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Diversity and biogeographical patterns of yeast communities in Antarctic, Patagonian and tropical lakes

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A B S T R A C T

We investigated the distribution patterns of yeast communities in freshwater lakes along a latitudinal gradient in order to evaluate yeast biogeography at intercontinental (501–8000 km), regional (0–500 km) and local (0–1 km) geographical scales. We identified 285 yeast isolates belonging to 64 species based on sequence analysis of the ITS-5.8S region and the D1/D2 domains of the large subunit of rRNA genes. Distance decay analysis showed a significant negative slope curve at the intercontinental scale. At the intercontinental and regional scales, the dissimilarity of the yeast communities was correlated with geographical distance, with community similarity decreasing with increasing distance. The physiological profiles of the yeast communities from tropical and Patagonian lakes were similar but were different from those of Antarctic lakes. This is the first report of latitudinal patterns of lake yeast diversity along a gradient extending from Antarctic to tropical environments.

1. Introduction

Biogeography is the study of organisms' distribution patterns in geographical space, both in contemporary terms and in the context of their evolution and development over time, and the processes determining the distribution of biodiversity (Meadows, 2004; O'Malley et al., 2007). A central goal of biogeography is to understand the mechanisms that generate and maintain diversity, such as dispersal, speciation, extinction and species interactions (Martiny et al., 2006). Distance decay analysis assumes that the similarity of communities decreases as the distance between them increases (Nekola and White, 1999) and is used to demonstrate how selection, drift, dispersal and mutation shape biogeographical patterns (Hanson et al., 2012). The distance decay relationship can be influenced by environmental conditions and/or dispersal limitations (Anderson et al., 2006; Martiny et al., 2011).

Micro-organisms are diverse and abundant, and have been regarded by some as cosmopolitan because they exhibit short generation times, large population sizes and long distance dispersal (Fenchel and Finlay, 2004). Molecular taxonomy, which allows the accurate identification of microbial species, has revealed that micro-organisms exhibit unique biogeographical distribution patterns. Previous biogeographical studies have described the variability and composition of communities of bacteria and yeasts in soil and plants (Taylor et al., 2006; Vishniac, 2006; Maksimova et al., 2009; Kachalkin and Yurkov, 2012; Yurkov et al., 2015, 2016), bacterioplankton in lakes, and microfungi associated with palm, fungal endophytes and other organisms (Taylor et al., 2000; Vaz et al., 2014; Hyde et al., 2016). These studies show that the distribution of a microbial species can be influenced by geographical distance, historical factors (geology, evolution and island biogeography), time since niche colonization and/or environmental factors, depending on the scale analysed.

Some studies have attempted to determine yeast distribution patterns. Yeasts form part of the microbiota of most, if not all, natural ecosystems and can be cosmopolitan or endemic to specific

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habitats or regions (Starmer and Lachance, 2011; Lachance et al., 2016). Environmental conditions, such as temperature, pH, light and concentration of readily available nutrients are some of the ecological factors that determine the metabolic activity, growth, survival and biodiversity of yeasts (Libkind et al., 2009; Yurkov et al., 2015). Yurkov et al. (2015) reported that at the community level, geographical region and type of substrate (phylloplane *vs.* soil) determine yeast species distribution in birch forests in Russia. Nagahama (2006) reported yeast distribution in nine deep-sea environments in the Pacific Ocean and found that *Rhodotorula sphaerocarpa* (=*Rhodosporidium sphaerocarpum*), *Cyberlindnera saturnus* (=*Williopsis saturnus*) and *Candida pseudolambica* (*Pichia* clade), were isolated from all deep-sea sites, while other species, such as *Kluyveromyces nonfermentans*, occurred only at some sites. Several yeast species associated with plants and insects have geographical distributions that mirror their host's distribution (Starmer and Lachance, 2011; Lachance et al., 2016).

Surveys of the geographical distribution of aquatic yeast species are sparse, with most being focused on the influence of water pollution (Nagahama, 2006). Few species of yeast appear to be specifically associated with aquatic habitats. *Debaryomyces hansenii* is the most common ascomycetous yeast isolated from marine waters. This yeast is considered to be a ubiquitous species because it is found in different environments and regions. Other ubiquitous species frequently associated with aquatic habitats such as *Aureobasidium pullulans*, *Rhodotorula mucilaginosa* and *Vishniacozyma victoriae* (= *Cryptococcus victoriae*) are also found in different regions and environments (de García et al., 2007; Brandão et al., 2011; Vaz et al., 2011; Yurkov et al., 2015). Some species are endemic to specific regions: for example, *Metschnikowia australis* is associated with algae, marine invertebrates and seawater in Antarctica (Lachance, 2011; Godinho et al., 2013), suggesting that the ecological distribution of aquatic yeast communities could be influenced by geographical patterns and the local conditions of each environment.

In the present study, we investigated the spatial distribution of cultivable yeasts on a geographical transect from polar to tropical lakes. This gradient included lakes in Antarctica, southern Argentina and southeastern and northern Brazil. We explored whether environmental and/or geographical distances explained yeast community composition at three different geographical scales (intercontinental, regional and local) and between different lakes.

2. Material and methods

2.1. Characteristics of the lakes and sampling sites

2.1.1. Antarctic lakes

Water samples were collected from five different lakes in the Antarctic Specially Managed Area (ASMA) in Admiralty Bay, King George Island, South Shetland Islands (Table 1), during the austral summer season between December 2008 and January 2009. The five lakes sampled in the ASMA represent different environmental conditions: Agat Point and Wanda Lakes are influenced by marine water and Machu Picchu, Stanhouse and Refuge II Lakes are subjected to long periods of ice and snow-cover in the winter. Water temperature and pH were measured *in situ* using an YSI 650 multiparameter display system (YSI Environmental, USA). Three water samples (500 mL) were collected in sterile bottles from five sites spaced approximately 50 m apart and were transported on ice to the laboratory within 24 h of sampling for processing.

2.1.2. Patagonian lake

Steffen Lake is located in Argentinian Patagonia in the Nahuel Huapi National Park (Table 1). It has an area of 6.3 km^2 and an average depth of 76.8 m. The lake is of glacial origin, is oligotrophic, has a high transparency (Secchi disk: 13 m), and has limited human influence. A native Andean Patagonian forest composed of *Nothofagus* spp. surrounds the lake. Mean annual surface water temperature is *c.* 17 °C (Quirós, 1988). Three water samples (300–400 mL) were collected in sterile bottles from four sites located approximately 200 m apart on a transect along the lake. The samples were transported on ice to the laboratory within 24 h for processing. Water temperature was measured *in situ* and pH was measured in the laboratory with a 3310 Jenway pH meter (Staffordshire, UK).

2.1.3. Tropical Brazilian lakes

Samples were obtained from three tropical lakes in Brazil (Table 1). Dom Helvecio Lake is located in the Ecological State Park of Rio Doce, which comprises an area of 36,113 ha and constitutes the largest relict area of Atlantic rain forest in Minas Gerais state. The lake has a surface area of 6.87 km^2 and is considered to be the largest and deepest lake of the middle Rio Doce lake system. It is one of the deepest natural lakes in Brazil, with an average depth of 32.5 m. The lake is oligotrophic, warm, monomictic and has one circulation period, usually between May and August (Matsumura-Tundisi and Tundisi, 1995). Three water samples (100 mL) were collected in sterile bottles from six sites located approximately 100 m apart on a transect along the lake. Samples were transported to the laboratory on ice within 24 h for processing. Temperature was measured *in situ* and pH was measured in the laboratory with a HI 211 combined meter (Hanna instruments, Rhode Island, USA). Rico and de Dentro Lakes are located in Cantão State Park (9°10′S, 50°10′W), a protected area located in the west of the Tocantins state, which represents an ecotone area among the Cerrado, Amazon forest and Pantanal ecosystems (Santos and Lolis, 2007). A dense Amazonian forest surrounds the lakes and, in the rainy season (October–April), the whole plain is flooded as the water level rises by 7–10 m (Pinheiro and Dornas, 2009). The presence of

Table 1
Description of study sites and diversity indexes of yeasts included in the present study.

Environment	Lakes	Geographical coordinates	Total yeast counts (CFU L^{-1})[a]	Temperature (°C)[b]	Mean pH	Number of isolates	Number of yeast species	Number of singletons	Shannon index (H′)
Tropical Brazil	Lago Rico	9° 21′S, 50°00′ W	721.6 ± 918.0	23.5	6.9	50	19	6	2.60
	Lago de Dentro	9°21′ S, 49°58′ W	373.3 ± 426.2	23.0	7.1	56	19	6	2.38
	Dom Helvécio	19°29′ S, 19° 48′ W	774.1 ± 590.2	24.4	6.2	52	17	3	2.57
Patagonian, Argentina	Steffen	41°31′ S, 71°33′ W	52.2 ± 35.5	17.0	7.0	51	17	5	2.43
Antarctic	Stanhouse	62°04′S, 58°22′ W	53 ± 25.1	0.2	9.1	16	5	1	1.94
	Refúgio II	62°04′ S, 58°25′ W	5.6 ± 2.85	4.2	8.5	14		1	1.99
	Wanda	62°04′ S, 58°19′ W	37.71 ± 9.0	1.8	7.4	8	3	–	1.77
	Machu Picchu	62°05′S, 58°19′ W	20.8 ± 17.9	0.7	7.1	22	8	1	2.07
	Agat Point	62°11′ S, 58° 26′ W	73.5 ± 58.4	2.8	7.5	15	4	–	1.76

[a] Mean ± standard deviation.
[b] Temperature values are point measurements.