FUNGAL ECOLOGY 19 (2016) 5–13

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/funeco

Commentary

Aquatic fungal ecology – How does it differ from terrestrial?

Introduction

Saline and brackish water accounts for 97.5% of total water and covers approx. 71% of the planet's surface (Shiklomanov 1993). Of the land surface, 1.8% is covered by lakes, and less than one-thousandth by rivers and streams (Hynes, 1970; Allan and Castillo, 2007). Despite the overwhelming preponderance of saline waters, estimated fungal diversity is lower in saline than in freshwater habitats (Shearer et al., 2007), though Jones (2011) argues that the estimated number of (obligate) marine fungal species of 537 is a gross underestimate.

Based on literature reports, Shearer et al. (2007) placed the combined fungal biodiversity in freshwater, brackish and marine habitats at approx. 3000 species. A more recent estimate puts it between 3069 and 4145 (including 49–87 Oomycota; Jones et al., 2014b). This is a small proportion of the total number (97,730) of described fungal species (Kirk et al., 2008). Until the 1970s, aquatic mycologists concentrated on zoosporic fungi and fungal-like organisms. These were assumed to be associated primarily with phytoplankton and pollen (Wurzbacher et al., 2010), though more recent studies have documented their occurrence on decaying plant detritus (Nikolcheva and Bärlocher, 2004; Das et al., 2007; Seena et al., 2008; Bärlocher et al., 2012; Duarte et al., 2015). Nevertheless, the nearly complete absence of planktonic organisms and scarcity of pollen has probably deterred many experts on Chytridiomycetes and other zoosporic fungi from working in streams. Chytridiomycota and Ascomycota (including mitosporic taxa) comprise most of the documented aquatic fungal diversity. Within the Ascomycota are roughly 300 aquatic hyphomycete species (Shearer et al., 2007), corresponding to 3.3% of all described hyphomycetes (Kirk et al., 2008). So far, 183 species of Trichomycetes have been reported from aquatic environments (Jones et al., 2014b; Lichtwardt, 2014). Very few Basidiomycota are aquatic.

Clearly, aquatic habitats have low fungal biodiversity compared to terrestrial habitats. This is in contrast with other organisms, for example, with insects where freshwaters are home to 6% of all insect species despite only covering only 1% of the earth's surface (Dijkstra et al., 2014). Not surprisingly, there are *Entomophthora* species that have adapted to parasitizing aquatic insects and which form tetraradiate propagules resembling the spores of aquatic hyphomycetes (Webster et al., 1978; Descals et al., 1981), though they have been little studied. If the diversity of fungi associated with aquatic insects parallels that of their terrestrial counterparts (Vega and Blackwell, 2005) then estimates of fungal diversity in freshwaters will be greater. Moreover, the extent of aquatic (and terrestrial) fungal biodiversity may need to be revisited in the light of recent molecular approaches, which have greatly increased the discovery of uncultured taxa from deep sea hydrothermal vents (Le Calvez et al., 2009) and marine sediments (Nagano and Nagahama, 2012; Nagano et al., 2010) Bass and Richards (2011) emphasize that current bases for estimating total fungal diversity are too incomplete to allow reliable estimates. Based on environmental rDNA sequences, Cryptomycota – an early diverging branch discovered in a freshwater pond – show diversity similar to that of the currently sampled fungal kingdom (Jones, 2011). Nonetheless, based on current knowledge, fungal diversity on land seems much greater than in aquatic ecosystems.

Not surprisingly, terrestrial fungi have been researched more intensively by more scientists than aquatic fungi. This is reflected, for example, by the topics of articles in the journal *Fungal Ecology*. In its first 10 volumes, 229 out of 275 articles dealt with terrestrial mycology (mycorrhiza, endophytes, soil and wood fungi, pathogens, etc.), 17 with zoosporic fungi and 22 with fungi in freshwater and marine habitats (commentaries and special issues of the journal were not counted). This presumably reflects financial support for these research areas. It is, therefore, not surprising that terrestrial fungal ecology often provides better examples of what can be and what has been achieved with molecular approaches.

This commentary explores how differences between aquatic and terrestrial habitats may account for differences in fungal diversity and decomposition processes (Table 1).

Abiotic and biotic differences between aquatic and terrestrial ecosystems

What are the basic differences between terrestrial and aquatic (in particular freshwater) habitats, and to what extent do they

Table 1 – Selected factors affecting fungal diversity and activities in aquatic and terrestrial ecosystems. Most statements on aquatic habitats refer to running waters and aquatic hyphomycetes.

	Aquatic	Terrestrial	Example references
Fungi			
Diversity: described species	<4000	100,000	Shearer et al., 2007; Kirk et al., 2008; Le Calvez et al., 2009; Bass and Richards 2011; Jones 2011; Jones et al., 2014b
Major taxa	Ascomycota, including aquatic hyphomycetes; Chytridiomycota and other zoosporic fungi; Trichomycetes; Oomycoata and fungus-like organisms;	Ascomycota, Basidiomycota, Glomeromycota, Zygomycota	Jones et al., 2014b; Lichtwardt 2014 Gulis et al., 2005 Duarte et al., 2015
Biomass	Streams: Mycelia in leaf substrata: average 40–60 mg g^{-1} detrital mass; maxima up to 249 mg g^{-1}. Production per area: 160–1930 kg ha yr^{-1}. >50% of production may be invested in conidia, which can reach 30,000 l^{-1} in autumn	Forests: Sporocarps: up to 3000 kg ha^{-1} yr^{-1}. Mycelia in litter: 0.66–6.24 mg g^{-1}. Mycelia in soil: 0.22–0.67 mg g^{-1}. Production by ectomycorrhizal fungi: Average – 205 kg ha^{-1} yr^{-1} Maximum – 1000 kg ha^{-1} yr^{-1}	Vogt et al., 1992; Gessner et al., 2007; Krebs et al., 2008 Bärlocher 2009; Suberkropp et al., 2010; Baldrian et al., 2013; Ekblad et al., 2013; Gulis et al., 2015
Spatial and temporal spread	Conidia: tens (summer) to 10,000s (autumn) l^{-1} water; sexual spores, mycelia in leaves and invertebrate faeces	Conidia, chlamydospores, sexual spores, sclerotia, mycelium, aggregated mycelium	Dix and Webster 1995; Bärlocher 1981, 2009;
Enzymic ability	Most species have modest to moderate activity against cellulose, hemicelluloses, pectin. Generally weak activity against lignin	Taken together the fungi can decompose all plant, animal and microbial compounds; ligninolysis is limited to a range of basidiomycetes and xylariacious ascomycetes	Suberkropp and Klug 1980; Chamier 1985; Zemek et al., 1985; Baldrian et al., 2012; Floudas et al., 2012
Abiotic drivers of diversity, abundance and activity			Cudowski et al., 2015
Temperature	Optima generally between 15 and 25 °C Some species occur in sulphur spring, but diversity very limited at 35 °C	Majority have optima between 20 and 25 °C, but psychrophilic and psychrotolerant species are common in arctic, Antarctic and alpine environments. Thermophilic and thermotolerant species occur in self-heating systems, e.g. compost, and even in temperate soils as well as tropical ones.	Boddy 1984; Dix and Webster 1995; Chandrashekar et al., 1991 Chauvet and Suberkropp 1998; Krauss et al., 2011
Water availability	Droughts or prolonged exposure to air lower activity and diversity of aquatic fungi	Most basidiomycetes cease growth below −4 MPa, but many other fungi can grow down to −10 MPa. High water content inhibits growth and decomposition.	Webster 1977; Boddy 1984, 1986; Chauvet et al., 2016
Oxygen and carbon dioxide	Hypoxic conditions lower diversity and activity	High water content inhibits decomposition due to elevated CO_2 and limited O_2; O_2 is essential for ligninolysis.Species have different tolerances, e.g. litter decaying basidiomycetes are less tolerant than wood decayers to high CO_2 and low O_2.	Boddy 1984; Field and Webster 1985; Medeiros et al., 2009
pH, electrolytes	Pristine streams: greatest diversity between 5 and 7; anthropogenically acidified streams: diversity declines (often due increased metal ions concentrations); decomposition rates (but not fungal biomass) decline at acid pH	pH varies considerably on a microspatial scale. Most prefer acidic conditions, and often lower the pH themselves. Most basidiomycetes do not tolerate pH much above 7, though most other taxa have a wide pH tolerance.	Bärlocher 1987; Dix and Webster 1995; Cornut et al., 2012; Dangles and Chauvet 2003;