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Diversity patterns of leaf-associated aquatic hyphomycetes along a broad latitudinal gradient

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ABSTRACT

Information about the global distribution of aquatic hyphomycetes is scarce, despite the primary importance of these fungi in stream ecosystem functioning. In particular, the relationship between their diversity and latitude remains unclear, due to a lack of coordinated surveys across broad latitudinal ranges. This study is a first report on latitudinal patterns of aquatic hyphomycete diversity associated with native leaf-litter species in five streams located along a gradient extending from the subarctic to the tropics. Exposure of leaf litter in mesh bags of three different mesh sizes facilitated assessing the effects of including or excluding different size-classes of litter-consuming invertebrates. Aquatic hyphomycete evenness was notably constant across all sites, whereas species richness and diversity, expressed as the Hill number, reached a maximum at mid-latitudes (Mediterranean and temperate streams). These latitudinal patterns were consistent across litter species, despite a notable influence of litter identity on fungal communities at the local scale. As a result, the bell-shaped distribution of species richness and Hill diversity deviated markedly from the latitudinal patterns of most other groups of organisms. Differences in the body-size distribution of invertebrate communities colonizing the leaves had no effect on aquatic hyphomycete species richness, Hill diversity or evenness, but invertebrates could still influence fungal communities by depleting litter, an effect that was not captured by the design of our experiment.

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Introduction

Global species diversity patterns of many taxonomic groups exhibit maxima at low latitudes in both terrestrial and marine ecosystems (Pianka 1966; Rosenzweig 1995; Gaston 2000; Hillebrand 2004). Though the mechanisms underlying this pattern are still not fully understood, several mutually non-exclusive hypotheses have been proposed (Rohde 1992; Rosenzweig 1995; Colwell & Lees 2000; Allen *et al.* 2002). In fresh waters, a meta-analysis encompassing a broad range of taxonomic groups has revealed a weaker increase in animal diversity with decreasing latitude compared with terrestrial and marine environments (Hillebrand 2004). Overall, however, the distribution of diversity in fresh waters has received less attention than in other ecosystems, and the existing data show conflicting gradients (Vinson & Hawkins 1998; González-Bergonzoni *et al.* 2012; Boyero *et al.* 2012).

Furthermore, very few studies have focused on aquatic fungal diversity patterns at large spatial scales (Ho *et al.* 2001; Arnolds 2007; Raja *et al.* 2009). Based on a compilation of data extracted from the literature, Shearer *et al.* (2007) concluded that the species richness of aquatic hyphomycetes in streams appeared to exhibit maxima in temperate rather than tropical climates, and suggested that this pattern might be driven by more varied ecological niches in temperate climates, resulting from stronger seasonality than in the tropics. It remains unknown, however, to what extent the latitudinal pattern identified by Shearer *et al.* (2007) reflected a geographical bias in the collection effort, since sampling of fresh water fungi in temperate regions has been much more intense than elsewhere. Studies encompassing broad geographical ranges across latitudinal gradients are restricted to literature analyses (Wood-Eggenschwiler & Bärlocher 1985; Shearer *et al.* 2007), since broad-scale coordinated surveys using identical methods have not been conducted.

Aquatic hyphomycetes, or Ingoldian fungi, are one of the most prominent groups of fresh water fungi (Bärlocher 1992a). As major drivers of leaf-litter decomposition, they are of primary importance in the functioning of forested stream ecosystems (Gessner *et al.* 2007). Notably, their productivity can be extraordinarily high (Suberkropp *et al.* 2010), in some cases resulting in more than 15 % fungal biomass in decomposing leaf litter (Gessner & Chauvet 1994). In addition, aquatic hyphomycetes stimulate litter consumption by detritivorous macroinvertebrates through the enzymatic 'conditioning' of leaf tissues (Bärlocher & Kendrick 1975; Suberkropp 1992). In turn, the feeding activity of these invertebrates could structure aquatic hyphomycete communities (Suberkropp 1992). Leaf-consuming invertebrates in streams often exhibit pronounced feeding preferences for particular fungal species (Arsuffi & Suberkropp 1985), which vary across invertebrate taxa (Arsuffi & Suberkropp 1989) and potentially alter fungal community composition or the relative abundances of species in a community. Smaller invertebrates, including early instars of litter-consuming detritivore larvae (Chung & Suberkropp 2009), may rely even more strongly on fungal hyphae rather than leaf tissue, and thereby could influence fungal communities as well. However, there is little information overall about how the feeding activity of invertebrates may affect the structure and composition of leaf-associated fungal communities in streams (Bärlocher 1980; Howe & Suberkropp 1994; Chung & Suberkropp 2008).

In the present study, we investigated aquatic hyphomycete communities colonizing leaf litter deployed in five streams located along a broad latitudinal gradient ranging from the subarctic to the tropics. By using strictly standardized procedures across locations we aimed at elucidating whether aquatic hyphomycete diversity in decomposing leaves can peak at mid-latitudes, as reported by Shearer *et al.* (2007). We expected fungal communities to vary across and within streams according to litter quality. Within locations, we varied litter quality by selecting native litter species belonging to four plant litter functional types. Furthermore, by enclosing litter in bags with one of three different mesh sizes, we tested whether the effects of litter consumers depend on the presence and size-class distribution of detritivorous invertebrates. We expected effects of invertebrates on fungal communities to be stronger for high-quality litter because of more intensive feeding. The influence of small invertebrates was expected to depend less on litter quality, because their feeding is likely to be mostly restricted to the litter surface. Exclusion of invertebrates by small mesh sizes also allowed us to assess interactions with latitude, as expected due to the scarcity of large detritivores in the tropics (Irons *et al.* 1994; Boyero *et al.* 2011, 2012).

Materials and methods

Study sites and litter functional types

We examined aquatic hyphomycete communities associated with native litter from five different forested low-order streams located across a 62° latitudinal range (Table 1): subarctic (Kopparåsen, Sweden), boreal (Krycklan, Sweden), temperate (Mosbeek, The Netherlands), Mediterranean (Maureillas, France), and tropical (Petit Saut, French Guyana). Stream characteristics are summarized in Table 1. To reflect locally available resource supply, four native litter species were selected in each location to represent four litter functional types: evergreen, nitrogen fixer, fast-decomposing deciduous and slow-decomposing deciduous (Table 2), which enabled comparisons of native plant litter species exhibiting similar sets of litter traits across sites (Fig S1; Table S1). In addition, we used *Ailanthus altissima* as a standard litter species at all sites. *A. altissima* is not native in any of the locations, and thus enabled comparison of fungal communities unconfounded by differences in litter quality across sites. Litter was collected shortly after natural abscission and was air-dried prior to the experiment. An exception was *Ilex aquifolium* litter, which was obtained by cutting branches in the field and simulating senescence in the laboratory for 3 weeks. Litter was collected during periods of most intense natural leaf abscission, which was normally in fall 2006, except for the tropical site (winter 2006) and *Quercus ilex* (summer 2007).

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