní, A.M.; Sabater, S.; Muñoz, I. Drought effects on resource quality in a Mediterranean stream: Fatty acids and sterols as indicators. *Limnetica* **2017**, *36*, 29–43. [CrossRef]
51. Bärlocher, F. Effects of drying and freezing autumn leaves on leaching and colonization by aquatic hyphomycetes. *Freshw. Biol.* **1992**, *28*, 1–7. [CrossRef]
52. Pölme, S.; Abarenkov, K.; Henrik Nilsson, R.; Lindahl, B.D.; Clemmensen, K.E.; Kauserud, H.; Nguyen, N.; Kjoller, R.; Bates, S.T.; Baldrian, P.; et al. FungalTraits: A user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Divers.* **2020**, *105*, 1–16. [CrossRef]
53. Boonmee, S.; Wanasinghe, D.N.; Calabon, M.S.; Huanraluek, N.; Chandrasiri, S.K.U.; Jones, G.E.B.; Rossi, W.; Leonardi, M.; Singh, S.K.; Rana, S.; et al. Fungal diversity notes 1387–1511: Taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Divers.* **2021**, *111*, 1–335. [CrossRef]
54. Kitching, R.L. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *J. Anim. Ecol.* **1971**, *40*, 281–302. [CrossRef]
55. Gönczöl, J.; Révay, Á. Treehole fungal communities: Aquatic, aero-aquatic and dematiaceous hyphomycetes. *Fungal Divers.* **2003**, *12*, 19–34. Available online: <https://www.fungaldiversity.org/fdp/sfdp/FD12-19-34.pdf> (accessed on 10 December 2022).
56. Koivusaari, P.; Tejesvi, M.V.; Tolkinen, M.; Markkola, A.; Mykrä, H.; Pirttilä, A.M. Fungi originating from tree leaves contribute to fungal diversity of litter in streams. *Front. Microbiol.* **2019**, *10*, 651. [CrossRef] [PubMed]
57. Leroy, C.J.; Fischer, D.G.; Halstead, K.; Pryor, M.; Bailey, J.K.; Schweitzer, J.A. A fungal endophyte slows litter decomposition in streams. *Freshw. Biol.* **2011**, *56*, 1426–1433. [CrossRef]
58. Veech, J.A. A probabilistic model for analysing species co-occurrence. *Glob. Ecol. Biogeogr.* **2013**, *22*, 252–260. [CrossRef]
59. Griffith, D.M.; Veech, J.A.; Marsh, C.J. cooccur: Probabilistic Species Co-Occurrence Analysis in R. *J. Stat. Softw. Code Snippets* **2016**, *69*, 1–17. [CrossRef]
60. Arias-Real, R.; Menéndez, M.; Muñoz, I.; Pascoal, C. Drying shapes the ecological niche of aquatic fungi with implications on ecosystem functioning. *Sci. Total Environ.* **2022**, *859*, 160374. [CrossRef]

61. Dolédec, S.; Chessel, D.; Gimaret-Carpentier, C. Niche separation in community analysis: A new method. *Ecology* **2000**, *81*, 2914–2927. [\[CrossRef\]](#)
62. Pavoine, S.; Vallet, J.; Dufour, A.-B.; Gachet, S.; Daniel, H. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos* **2009**, *118*, 391–402. [\[CrossRef\]](#)
63. Maire, E.; Grenouillet, G.; Brosse, S.; Villéger, S. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob. Ecol. Biogeogr.* **2015**, *24*, 728–740. [\[CrossRef\]](#)
64. Legendre, P.; Legendre, L. *Numerical Ecology*; Elsevier: Amsterdam, The Netherlands, 2012.
65. Arias-Real, R.; Gutiérrez-Cánovas, C.; Menéndez, M.; Muñoz, I. Drying niches of aquatic macroinvertebrates identify potential biomonitoring indicators in intermittent and ephemeral streams. *Ecol. Indic.* **2022**, *142*, 109263. [\[CrossRef\]](#)
66. Villéger, S.; Mason, N.W.H.; Mouillot, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **2008**, *89*, 2290–2301. [\[CrossRef\]](#)
67. Fox, J.W. Interpreting the ‘selection effect’ of biodiversity on ecosystem function. *Ecol. Lett.* **2005**, *8*, 846–856. [\[CrossRef\]](#)
68. Melbinger, A.; Vergassola, M. The Impact of Environmental Fluctuations on Evolutionary Fitness Functions. *Sci. Rep.* **2015**, *5*, 15211. [\[CrossRef\]](#)
69. Gulis, V. Are there any substrate preferences in aquatic hyphomycetes? *Mycol. Res.* **2001**, *105*, 1088–1093. [\[CrossRef\]](#)
70. Thomas, K.; Chilvers, G.A.; Norris, R.H. Aquatic hyphomycetes from different substrates: Substrate preference and seasonal occurrence. *Mar. Freshw. Res.* **1992**, *43*, 491–509. [\[CrossRef\]](#)
71. Denelle, P.; Violle, C.; Consortium, D.; Munoz, F. Generalist plants are more competitive and more functionally similar to each other than specialist plants: Insights from network analyses. *J. Biogeogr.* **2020**, *47*, 1922–1933. [\[CrossRef\]](#)
72. Morris, D.W. Coexistence of specialist and generalist rodents via habitat selection. *Ecology* **1996**, *77*, 2352–2364. [\[CrossRef\]](#)
73. Badyaev, A.V. Stress-induced variation in evolution: From behavioural plasticity to genetic assimilation. *Proc. R. Soc. B Biol. Sci.* **2005**, *272*, 877–886. [\[CrossRef\]](#) [\[PubMed\]](#)
74. Arribas, P.; Gutiérrez-Cánovas, C.; Botella-Cruz, M.; Cañedo-Argüelles, M.; Carbonell, J.A.; Millán, A.; Pallarés, S.; Velasco, J.; Sánchez-Fernández, D. Insect communities in saline waters consist of realised but not fundamental niche specialists. *Philos. Trans. R. Soc. B Biol. Sci.* **2019**, *374*, 20180008. [\[CrossRef\]](#)
75. Gutiérrez-Cánovas, C.; Millán, A.; Velasco, J.; Vaughan, I.P.; Ormerod, S.J. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Glob. Ecol. Biogeogr.* **2013**, *22*, 796–805. [\[CrossRef\]](#)
76. Herbst, D.B. Gradients of salinity stress, environmental stability and water chemistry as a templet for defining habitat types and physiological strategies in inland salt waters. *Hydrobiologia* **2001**, *466*, 209–219. [\[CrossRef\]](#)
77. Liancourt, P.; Callaway, R.M.; Michalet, R. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* **2005**, *86*, 1611–1618. [\[CrossRef\]](#)
78. Noel, L.; Bärlocher, F.; Culp, J.M.; Seena, S. Nutrient enrichment and flow regulation impair structure and function of a large river as revealed by aquatic hyphomycete species richness, biomass, and decomposition rates. *Freshw. Sci.* **2016**, *35*, 1148–1163. [\[CrossRef\]](#)
79. Gonçalves, A.L.; Lirio, A.V.; Graça, M.A.S.; Canhoto, C. Fungal species diversity affects leaf decomposition after drought. *Int. Rev. Hydrobiol.* **2016**, *101*, 78–86. [\[CrossRef\]](#)
80. Sommer, B.; Harrison, P.L.; Beger, M.; Pandolfi, J.M. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* **2014**, *95*, 1000–1009. [\[CrossRef\]](#) [\[PubMed\]](#)
81. Soliveres, S.; Maestre, F.T.; Bowker, M.A.; Torices, R.; Quero, J.L.; Garcia-Gomez, M.; Cabrera, O.; Cea, A.P.; Coaguila, D.; Eldridge, D.J.; et al. Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands. *Perspect. Plant Ecol. Evol. Syst.* **2014**, *16*, 164–173. [\[CrossRef\]](#)
82. Medeiros, A.O.; Pascoal, C.; Graça, M.A.S. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshw. Biol.* **2009**, *54*, 142–149. [\[CrossRef\]](#)
83. Duarte, S.; Cássio, F.; Pascoal, C. Environmental drivers are more important for structuring fungal decomposer communities than the geographic distance between streams. *Limnetica* **2017**, *36*, 491–506. [\[CrossRef\]](#)
84. Gulis, V.; Su, R.; Kuehn, K.A. Fungal decomposers in freshwater environments. In *The Structure and Function of Aquatic Microbial Communities*; Springer: Berlin, Germany, 2019; pp. 121–155. [\[CrossRef\]](#)
85. Naranjo-Ortiz, M.A.; Gabaldón, T. Fungal evolution: Diversity, taxonomy and phylogeny of the Fungi. *Biol. Rev.* **2019**, *94*, 2101–2137. [\[CrossRef\]](#)
86. Kakumanu, M.L.; Cantrell, C.L.; Williams, M.A. Microbial community response to varying magnitudes of desiccation in soil: A test of the osmolyte accumulation hypothesis. *Soil Biol. Biochem.* **2013**, *57*, 644–653. [\[CrossRef\]](#)
87. Hernandez, D.J.; David, A.S.; Menges, E.S.; Searcy, C.A.; Afkhami, M.E. Environmental stress destabilizes microbial networks. *ISME J.* **2021**, *15*, 1722–1734. [\[CrossRef\]](#) [\[PubMed\]](#)
88. Menezes, B.S.; Martins, F.R.; Dantas Carvalho, E.C.; Souza, B.C.; Silveira, A.P.; Loiola, M.I.B.; Araújo, F.S. Assembly rules in a resource gradient: Competition and abiotic filtering determine the structuring of plant communities in stressful environments. *PLoS ONE* **2020**, *15*, e0230097. [\[CrossRef\]](#) [\[PubMed\]](#)
89. Le Bagousse-Pinguet, Y.; Gross, N.; Maestre, F.T.; Maire, V.; de Bello, F.; Fonseca, C.R.; Kattge, J.; Valencia, E.; Leps, J.; Liancourt, P. Testing the environmental filtering concept in global drylands. *J. Ecol.* **2017**, *105*, 1058–1069. [\[CrossRef\]](#)

90. Díaz, S.; Lavorel, S.; De Bello, F.; Quétier, F.; Grigulis, K.; Robson, T.M. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 20684–20689. [[CrossRef](#)]
91. Flynn, D.F.B.; Gogol-Prokurat, M.; Nogeire, T.; Molinari, N.; Richers, B.T.; Lin, B.B.; Simpson, N.; Mayfield, M.M.; DeClerck, F. Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* **2009**, *12*, 22–33. [[CrossRef](#)] [[PubMed](#)]
92. Delgado-Baquerizo, M.; Giaramida, L.; Reich, P.B.; Khachane, A.N.; Hamonts, K.; Edwards, C.; Lawton, L.A.; Singh, B.K. Lack of functional redundancy in the relationship between microbial diversity and ecosystem functioning. *J. Ecol.* **2016**, *104*, 936–946. [[CrossRef](#)]
93. Mori, A.S.; Isbell, F.; Fujii, S.; Makoto, K.; Matsuoka, S.; Osono, T. Low multifunctional redundancy of soil fungal diversity at multiple scales. *Ecol. Lett.* **2016**, *19*, 249–259. [[CrossRef](#)]
94. Louca, S.; Polz, M.F.; Mazel, F.; Albright, M.B.N.; Huber, J.A.; O'Connor, M.I.; Ackermann, M.; Hahn, A.S.; Srivastava, D.S.; Crowe, S.A.; et al. Function and functional redundancy in microbial systems. *Nat. Ecol. Evol.* **2018**, *2*, 936–943. [[CrossRef](#)]
95. Granados, V.; Gutiérrez-Cánovas, C.; Arias-Real, R.; Obrador, B.; Harjung, A.; Butturini, A. The interruption of longitudinal hydrological connectivity causes delayed responses in dissolved organic matter. *Sci. Total Environ.* **2020**, *713*, 136619. [[CrossRef](#)]
96. Li, Y.; Ge, Y.; Wang, J.; Shen, C.; Wang, J.; Liu, Y.-J. Functional redundancy and specific taxa modulate the contribution of prokaryotic diversity and composition to multifunctionality. *Mol. Ecol.* **2021**, *30*, 2915–2930. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.