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

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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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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)