



## Diverse fungal lineages in subtropical ponds are altered by sediment-bound copper

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### ABSTRACT

Ponds represent a black box for fungal ecology. Compared to terrestrial environments, the fungal ecology of aquatic environments is rarely studied, and the few published studies have tended to be of lotic habitats in the northern hemisphere. We explored fungal communities and their responses to a gradient of copper in five year old artificial, replicated ponds in Australia. Ponds were subject to natural variations in temperature, precipitation and biotic colonisation. To explore the fungal communities, we amplified the ITS1 region of rDNA from samples of the water column, the sediment and cellulose baits (analogues to leaf fall) alone and in the presence of a gradient of copper. Fungal amplicon data revealed almost 800 fungal species from these habitats within the ponds. Interestingly, no chytrids from the Cladochytriales and Rhizophlyctidales were detected on cellulose baits, instead, putatively novel zoosporic taxa in the Chytridiomycota and the Rozellomycota were observed. Given the keystone role zoosporic fungi are thought to play in aquatic food webs, along with their role as primary decomposers of plant material, improved knowledge of their diversity and distribution is vital for understanding ecosystem function in standing water habitats. In aquatic environments copper tends to be bound to sediment and is not especially mobile in the water phase. The presence of copper in our sediment samples was correlated with repeatable and profound shifts in the fungal community, with chytrid species appearing to be the most sensitive, suggesting that they may be useful indicator organisms. Indirect effects of copper on fungal communities living on leaf analogues and in the water column were also explored.

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## 1. Introduction

Fungi support ecosystem processes in terrestrial habitats worldwide, playing key roles in nutrient translocation and carbon cycling (Boddy and Watkinson, 1995). They translocate nutrients, sometimes over many metres, through the formation of extensive hyphal networks (Boddy, 1993). Translocation has been demonstrated in various fungi engaging in diverse life strategies, including plant-associated fungi, both pathogenic and mutualistic, and saprotrophic fungi (Bolan, 1991; Cairney, 1992; Wells and Boddy, 1995). These hyphal networks allow a fungus to colonise and exploit multiple niches, for example, multiple plant hosts and/or aggregates of organic matter (Simard et al., 1997; Hättenschwiler et al., 2005). By colonising diverse sources of carbon, nitrogen and

phosphorous, fungi are able to overcome heterogeneous nutrient availability in the environment (Hättenschwiler et al., 2005; Tiunov, 2009; Gessner et al., 2010). Fungi also play a key role in carbon cycling through saprotrophic activities, producing a suite of hydrolases capable of decomposing recalcitrant organic material, and acting as the primary decomposers of moribund plant material in terrestrial settings (reviewed in Kirk and Farrell, 1987; Martínez et al., 2005).

While extensive fungal literature concerns soils, few studies have investigated freshwater systems (Lategan et al., 2012; Bärlocher and Boddy, 2016). Although freshwater environments account for less than 1% of the Earth's surface, they are disproportionately important in terms of their contribution to the overall environment (Dudgeon et al., 2006). Freshwater fungi are important components of communities in the water column and sediments of both lentic and lotic systems. For example, mycorrhizal and mycorrhizal-like associations between fungi and aquatic plants

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have been observed (reviewed in Xu (Xu et al., 2016)) and include arbuscular mycorrhiza and dark septate endophytes. Saprotrophic fungi remain the dominant decomposers of leaf litter in freshwater streams and lakes (Komínková et al., 2000; Gulis and Suberkroop, 2003; Hieber and Gessner, 2002).

Ascomyceteous fungi are typically abundant in all aquatic environments. For example, a review of largely culture-dependent surveys in 2007 reported that ascomycetes accounted for ~50% of all species identified from freshwater, brackish and marine environments (Shearer et al., 2007). Subsequent molecular surveys of these environments support these findings, however, numerous basidiomycetes have been detected that were mostly absent from culture-based surveys (Panzer et al., 2015). These aquatic basidiomycetes predominately belonged to clades of yeasts, and were not the more common hyphal taxa that frequently colonise terrestrial environments (Panzer et al., 2015). In terrestrial settings, hyphal basidiomycetes are primary decomposers of lignin (e.g. white and brown rot fungi) (Kirk and Farrell, 1987; Martínez et al., 2005) and their absence in aquatic environments corresponds with comparatively slower decomposition rates for lignified material in these systems (Bucher et al., 2004; Bärlocher and Boddy, 2016). Indeed, in aquatic ecosystems less-efficient soft rot ascomycetes may play the primary role in lignin degradation (Savory, 1954; Bucher et al., 2004; Simonis et al., 2008). Such findings suggest that changes in fungal assemblages affect important ecological processes.

Aquatic fungal communities differ markedly from their terrestrial counterparts in the elevated representation of zoospore fungal lineages; namely Chytridiomycota, Blastocladiomycota and Rozellomycota (Shearer et al., 2007; Panzer et al., 2015; Grossart et al., 2016). These groups are particularly prevalent in the water column of freshwater ecosystems, with molecular techniques identifying them as the most dominant taxonomic grouping in fungal assemblages (Panzer et al., 2015). In sediments, these basal fungal lineages are of approximately equal abundance to Ascomycota and Basidiomycota (Panzer et al., 2015). Traditionally, saprotrophic chytrids have been recovered from aquatic systems by baiting (Sparrow, 1960), often with cellulosic materials such as filter paper or onion skin (Haskins, 1946; Dogma, 1969). Along with saprotrophic activities, however, Chytridiomycota, Blastocladiomycota and Rozellomycota also engage in varied lifestyles, including parasitism of other fungi and phytoplankton (reviewed in Gleason et al., 2008; Grossart et al., 2016). In their role as phytoplankton parasites, these basal fungal groups have been implicated as keystone taxa in aquatic food webs (Kagami et al., 2014; Grossart et al., 2016).

Copper is a trace metal and essential micronutrient, however, at elevated concentrations it can be toxic to life. Both naturally occurring and anthropogenically derived copper enrichments have been reported for numerous aquatic settings. For example, Kendrick (1962) measured copper concentrations of up to 68,000 mg kg<sup>-1</sup> occurred naturally in swamp sediments while concentrations of 7,650 mg kg<sup>-1</sup> have been reported for mine-impacted lake sediments (Kendrick, 1962; Flemming and Trevors, 1989). While copper originating from anthropogenic sources is often introduced to sediments via the water column, this is typically transitory and elevated concentrations in the water column do not persist, instead, copper has a high affinity for organic carbon and thus readily binds to sediment particulates (reviewed in Gardham et al., 2014a). This phenomenon causes copper to be less bioavailable and hence, less toxic to aquatic organisms (Gardham et al., 2014a).

Many fungal species are especially sensitive to copper, with copper being a major constituent of antifungal compounds used in the prevention of plant infections by fungal pathogens and in the preservation of wood (Freeman and McIntyre, 2008; Kanhed et al., 2014). The mechanism for copper toxicity in fungi primarily involves disruption of the cell membrane, as well as the inhibition of

enzymes (reviewed in Baldrian, 2003). A number of extracellular enzymes produced by fungi to catabolise plant-derived polymers, for example cellulase,  $\beta$ -glucosidase and pectin hydrolase, are inhibited by copper (Baldrian, 2003; Lebrun et al., 2010). Additionally, field surveys of soils containing ~120 mg kg<sup>-1</sup> copper, along with other metals, identified a significant decrease in the activity of many of these enzymes (Kuperman and Carreiro, 1997). Contrasting with this, the ligninolytic enzyme, laccase, uses copper as a cofactor and is upregulated by fungal cultures exposed to 200–25,000 mg L<sup>-1</sup> of copper (Collins and Dobson, 1997; Baldrian, 2003; Lebrun et al., 2010).

At the community level, few researchers have investigated the effect of copper on fungal assemblages. Numerous studies, however, have examined the copper sensitivity of individual taxa in axenic culture. For example, *Penicillium* spp. have been isolated from multiple copper-enriched soils and grown in media containing >1,000 mg kg<sup>-1</sup> copper (Stoke and Lindsay, 1979; Yamamoto et al., 1985; Arnebrant et al., 1987). Additionally, the entomopathogenic fungi *Isaria farinosa* and *Beauveria bassiana* from the Hypocreales, along with multiple species of *Verticillium*, were isolated from a brass mill site with copper concentrations of 3,000–6,000 mg kg<sup>-1</sup>, and could be grown on media containing >1,000 mg L<sup>-1</sup> copper (Arnebrant et al., 1987). Conversely, substantial growth inhibition has been observed for saprotrophic basidiomycetes (*Agaricus bisporus*, *Stropharia* spp. and *Mycena galericulata*) and ascomycetes (*Sordaria* sp., *Pyrenophora* sp. and *Chaetomium* sp.) in media containing just 100 mg kg<sup>-1</sup> of Cu, suggesting that these taxa may be particularly sensitive to copper (Hartikainen et al., 2012). A handful of studies have also reported the sensitivity of species within the saprotrophic zygomycete genus, *Mortierella* (Arnebrant et al., 1987; Hartikainen et al., 2012), with multiple isolates being sensitive to copper concentrations of <60 mg L<sup>-1</sup> (Arnebrant et al., 1987).

The current study used high throughput, amplicon sequencing, to survey fungal communities in outdoor freshwater mesocosm ponds, with varying copper concentrations. Such high throughput sequencing surveys have revolutionised our understanding of fungal communities, providing researchers with an ability to sample complex environmental communities at exceptional sampling depth, and without culture bias (reviewed in Lindahl et al., 2013). The Illumina MiSeq platform has an advantage over earlier sequencing technologies (i.e. Sanger sequencing and Roche 454 pyrosequencing), due to its cheaper sequencing costs and greater sequencing depth (Schmidt et al., 2013; Smith and Peay, 2014; Tedersoo et al., 2015). One draw-back of this method, however, is the shorter read lengths provided by this technology (~250 bases). In contrast to earlier molecular surveys which sequenced the entire 18S rRNA gene or ITS region (including ITS1, 5.8S rRNA and ITS2), surveys with the MiSeq platform sequence only the ITS1 or ITS2 region (Lindahl et al., 2013; Tedersoo et al., 2015). While studies have found the ITS1 and ITS2 regions sequenced using the MiSeq platform are sufficient for capturing the biodiversity of fungal communities in environmental samples (Nilsson et al., 2009; Schmidt et al., 2013; Smith and Peay, 2014), taxonomic resolution from these shorter reads is poorer.

The aims of the present study were to: (1) develop an understanding of cellulolytic and sediment fungal communities in freshwater ponds and (2) to understand the effects of copper on these communities.

## 2. Methods

### 2.1. Ponds

Mesocosms (ponds) were established by Gardham et al. (2014a)

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