FUNGAL ECOLOGY 19 (2016) 14–27

available at www.sciencedirect.com
ScienceDirect
journal homepage: www.elsevier.com/locate/funeco

Aquatic hyphomycetes in a changing environment

F. BÄRLOCHER*

Department of Biology, Mt. Allison University, Sackville, NB E4L 1G7, Canada

A R T I C L E I N F O

Article history:
Received 6 March 2015
Revision received 12 May 2015
Accepted 12 May 2015
Available online 29 July 2015
Corresponding editor:
Lynne Boddy

Keywords:
Aquatic hyphomycetes
Big data
Bioinformatics
Fungal diversity
Molecular ecology

A B S T R A C T

In 1942, Ingold documented an ecologically defined group of fungi, aquatic hyphomycetes, on autumn-shed leaves decaying in streams. They were shown to be vital intermediaries between the nutritionally poor leaf substratum and leaf-eating invertebrates. Research has subsequently emphasized functional aspects such as leaf decomposition and nutritional conditioning by fungi. Structural aspects (community composition) have attracted less attention, partly because of the difficulties of identifying fungal mycelia *in situ*. Extraction, amplification (PCR, qPCR) and characterization of DNA and RNA, and, more recently, of proteins, allow much greater insights into the presence of fungal taxa, their metabolic status (dead, dormant or active), and their potential and actual participation in decomposition processes. This approach can yield huge amounts of data, and major challenges today are the development and application of suitable bioinformatics techniques. The complexity of data collection and evaluation favour interdisciplinary teams of researchers. Fungi are major players in most ecosystems and are increasingly affected by human impacts. Changing land use, eutrophication/pollution and climate change are among the major factors that affect diversity and ecological functions of aquatic hyphomycetes.

Introduction

Aquatic hyphomycetes (or freshwater fungi, amphibious fungi, Ingoldian fungi) are an ecologically defined, polyphyletic group of true fungi. Even though some species had previously been reported, the decisive breakthrough was Ingold's (1942) observation that these fungi occur most commonly and most abundantly on deciduous leaves decaying in running waters. They are also found on wood if placed in a bubble chamber (e.g., Hyde *et al.* 2016; Tsui & Hyde 2003). Traditionally, the taxonomy of aquatic hyphomycetes has been based on the morphology and development of their mitospores or conidia. Conidia are predominantly multiradiate (often tetraradiate) or sigmoid, suggesting convergent evolution due to a common advantageous trait, which has been identified as their propensity to become attached to smooth substrata such as leaves in running water (Webster 1959, 1987; Dang *et al.* 2007; Kearns & Bärlocher 2008). This morphological convergence can make spore shapes unreliable proxies for phylogenetic relationships, which had to be unraveled by comparing rarely observed sexual states, or, more recently, by evaluating DNA sequences. Such studies have demonstrated that the majority of aquatic hyphomycetes belong to the Ascomycota, with the remaining belonging to the Basidiomycota. When using spore morphology as a criterion, many species appear to be globally distributed; one recent study using molecular markers distinguished several haplotypes with restricted distributions (Duarte *et al.* 2012, 2016).

---

* Tel.: +1 506 364 3501; fax: +1 506 364 2505.
E-mail address: fbaerlocher@mta.ca

http://dx.doi.org/10.1016/j.funeco.2015.05.005

Limnologists largely ignored aquatic hyphomycetes until they recognized the often dominant contribution of allochthonous organic materials (leaves, needles, twigs and branches of terrestrial plants) to food webs of low-order streams (Hynes 1975). Palatability and nutritional quality of this detritus are improved by fungal colonization (Kaushik & Hynes 1971). Bärlocher & Kendrick (1974) and Suberkropp & Klug (1976) showed that aquatic hyphomycetes are the dominant fungal colonizers. These observations have stimulated considerable research on various aspects of aquatic fungal biology, particularly regarding their involvement in decomposition and food webs. Much of this research has concentrated on process-oriented aspects (degradative enzymes, decomposition rates, fungal biomass, fungal productivity). The recognition that ecological processes are influenced by species richness and/or identity has renewed interest in fungal taxonomy and potential connections between biodiversity and ecological functions. Ongoing climate change and other anthropogenic impacts have stimulated research on the occurrence and ecology of aquatic hyphomycetes in extreme habitats and in little explored ecoregions (e.g., subtropics and tropics). Table 1 lists major reviews of some of these topics.

Progress in fungal ecology has long been hampered by the difficulty of identifying species and measuring their activities *in situ*. Microscopic observations for the most part revealed sterile (non-reproductive) mycelia that could not be identified. They were, therefore, complemented by attempts to isolate pure cultures (e.g., by plate counts) and inducing them to reproduce. The long-standing dilemma has been characterized by Garrett (as quoted by Warcup 1967) as follows: “With the plate count one identifies what one cannot see (i.e. *in situ*), whereas with the direct method one sees what one cannot identify”. A partial solution was inducing sporulation on the substratum by exposing it to turbulence in an aqueous environment, which demonstrated the presence of viable fungal structures capable of reproduction (Bärlocher 1982). However, this approach overlooks non-reproductive but metabolically active mycelia.

A major breakthrough has been the development and application of molecular methods, allowing the identification and characterization of species based on analysing DNA from fungal cultures and from detrital substrata (Bärlocher 2010). This approach was initially applied to aquatic hyphomycetes to study genetic variation in species (Peláez *et al.* 1996; Charcosset & Gardes 1999). The first comparison of conventional (microscopy and culture based) and molecular methods (based on extraction and characterization of DNA) for detecting aquatic fungi was published by Nikolcheva *et al.* (2003).

Molecular and other modern techniques have profoundly affected the research environment in microbial and fungal ecology (Andrew *et al.* 2013; Barberán *et al.* 2012, Cuadros-Orellana *et al.* 2013; Joly *et al.* 2014; for methodological reviews, see Hause & Hause 2015; Schaumlöffel 2015). There is an increasing trend toward larger studies involving scientists from several disciplines. The potential for generating enormous amounts of data is starting to influence the type of questions we ask and the interpretation of our results.

As in most fields of biology, research in fungal ecology is becoming more responsive to problems associated with anthropogenic change. Many of these topics are a simple extension of existing themes, e.g., physiological or ecological responses to temperature or hydrological regimes. Others present entirely new challenges (e.g., nanoparticles, xenobiotics).

The impact of molecular methods

Shearer *et al.* (2007) estimated fungal biodiversity in freshwater, brackish and marine habitats based on literature reports. They arrived at approx. 3 000 species. A recent estimate puts it between 3 069 and 4 145 (includes 49–87 Oomycota; Jones *et al.* 2014). This is a small proportion of 97 730, the total number of described species as of 2008 (Kirk *et al.* 2008). The greatest number of aquatic fungi belong to the Ascomycota (including asexual taxa) and Chytridiomycota, and very few to the Basidiomycota. Included with the Ascomycota are roughly 300 aquatic hyphomycete species (Shearer *et al.* 2007). This corresponds to 3.3 % of all described hyphomycetes (Kirk *et al.* 2008). Clearly, aquatic habitats have low fungal biodiversity compared to terrestrial habitats (Bärlocher and Boddy 2016). 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. I will therefore often rely on insights from these areas as well as from marine microbiology to discuss potential avenues of future research.

When studying decomposition in aquatic ecosystems, the emphasis has often been on rates and processes, reminiscent of “empirical limnology” (Rigler 1982; Peters 1991). This approach seeks relationships by regression models, and argues that many phenomena studied by ecologists are conceptually obscure and inherently unpredictable from first principles. As pointed out before (Bärlocher 2010), this dispenses with the widely accepted statement “Nothing in biology makes sense except in the light of evolution” by Dobzhansky (1973), who wrote: “Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts some of them interesting or curious but making no meaningful picture as a whole”.

To what extent have molecular techniques contributed to a deeper understanding of evolution and ecology, beyond the mere accumulation of “sundry facts”? According to Johnson *et al.* (2009), their impact has been decisive in phylogenetic analyses and biogeography, while they have contributed little to explaining community patterns (but see Schneider *et al.* 2012a, b; Peay 2014; Alvarez *et al.* 2015). Thus far, they have played a negligible role in approaching the central questions that May (1999) expected to guide the ecological research agenda in the 21st century. May be ecologists have been slow to adapt molecular tools, or, conventional approaches were adequate, at least when dealing with macroorganisms (Johnson *et al.* 2009). Johnson *et al.* (2009), Pauls *et al.* (2014), and Peršoh (2015) list several broad topics providing opportunities for exploiting the vast potential of meta-genomic approaches. Sutherland *et al.* (2013) identified 100 fundamental ecological questions. Molecular techniques are mentioned specifically in the context of micro-organisms and disease; microbial