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ECOSYSTEMS

Studies on aquatic fungi in Dikarya: a review of the literature from Southern Cone of South America

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Abstract: A bibliographic analysis was carried out to update the state of knowledge about aquatic fungi belonging to the subkingdom Dikarya in the Southern Cone of South America. The exhaustive search resulted in 38 articles reported. These papers correspond to those on taxonomic, ecological and biogeographic topics and include studies from lotic environments of the temperate ecoregions of Chile and Argentina. A total of 325 aquatic fungal taxa were reported, of which 318 belong to the phylum Ascomycota and 7 to the phylum Basidiomycota. According to the subgroups of these aquatic fungi 17 taxa were aero-aquatic, 199 facultative and 109 Ingoldian fungi. Regarding the methodologies, in these studies the information was obtained mainly by using lignocellulosic substrates such as leaf litter and wood as fungal source and wet chamber traditional working technique. However, more studies are still needed using other few-reported perspectives for the region such as ecological and molecular approaches as well as analyses of water environments belonging to unexplored biomes. This information can contribute to a better understanding of aquatic fungal communities and their role in ecosystems of the Southern Cone of South America.

Key words: Biogeography, freshwater environments, fungal source, hyphomycetes, Ingoldian fungi.

INTRODUCTION

Aquatic fungi are a group of organisms whose life cycle takes place completely or partly on aquatic habitats (Grossart et al. 2019). They participate in different ecological processes and are key elements in the decomposition of organic material, both autochthonous and allochthonous (Goh & Hyde 1996, Romaní et al. 2009). Phylogenetically, these fungi are represented by different phyla, mainly the Ascomycota (Webster 1992). From an ecological and morphological perspective, they are classified into three categories: Ingoldian (also called aquatic hyphomycetes), aero-aquatic (Beverwijk 1951) and facultative (Shearer et al. 2007, Goh & Hyde 1996, Tsui et al. 2016); each group being characterized mainly by the morphology of its spores (a feature that has a close relationship with the environments where they live) and type of sporulation (Tsui et al. 2016).

Several studies indicate that the main factors that modulate fungal diversity in aquatic ecosystems are temperature, turbidity, nutrient concentration, quality of organic matter, spore production, and competition with other fungi in freshwater environments (Bärlocher et al. 2011, Graca et al. 2016, Shearer et al. 2007, Kominoski et al. 2015).

Recent estimations report more than 3,000 species of aquatic fungi worldwide, taking into account the main fungal groups such as the

phyla Ascomycota, Blastocladiomycota and Chytridiomycota (Shearer et al. 2007, Abdel-Aziz 2008, Tsui et al. 2016). However, when the richness of asexual aquatic taxa belonging to the sub-kingdom Dikarya (phyla Ascomycota and Basidiomycota), frequently found in freshwater environments, is quantified, about 335 correspond to Ingoldian forms (Duarte et al. 2016), 90 to aero-aquatic and 405 to facultative ones (Shearer et al. 2007). Specifically, current data show that up to 128 of the Ingoldian fungal species have been recognized in South America (Schoenlein-Crusius & Grandi 2003, Fiuza et al. 2017).

According to Duarte et al. (2016) the greatest diversity of Ingoldian fungi has been reported for temperate regions. Considering that temperate climate prevails in the Southern Cone of South America, it is important to have an updated review of the reported taxa. This area of the American continent, which extends from the Tropic of Capricornio to Cabo de Hornos (including Argentina, Chile and Uruguay) is potentially favourable to host an important diversity of aquatic fungi, exhibiting a variety of biomes and landscapes. In addition, hydrologically, it a wide range of freshwater habitats, rivers of different orders, lakes, lagoons, peatlands, among other wetlands.

The aim of this review was to explore through information from different bibliographic sources:

I. Biogeographic distribution of taxa in the Southern Cone of South America.

II. Habitats where they were found.

III. Methodology used for their study.

IV. Substrates used.

Despite that reviews on aquatic fungi have been carried out in South America, with emphasis on data from Brazil (Schoenlein-Crusius & Grandi 2003, Fiuza et al. 2017), the aim of this study was to obtain a current state of knowledge on aquatic fungi in the Southern Cone of South America, which is still little explored in aquatic mycology, to have fundamental information and, therefore, to project future studies that can contribute to expand existing information.

MATERIALS AND METHODS

The search for journal articles dealing with aquatic fungi reported from the Southern Cone of South America was carried out using "Google scholar" (https://scholar.google.com), "Scopus" (https://www.scopus.com), "Scielo" (https://scielo.org/es),"Science direct" (https://www.sciencedirect.com/), and "Dimensions" (https://app.dimensions.ai/) from December 2019 to January 2020. Each database was screened using key words such as "fungi", "freshwater", "Ingoldian", "hyphomycetes", "aquatic", "South America" or a combination of these. The bibliographic analysis was carried out taking into account the following information: taxonomic, ecological and biogeographic features, methodologies used for their study, as well as the type of substrate and the aquatic environment where the fungi were found. Nomenclature of fungi was validated through the Mycobank website (http://www.mycobank.org) and for some taxa following recent publications (Johnston et al. 2019, Anderson & Marvanová 2020, Johnston & Baschien 2020).

RESULTS AND DISCUSSION

Out of the 38 articles reported, studies about taxonomical features (76 %), followed by those of ecological analysis, which have been considered to be only of local relevance, were found from the database consulted (Supplementary Material-Table SI). The first published paper was carried out in 1970 analyzing freshwater fungi from Chile (Lindquist 1970), eight years after

the first report for South America by Nilsson 1962 on Venezuela. The largest amount of data about freshwater fungi from the Southern Cone of South America were between the 1980s and 1990s, with information corresponding to Argentina and Chile. (Figure 1.)

Regarding the distribution of references, we have observed that there are only reports from five bio-geographic provinces (Figure 2), of the 20 ones recognized in the Southern Cone of South America, of which Pampa and Bosques Valdivianos have 49% and 24%, respectively. Considering that both ecoregions correspond to temperate climate, this information is in agreement with that of the Northern Hemisphere (Europe and east of United States), where the research of these fungi is greater compared to tropical areas (Jabiol et al. 2013, Duarte et al. 2016). On the other hand, the analysis of environments in which the studies were conducted reveals that lotic habitats have been more explored (76%) than lentic ones, which have also been less explored worldwide (Descals & Moralejo 2001, Wurzbacher et al. 2010).

Analyzing the fungal richness, a total of 325 taxa were reported, being *Aegerita candida* Pers., *Fibulotaeniella* sp., *Papiliotrema laurentii* (Kuff.) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout, *P. pseudoalba* (Nakase & M. Suzuki) Xin Zhan Liu, F.Y. Bai, M.Groenew. & Boekhout, *Rhodotorula mucilaginosa* (A. Jörg.) F.C. Harrison, *Tausonia pullulans* (Lindner) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout and *Tricladiomyces geniculatus* Nawawi & Kuthub. the only

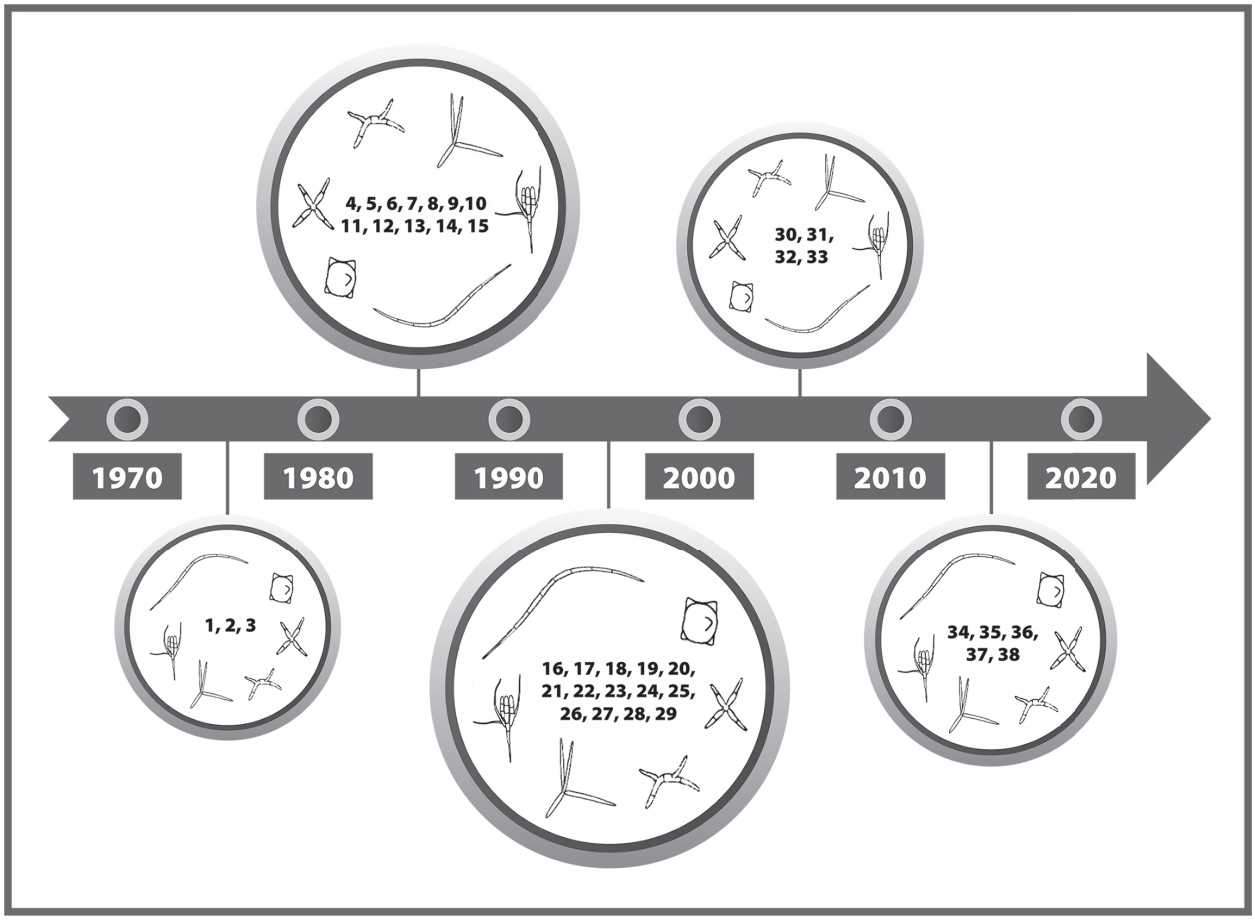

Figure 1. Timeline of studies published in each decade on the Southern Cone of South America (Table SI).

representatives of the Basidiomycota and the others belonged to the Ascomycota (Table SII). Only *Alatospora acuminata* Ingold, *Tetracladium marchalianum* De Wild., and *T. setigerum* (Grove) Ingold were reported in all provinces analyzed (Table SII).

Alatospora acuminata was also reported in Duarte et al. (2016) biogeographic studies in all the regions analyzed worldwide. Of the total species reported for the Southern Cone of South America, 199 corresponded to facultative, followed by 109 Ingoldian and only 17 to aero-aquatic fungi. These Ingoldian fungi represent 32 % of the known species worldwide. This suggests the need of more studies on this aquatic fungal group, since it is known that they play a key role in litter decomposition (Gessner & Chauvet 1994, Graça & Ferreira 1995, Gulis & Suberkropp 2003) and as pollution bioindicators in freshwater ecosystems (Solé et al. 2008, Dubey 2016, Tarda et al. 2019). In addition, molecular studies have shown that Ingoldian fungi are

Figure 2. Map of the Southern Cone of South America (shaded area), showing the biogeographic provinces (Morrone 2001) where studies on aquatic fungi (stars) were recorded. Additionally, the taxa reported in each provinces biogeographic were indicated in Table SII.

dominant representatives of the mycobiota associated with leaf litter decomposition in streams (Nikolcheva & Bärlocher 2004).

The substrates mostly used as fungal source from freshwater environments of the Southern Cone of South America were leaf litter (31 %) and woody substrates (24 %, Figure 3a). The main technique used for detecting fungi was the wet chamber (44 %, Figure 3b). Also different methodological strategies have been employed such as those using leaf litter as source of incubations in chambers assisted with aeration (Chan et al. 2000) or by shaking (Bärlocher et al. 2005), while the incubation on solid support under wet chamber, when wood is the inoculum source, is mostly used (Tsui et al. 2000). The aeration condition in water incubations facilitates mainly the recovery of Ingoldian fungi, while the wet chamber technique does so for obtaining mostly facultative fungi (Roldán et al. 1989). Therefore, the methodology conditions the composition of the fungal assemblage obtained from a specific substrate (Sridhar et al. 2010). Consequently, the dominance of facultative aquatic fungi reported in these studies for freshwater environments of the Southern Cone of South America could be due to technical limitations of the methodology applied for the detection of other categories of aquatic fungi. This is outstanding in articles from the Pampa province, where facultative fungi reached 139 taxa while Ingoldian and aero-aquatic ones, were 32 and 9, respectively.

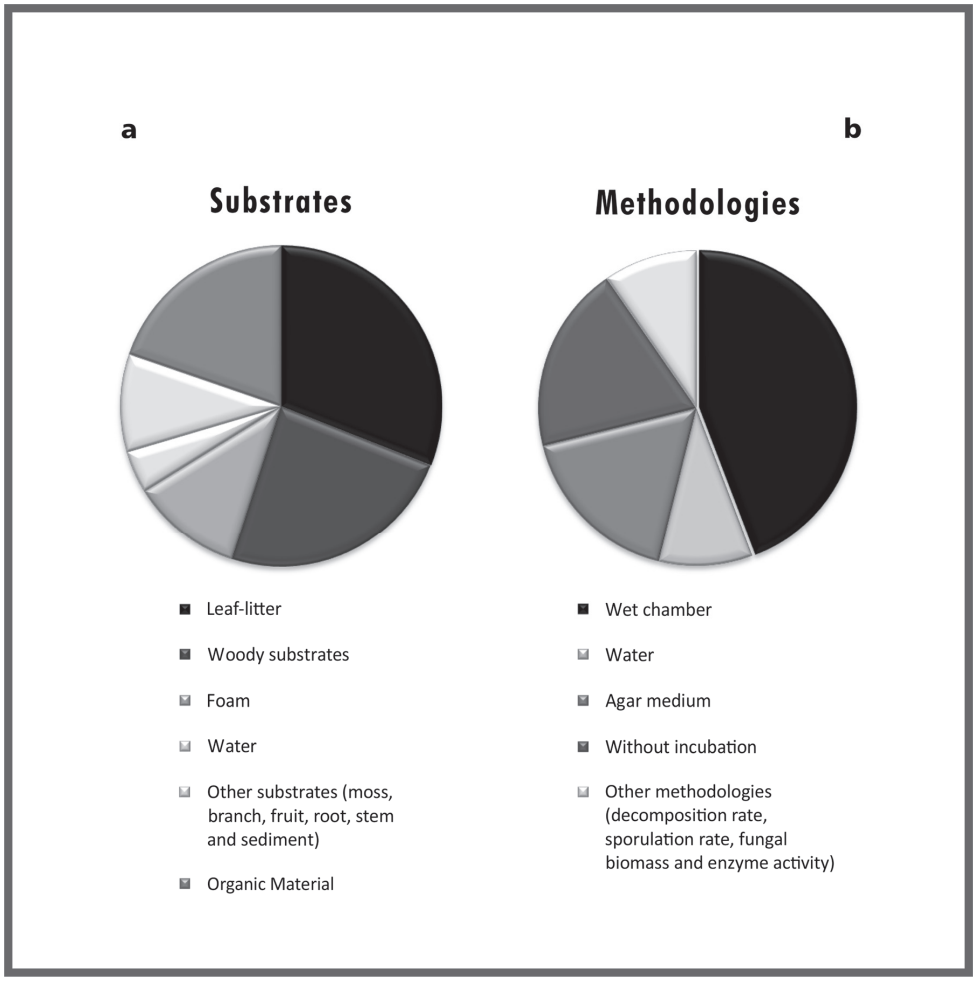

Figure 3. Percentage of substrates (a) and methodologies (b) reported in each publication.

The procedures used in all the studies of the Southern Cone of South America are traditional ones based on culture and morphology; only a recent article used molecular approach (Seena et al. 2019). Therefore, it is imperative that future studies on aquatic fungi from the Southern Cone of South America include methodologies that apply technological advances such as non-culturing techniques and bioinformatic tools as such metagenomic studies. This will contribute to overcome the limitations found by most of the classical mycologists when characterizing the fungal assemblages involved in aquatic environments such as those reported by Panzer et al. (2015) and Valderrama et al. (2016). Lepère et al. (2019) reported that still today there are also several limitations in the molecular studies about aquatic fungi since there are not specific molecular markers or well-represented reference databases, which prevent the exploration of the metabolic capacities of aquatic fungi through metagenomic and metatranscriptomic studies and their accurate taxonomic identification.

CONCLUSION

Since the data available about aquatic fungi from freshwater ecosystems reported for the Southern Cone of South America correspond mostly to taxonomical articles, more studies using innovative perspectives such as ecological and molecular ones are still necessary. Therefore, the availability of isolates of these fungi in axenic culture and their housing in culture collections such as in the Instituto Spegazzini (LPSC, Argentina), Facultad de Ciencias Exactas y Naturales, at the University of Buenos Aires (BAFCcult, Argentina), Westerdijk Fungal Biodiversity Institute (CBS, Netherland) or American Type Culture Collection (ATCC, United States of America), where they can be well preserved and used as reference, should be a high priority to decipher the structure and ecology of communities of fungi associated to freshwater ecosystems from the Southern Cone of South America (The cultures were indicated in the Table SII). Finally, our study highlights the need to increase the sampling effort at a regional scale by conducting as many surveys in the most diverse sets of aquatic ecosystems as possible, by exploring different habitats, as well as increasing the resolution of the fungal diversity by performing temporal surveys at the scale of some particular ecosystems. Moreover, it is necessary to emphasize the studies in lentic environments, which have been less explored in the Southern Cone of America so far.

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SUPPLEMENTARY MATERIAL

Tables SI-SII

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AST, MCNS and NG wrote the manuscript; AST conducted the data analysis and prepared the figures; all authors contributed to the interpretation of the results, critically revised the manuscript, and approved the final version.