FUNGAL ECOLOGY 17 (2015) 96–102

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Is diversity a buffer against environmental temperature fluctuations? – A decomposition experiment with aquatic fungi

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ARTICLE INFO

Article history:
Received 6 January 2015
Revision received 5 May 2015
Accepted 6 May 2015
Available online xxx
Corresponding editor:
Felix Bärlocher

Keywords:
Aquatic hyphomycetes
Environmental oscillations
Species richness
Streams

ABSTRACT

We tested if species-rich fungal assemblages are functionally more efficient in leaf decomposition under environmental fluctuations than species-poor assemblages. We manipulated temperature fluctuations in laboratory microcosms in which oak leaf discs were inoculated with monocultures of aquatic hyphomycetes or random mixtures of three or eight species and subjected to different temperature regimes, including three constant temperatures and temperature fluctuation regimes. Temperature regime and identity of fungal species inoculated in monoculture microcosms significantly affected decomposition rates: these increased with temperature, but across all temperature regimes species diversity promoted higher decomposition rate, although functional saturation seemed to occur above three species. In assemblages with at least eight species, litter decomposition was not inhibited by temperature fluctuating regime when compared with constant temperature conditions. Ecosystem function under environmental changes seems to benefit from the presence of multiple species.

Introduction

The study of biodiversity–ecosystem function (B–EF) relationship has been stimulated by the current rapid worldwide species loss and its potential effects on ecosystem services (Dudgeon et al., 2006; Rockström et al., 2009). Freshwater biotas are subjected to high anthropogenic extinction rates (Malmqvist and Rundle, 2002; Dudgeon et al., 2006; Rockström et al., 2009), emphasizing the importance of evaluating the relationships between diversity and function in these systems.

Forested low order streams rely on riparian leaf litter and are inhabited by diverse assemblages of aquatic hyphomycetes, which perform an important ecosystem function, the decomposition of leaf litter (Abelho, 2001; Gessner et al., 1999, 2007). Aquatic hyphomycetes can, therefore, be used as model organisms to investigate the relationships between structure (number and type of species) and function (litter decomposition). Some studies here suggested that high fungal

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http://dx.doi.org/10.1016/j.funeco.2015.05.013
1754-5048/

diversity increases the litter decomposition efficiency (Duarte et al., 2006; Costantini and Rossi, 2010; Pascoal et al., 2010), while others have shown no such relationship (*i.e.* Dang et al., 2005; Ferreira and Chauvet, 2012; Geraldes et al., 2012). These studies have typically been performed under constant conditions. However, actual streams experience natural fluctuations in current, temperature and/or availability of resources, which may profoundly affect the persistence and activity of individual species and their function in the ecosystem (Riedl et al., 2013; Martínez et al., 2015). In fact, the functional response of communities to abiotic factor fluctuations may be dependent on the proximity of the functional optimum of the consortium: species that periodically experience their ecological optima may fully play out their ecological function, whereas species exposed to suboptimal conditions may display more reduced performances (Ruel and Ayres, 1999). Oscillations of the environmental conditions may allow different species to experience their ecological optimum and function as "process-drivers", at distinct times and conditions.

Several hypotheses have been proposed to explain the response of an ecosystem to changes in biodiversity. The linear or diversity-stability hypothesis (MacArthur, 1955) postulates that the number of species and functioning of the ecosystem are linearly related, making rich ecosystems more stable and more resistant to perturbations and disturbances, while the Rivet hypothesis (Ehrlich and Ehrlich, 1981; Naeem et al., 2002) describes a positive, but nonlinear, biodiversity–ecosystem function (B–EF) relationship; in this case, species loss is predicted to have a slightly negative effect on ecosystem function until a critical point is reached, after which the system fails. The Redundancy hypothesis (Walker, 1992) assumes a positive but asymptotic B–EF relationship, with species losses being compensated by other functionally equivalent species. Finally, the Idiosyncratic hypothesis (Lawton, 1994) considers a non-monotonic relationship between richness and functioning, because impacts or losses of species are context-dependent (e.g. community composition, environmental conditions), which limits the prediction of the effects of the loss of any particular species (Cardinale et al., 2000; Naeem et al., 2002). Despite distinct explanations, all these hypotheses predict a positive B–EF relationship – species-poor communities are more unstable and susceptible to imbalances than the species-rich communities (Insurance hypothesis; Loreau et al., 2002; Yachi and Loreau, 1999). However, although changes in the composition of a community can be considered a form of instability, it may also constitute an important mechanism to promote the stability of the ecosystem under environmental variability (Lehman and Tilman, 2000; Hooper et al., 2005).

Water temperature is a prominent ecological condition affecting species metabolism and consequently the use of resources (Brown et al., 2004). The function–temperature relationship has been recently investigated in an attempt to predict the effects of global warming (e.g. Woodward et al., 2010a,b). Such studies have shown that increased temperatures (within the physiological limits) result in faster microbial decomposition rates (Ferreira and Chauvet, 2011a,b; Bergfur and Friberg, 2012; Geraldes et al., 2012) and changes in fungal assemblages composition (Bärlocher et al., 2008; Fernandes et al., 2009, 2012; Ferreira and Chauvet, 2011a). However, biodiversity–function experiments under constant temperature conditions could be far from realistic. As far as we know, only Dang et al. (2009) have investigated temperature oscillation, and concluded that this may increase litter decomposition rates when compared to constant temperature regimes.

Here we tested the hypothesis that species-rich fungal assemblages perform better at leaf decomposition than species poor ones under fluctuating temperature regimes. To test this hypothesis, we manipulated species richness of aquatic decomposers and measured leaf litter (*Quercus robur*) decomposition in sets of microcosms exposed to constant and to fluctuating temperatures.

Materials and methods

Microcosms and experimental setup

Leaf discs (9 mm diameter) were punched out from senescent oak (*Q. robur*) leaves with a cork borer. Discs were oven dried (105 °C, 24 hr) and individually pre-weighed (6.0–10.0 mg). Groups of ten leaf discs were placed in 100 ml Erlenmeyer flasks with 40 ml of distilled water and autoclaved (20 min, 121 °C). Two hundred and ninety four flask replicates were set up (294 × 10 = 2 940 disc). After autoclaving, leachates were removed and microcosms filled with 40 ml of nutrient solution (75.5 mg $CaCl_2$, 10 mg $MgSO_4.7H_2O$, 0.5 g 3-morpholino propanesulfonic acid (MOPS), 5.5 mg K_2HPO_4 and 100 mg KNO_3 per litre of sterile distilled water; Dang et al., 2005). Microcosms were allocated to three groups of 98 microcosms, closed with cotton bungs, and continuously aerated in orbital shakers for 24 hr at 5, 11 and 17 °C respectively, to allow additional leaching at different temperatures. After 24 hr four microcosms from each temperature were sacrificed to determine leaching mass loss. The mineral salt solution was replaced in the remaining microcosms, which were then inoculated with 5 000 conidia each (Treton et al., 2004) from mixed assemblages in equal proportions or single aquatic hyphomycete species (see below).

Thirteen fungal species were used in the experiments (Fig 1): *Tetrachaetum elegans* Ingold, *Heliscus lugdunensis*, *Tetracladium marchalianum*, *Clavariopsis aquatica*, *Articulospora tetracladia*, *Flagellospora curvula*, *Tricladium chaetocladium*, *F. curta*, *H. submersus*, *Varicosporium elodeae*, *T. splendens*, *Fontanospora fusiramosa* and *Anguillospora filiformis*. Microcosms were inoculated with: (1) single species (3 replicates × 13 species × 6 temperature regimes = 234), or (2) a random combination of three fungal species (species poor treatment; 4 replicates × 6 temperature regimes = 24); or (3) a random combination of eight species (species rich treatment; 4 replicates × 6 temperature regimes = 24). Within each species richness level, each replicate *per* temperature regime was inoculated with a different random fungal composition from the pool of fungal species. In total, four different assemblages were obtained for each fungal richness level.

Microcosms from the three diversity treatments (single species, 3-species and 8-species) were allocated to two treatments, (a) constant temperatures for 27 d and (b) fluctuating temperatures. The three constant temperatures were 5, 11 and 17 °C (Fig 1A). All microcosms were aerated on an orbital shaker (100 rpm) under photoperiod conditions (12 hr light/12 hr dark)

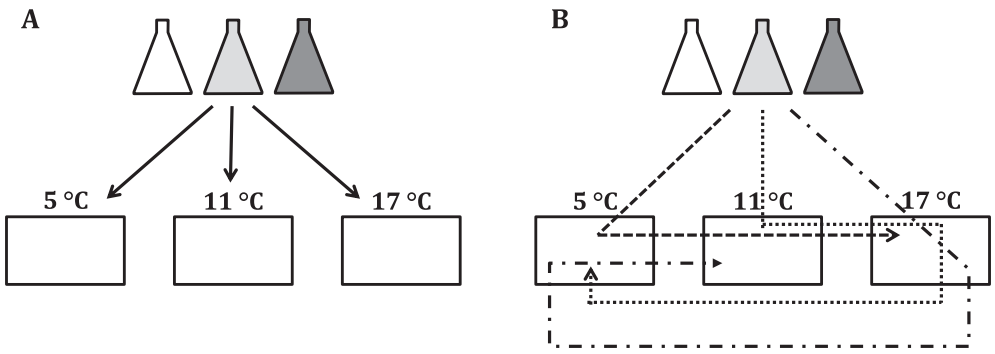

Fig 1 – Experimental design. Three diversity treatments (all single species – white, three species – light grey, eight species – dark grey) were submitted to (A) three constant temperatures or (B) to three variable temperature regimes (for simplicity, only three species treatment are indicated).

and the nutrient solution was replaced and discharged after 24 hr.

The fluctuating temperature treatments were arranged in three sets exposed for 9 d at each of the three temperatures (total 27 d). The sequence of temperatures varied across the three sets: 5 → 11 → 17 °C, 11 → 17 → 5 °C and 17 → 5 → 11 °C (Fig 1B). In fluctuating temperature treatments the average temperature was the same (11 °C).

In all cases the medium was renewed every 2 d. After 27 d the discs from each microcosm were oven-dried (105 °C for 48 hr) and weighed (±0.1 mg). Dry mass loss (% DM) was calculated as the difference between initial and final mass of each batch of discs.

Statistical analysis

Data satisfied assumptions of normality and homoscedasticity. Two-way Analysis of Variance (ANOVA) was performed to compare leaf mass loss among treatments, with fungal diversity and temperature regimes as categorical factors. When significant statistical differences were detected ($P < 0.05$), planned comparisons were used to identify the significant effects of one factor within the other; Tukey's HSD test was performed when necessary. Since mass loss in the three temperature sequences (5 → 11 → 17 °C, 11 → 17 → 5 °C and 17 → 5 → 11 °C) was not statistically different (two-way ANOVA, $F_{2,132} = 0.048$, $P = 0.954$), those treatments were pooled as "fluctuating treatment".

To evaluate direction and magnitude of treatment effects on leaf mass loss, effect sizes for fungal species number and temperature regimes were calculated based on the difference between each treatment mean and the grand mean (*i.e.* the mean of all treatments; according to Bärlocher and Corkum, 2003). The differences obtained were tested against the null hypothesis that the average difference equalled 0 by a t-test (Zar, 1999). All statistical analyses were performed using STATISTICA 7 software (StatSoft, Tulsa, Oklahoma).

Results

In single fungal species treatments, leaf mass loss was significantly affected by temperature (two-way ANOVA, $F_{2,77} = 25.880$, $P < 0.001$; Fig 2) and fungal identity (two-way ANOVA, $F_{12,77} = 52.330$, $P < 0.001$), but not by their interaction (two-way ANOVA, $F_{24,77} = 1.140$, $P = 0.322$). Although the thirteen aquatic hyphomycete species differed in their decomposition capabilities, in general, they exhibited a maximum activity at 11 °C and minimum at 5 °C. In a few species, such as *T. elegans*, decomposition increased linearly with increasing temperature.

Mass loss at constant temperatures varied between 32.3 % ± 0.8 % (mean ± SE) in monocultures permanently exposed to 5 °C and 43.1 % ± 0.9 % (species-rich assemblage) exposed to constant 11 °C. Leaf mass loss increased as a function of the number of fungal species across the three constant temperatures (two-way, $F_{2,131} = 8.086$, $P < 0.001$,

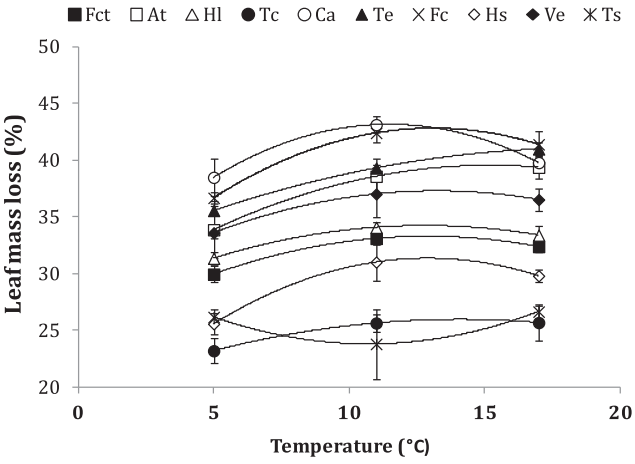

Fig 2 – Leaf mass loss of oak leaf discs in microcosms (means ± 1SE), incubated with single cultures of aquatic hyphomycetes species at three constant temperatures. Fct – *Flagellospora curta*, At – *Articulospora tetracladia*, Hl – *Heliscus lugdunensis*, Tc – *Tricladium chaetocladium*, Ca – *Clavariopsis aquatica*, Te – *Tetrachaetum elegans*, Fc – *Flagellospora curvula*, Hs – *Heliscus submersus*, Ve – *Varicosporium elodeae*, Ts – *Tricladium splendens*. The species Tm – *Tetracladium marchalianum*, Ff – *Fontanospora fusiramosa* and Af – *Anguillospora filiformis* also followed a quadratic pattern but were not plotted to avoid overlapping.

Tukey's test, P = 0.015; Fig 3), but no differences were detected among the two mixed species treatments. As with single fungal species treatments, in multiple species microcosms mass loss was significantly lower at 5 °C than at 11 and 17 °C (two-way ANOVA, $F_{2,131} = 4.267$, P = 0.016; Tukey's test, P < 0.006). No interaction between the main factors was observed (two-way ANOVA, $F_{4,131} = 0.409$, P = 0.802).

Mass loss was affected by species richness under fluctuating regimes of temperatures (two-way ANOVA, $F_{2,132} = 7.068$, P = 0.001). However, Tukey's test did not detect significant differences between treatments (Tukey's test, P > 0.088; data not shown).

The effect sizes of fungal species richness (t-test (23) < 1.183, P > 0.249; Fig 4B) and fluctuating treatment (t-test (23) = 1.324, P > 0.198) did not differ from 0. However, constant temperature regimes induced different deviations from the grand mean: the effect of the 5 °C temperature was negative on leaf decomposition (t-test (7) = −4.996, P = 0.002), while it was positive at 11 °C (t-test (7) = 2.530, P = 0.039; Fig 4A).

Decomposition in temperature fluctuation treatments was not significantly different from that observed at the constant temperature of 11 °C (two-way ANOVA, $F_{1,182} = 0.035$, P = 0.851; Fig 5). The interaction between factors was also not significant (two-way ANOVA, $F_{2,182} = 0.073$, P = 0.930). Leaf mass loss was higher in both mixed assemblages than in single microcosms (two-way ANOVA, $F_{2,182} = 7.946$, P < 0.001; Tukey's test, P < 0.049).

Discussion

Our results showed that the number of species was important for litter decomposition (within the range of tested numbers). Rich fungal assemblages are more efficient in decomposition of leaves than single species under constant thermal regime and when temperature fluctuates. However, the three and the eight species assemblage did not differ in their decomposition capabilities, possibly due to a high functional redundancy among fungal species. Despite the confirmed susceptibility of overall species richness treatments to temperature, mass loss was similar at constant temperature of 11 °C or under fluctuations.

Degradative differences among species

Aquatic hyphomycete species differed in their ability to decompose leaves. In agreement with previous results, *H. submersus* (Duarte et al., 2006; present study) caused low mass loss when compared with other species, and *A. tetracladia* caused comparatively high litter mass loss (Duarte et al., 2006). The functional response (*i.e.* leaf litter decomposition) to temperature by individual aquatic hyphomycetes was species-specific. This was not surprising as several previous laboratory studies indicate that aquatic hyphomycetes differ in their optimal growth and sporulation temperatures (Chauvet and Suberkropp, 1998; Rajashekhar and Kaveriappa, 2000) and in their ability to decompose leaves (Duarte et al., 2006; Fernandes et al., 2011).

As with individual species treatment, decomposition in multiple species treatments was sensitive to temperature, being lower at 5 °C than at 11 and 17 °C. Fernandes et al. (2012) also reported a stimulation of decomposition of oak leaves, previously colonized in a stream, by an increase from 16 °C to 24 °C after 21 d in microcosms. Our data on leaf decomposition capabilities of aquatic hyphomycetes and their relationship with temperature are, therefore, consistent with the literature. Effect size analyses indicate that lower constant temperatures (5 °C) tend to be responsible for the inhibition of activity of fungal assemblages, as opposed to the intermediate temperature (11 °C), which could stimulate the performance of the decomposers. Activity, growth and survival of freshwater organisms, fungi included, seem to be directly (e.g. metabolic rates, physiological stress) and/or indirectly (e.g. species interactions and distributions) affected by the water temperature (Friberg et al., 2009; Madigan et al., 2009; Woodward et al., 2010a,b; Bergfur and Friberg, 2012).

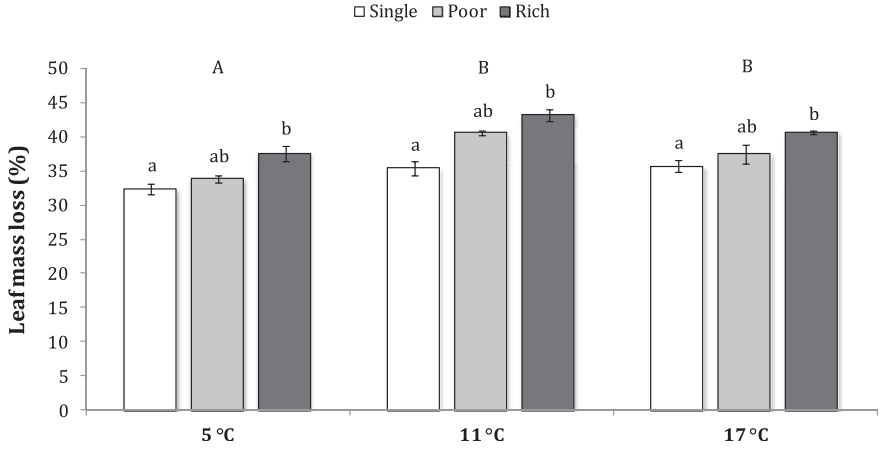

Fig 3 – Leaf mass loss of oak leaf discs in microcosms (means ± 1SE), incubated with three diversity treatments (monocultures – white, three species – light grey, eight species – dark grey) of aquatic hyphomycetes and three constant temperatures. Different letters indicate significant differences across pooled treatments (lowercase – richness; uppercase letters – temperature), because the interaction effect between the two main factors was not significant.

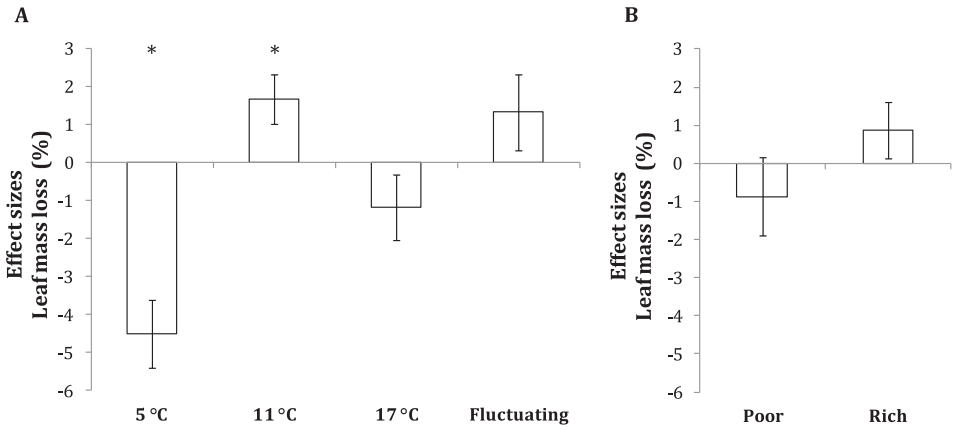

Fig 4 – Effect sizes of temperature regime (A) and fungal species richness (B) on leaf mass loss of mixed assemblages, expressed as the percentage of deviation between each treatment mean and the grand mean. Bars with (*) are significantly different when tested against the null hypothesis that the average difference equalled 0 by a t-test.

Fungal diversity effects on decomposition

Leaf decomposition tended to be higher in mixed assemblages in comparison to single species treatments at constant temperatures. This may suggest that the ecological function increases with diversity up to a certain richness level and then stabilizes. In our experiments this plateau was reached with eight species at constant temperatures but only three species under fluctuating conditions. This may suggest that tests performed under constant temperatures may overestimate the importance of species richness.

The absence of the effects of the number of species on decomposition observed between both mixed assemblages in all thermal regimes, corroborated by the absence of positive/negative effect sizes in both cases, implies considerable functional equivalency (redundancy, *sensu* Walker, 1992) among the tested aquatic hyphomycete species. Whether tolerant species compensate for the functional loss of sensitive species is unknown, as we did not measure fungal biomass, nor enzymatic activity. Several other authors reported no differences in litter decomposition across several species diversity combinations, including single-species treatments (e.g. Dang et al., 2005; Duarte et al., 2006), while some studies reported faster decomposition rates in multiple than single species microcosms (e.g. Bärlocher and Corkum, 2003; Pascoal et al., 2010; Fernandes et al., 2011; Geraldes et al., 2012). If our results can be extrapolated to stream conditions, it seems that diversity is important, but a lower number of species seems to be enough to achieve the maximum decomposition. However, we should consider that several abiotic factors, other than temperature, may oscillate and affect fungal diversity and performance. Indeed, in temperate streams several leaf species with distinct traits may be available affecting fungal richness and consequent microbial-mediated decomposition (e.g. Gessner et al., 1999, 2007; Lecerf et al., 2005; Lecerf and Chauvet, 2008). Finally, our approach only considered two trophic levels and in freshwater environments multiple levels of organization modulate the response to temperature (Perkins et al., 2010).

Consistently, in all previous studies assemblage composition (*i.e.* species identity) was a very important factor explaining litter decomposition. In these cases some species benefited at the expense of others, with species identity mitigating the potentially negative effect of low diversity. With our experimental design, we dissolved the importance of fungal species composition using random fungal assemblages (within the same richness level); this procedure may have limited the existence of complementary interactions among species (by niche differentiation or facilitation; Loreau and Hector, 2001), as the collective activity did not outperform the most active species.

Fluctuating temperature effects on decomposition

Having shown that species respond to changes in temperature, we tested the effect of temperature fluctuations on litter decomposition. If the insurance hypothesis applies, we expect function (*i.e.* decomposition) to remain relatively unchanged under fluctuating temperatures in multiple species treatments because of functional species replacements. Otherwise, function (decomposition) could decrease or increase with changes in temperature (favouring or inhibiting the whole assemblage in the case of equivalent functional traits). Our results were consistent with the insurance hypothesis: decomposition remained the same at the constant temperature of 11 °C or any of the tested fluctuations (with the same mean of 11 °C). This lack of differences contrasts with a previous study reporting higher decomposition rates of softer leaves with temperature oscillations (3 or 8 °C) in comparison with constant temperatures (Dang et al., 2009). The authors attributed the results to the relative importance of the identity of the dominant species. Although this explanation remains valid, the identity effect was greatly reduced in our case since all fungal assemblages varied in terms of species composition, and were randomly obtained from a pool of species.

Overall, our results suggest a functional saturation with a low number of species of aquatic hyphomycetes regarding biodiversity-temperature fluctuations. Our temperature oscillation results suggest that, if the temperature deviations are

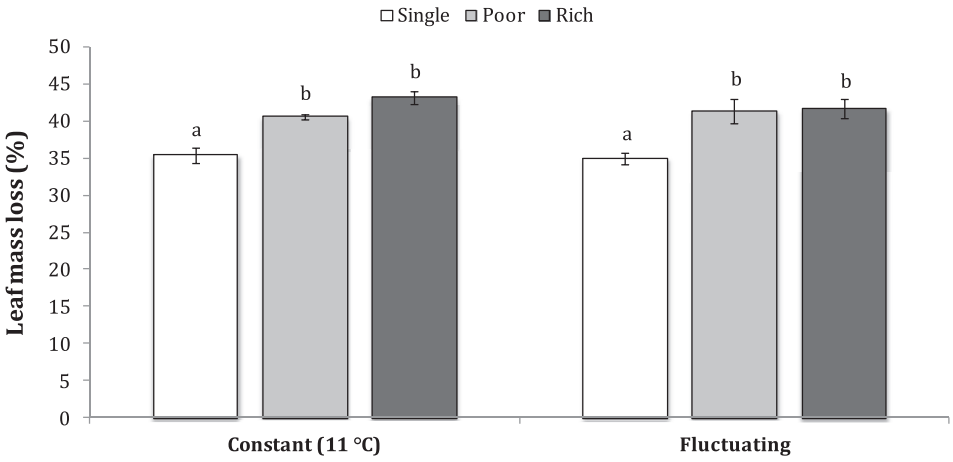

Fig 5 – Leaf mass loss of oak leaf discs in microcosms (means + 1SE), in three diversity treatments (average of all monocultures – white, three species – light grey, eight species – dark grey) of fungal species and incubated at (A) a constant temperature of 11 °C and (B) the pooled mean of all fluctuating temperature treatments. Different letters indicate significant differences, referring to pooled single, poor and rich replicates (lowercase letters) within each temperature regime. No significant differences were observed concerning the temperature regime and the interaction effect between the two main factors.

close to the species optimum, there may not be functional advantage of multispecies assemblages (>3 species). However, regarding the functional species redundancy and its plasticity, aquatic hyphomycetes respond to other fluctuating conditions in streams. We argue that oscillations in environmental parameters should be further investigated in experiments on diversity effects in stream ecosystems, particularly when considering global change, including warming, changes in hydrology, nutrient enrichment and/or riparian vegetation cover.

Declaration of authorship

All authors conceived and designed the experiments. ALG performed the experiments and wrote the first draft of the manuscript, and all authors collaborated on writing the final version.

Acknowledgements

We thank Ana Virgínia Lírio, Cátia Domingos and Inês Santos for the assistance in the lab experience. Financial support by the Portuguese Science and Technology Foundation (reference SFRH/BD/47089/2008; SFRH/BPD/94820/2013) to ALG is gratefully acknowledged. This study was supported by the European Regional Development Fund (ERDF) through the COMPETE – Operational Factors of Competitiveness Program (POFC-COMPETE) and national funds through FCT – Foundation for Science and Technology, under the projects: "Predicting the effect of global warming on stream ecosystems" (FCT Ref: PTDC/CLI/67180/2006; COMPETE Ref: FCOMP-01-0124-FEDER-007112) and "Effects of pollution on estuarine zooplankton-zooplanktivorous fish ecological interactions in relation to climate changes" (FCT Ref.: PTDC/AAC-AMB/110331/2009; COMPETE Ref: FCOMP-01-0124-FEDER-013876).

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