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ORIGINAL PAPER

Endophytic symbiont yeasts associated with the Antarctic angiosperms *Deschampsia antarctica* and *Colobanthus quitensis*

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Abstract Fungal diversity in Antarctic seems to be greater than what is known and remains largely unexplored. In this study, we identified the endophytic symbiont yeasts associated with leaves of the angiosperms *Deschampsia antarctica* and *Colobanthus quitensis* living on King George Island, Antarctica using a culture-based approach. One hundred and twelve yeast isolates were obtained from the tissue of the different plants sampled. These yeasts were identified using sequencing of the D1/D2 domains of the LSU region of the rRNA gene as *Cryptococcus victoriae*, *Cystobasidium laryngis*, *Rhodotorula mucilaginosa*, *Sporidiobolus ruineniae* and *Leucosporidium* aff. *golubevii*. The psychrophilic yeast *C. victoriae* was the most abundant species associated with the two angiosperms. *Cystobasidium laryngis* occurs only in the leaves of *D. antarctica*. In contrast, *R. mucilaginosa*, *S. ruineniae* and *L.* aff. *golubevii* occurred only in *C. quitensis*. Phylogenetic analysis indicates the Antarctic endophytic yeast strains are closely related to taxa obtained from substrates located in different habitats of the world. However, the endophytic yeast *C. victoriae* was closely related to psychrophilic taxa isolated from Antarctica, but also from the Arctic, Alpine and Himalayan environments. The abundance of endophytic yeasts associated with Antarctic angiosperms suggests a possible symbiotic relationship with their plant hosts, which may provide shelter and growing conditions suitable for the yeasts' survival, dispersal and colonization other Antarctic environments. In contrast, the endophytic yeasts might directly or indirectly promote the fitness of their host plants by producing metabolites beneficial to plant survival in the extreme environments of Antarctica.

Keywords Antarctica · Endophytes · Extremophile · Symbiosis

Introduction

Antarctica is a relatively pristine region of planet Earth. The fungal presence and diversity of some Antarctic ecosystems have been investigated. However, fungal occurrence and diversity in Antarctic may be greater than what is known, mainly because the environments and substrates of continental and oceanic Antarctica remain largely unexplored. The diversity of the fungal communities in Antarctica varies with the studied substrate, examples of which have included samples of soils, rocks, freshwater, plants, macroalgae, permafrost, rocks, ice and historic wood (Ruisi et al. 2007). As symbionts of Antarctic plants, plant-associated fungi have previously been recovered from mosses (Bradner et al. 2000; Tosi et al. 2002; Zhang et al. 2013), as well as two vascular plants native to Antarctica: *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) (Rosa et al. 2009, 2010; Uspon et al. 2009).

Endophytic fungi, which live asymptomatically in plant tissues, have been obtained from every major plant lineage in the world, and these microorganisms represent an important part of the global mycobiome diversity. The majority of described endophytic fungi are filamentous fungi of the phylum Ascomycota, although some species are members of the phyla Basidiomycota and Zygomycota (Huang et al. 2001). According to Isaeva et al. (2010),

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yeasts are common epiphytic fungi that inhabit the surfaces of various plant parts, including leaves, flowers and fruits. However, reports of yeasts as endophytes are scarce when compared with the reports of filamentous fungi. Nassar et al. (2005), Gai et al. (2009), Xin et al. (2009), Khan et al. (2012) Solis et al. (2015) and Zhang and Yao (2015) reported endophytic yeasts associated with plants from different parts of the world, including those present in the Arctic ecosystem. Endophytic fungal communities have been reported as important symbionts for their host plants; however, their biological significance in polar ecosystems remains poorly characterized.

The plant diversity in Antarctica is restricted to several species of mosses and two angiosperms. *D. antarctica* (Antarctic hair grass), a monocot, and *C. quitensis* (Antarctic pearlwort), a dicot, are the only two plants able to grow in the Antarctic ecosystem that extends from the maritime Antarctic (Lewis-Smith and Poncet 1987). According to Fowbert and Smith (1994), Smith (1994), Grobe et al. (1997) and Convey (2003), the populations of *D. antarctica* and *C. quitensis* have been growing in the Argentine Island archipelago and in the western Antarctic Peninsula in recent years, which may be considered a response to the increasing summer air temperatures and local snow recession, possibly caused by global climate changes. For this reason, these Antarctic angiosperms represent interesting models to study the dispersal of their associated microbiome communities. Additionally, studies of the biology of fungal communities present in Antarctic environments are very important because they may clarify the ecological roles of the fungal species and other organisms, the complexity, evolution and speciation of the fungal webs under extreme conditions, as well as the influence of climate change on the Antarctic biota (Santiago et al. 2015). These two angiosperms have been investigated for filamentous fungal endophytes in their leaves (Rosa et al. 2009, 2010) and roots (Uspon et al. 2009), but the present study represents the first focused work on the endophytic yeasts associated with these species.

Materials and methods

Host plants and isolation of the endophytic yeasts

The study area is located at Admiralty Bay, King George Island, one of the South Shetland Islands, Antarctica. Leaves of *D. antarctica* and *C. quitensis* were sampled from six different sites (Botany Point, Ullman Point, Brazilian Refuge II, Macchu Picchu Station, Hennequin Point and Demay Point) forming a 25.5-km transect through Admiralty Bay (Fig. 1). The collection was performed during the austral summer in January and February of 2008. Healthy leaves were cut into pieces and stored in plastic bags at 10 °C for no more than 24 h before isolation of the endophytes. Five leaf fragments 1 cm in length were dipped in 70 % ethanol (1 min) and 2 % sodium hypochlorite (3 min), followed by one wash with sterile distilled water (2 min) (Rosa et al. 2009). The fragments were plated on Petri plates containing potato dextrose agar (PDA; Difco, USA) supplemented with chloramphenicol (100 μg mL^{-1}). The plates were incubated at 15 °C for up to 60 days, and individual colonies were transferred to the PDA and stored at 4 °C. Yeasts were stored in cryotubes with 15 % sterilized glycerol at −80 °C for the long-term preservation and later deposited in the Culture Collection of Microorganisms and Cells at the Universidade Federal de Minas Gerais under UFMGCB codes.

Yeasts identification

The yeasts were grouped and identified according to protocols established by Kurtzmam et al. (2011). Yeast molecular identities were confirmed by sequencing the D1/D2 variable domains of the large-subunit rRNA gene using the primers NL1 and NL4 as described by Lachance et al. (1999). Yeast isolates with query coverage and identity ≥99 % were considered to represent the same taxon. To sequence the purified PCR products of all endophytic yeast, we used the BigDye reaction kit (Applied Biosystems, USA). Sequencing was performed using an ABI 3730 (Life Technologies, USA) automated sequencing system in the Fundação Oswaldo Cruz (FIOCRUZ, MS), Brazil. The consensus sequences (forward/reverse) of all yeasts were obtained and compared with those included in the GenBank database using the Basic Local Alignment Search Tool (BLAST at http://www.ncbi.nlm.nih.gov). Alignments were performed using MUSCLE (Edgar 2004). Representative consensus sequences of fungal taxa were deposited into GenBank (Table 1). To achieve species-rank identification based on the D1/D2 variable domain, the consensus sequence (four different sequences) was aligned with the nearest (≥99 % of query cover and ≥98 % of identity) sequences of type species retrieved from the NCBI GenBank database using BLAST (Altschul et al. 1997). The followed criteria were used to interpret the sequences from the GenBank database: For query coverage and sequence identities ≥99 %, the genus and species were accepted; for sequence identities showing ≤98 %, the genus and species were accepted, but the term 'aff.' (species affinis = species related to) was used to indicate that the specimen resembles the reference species, yet has certain minor features not found in the reference. The

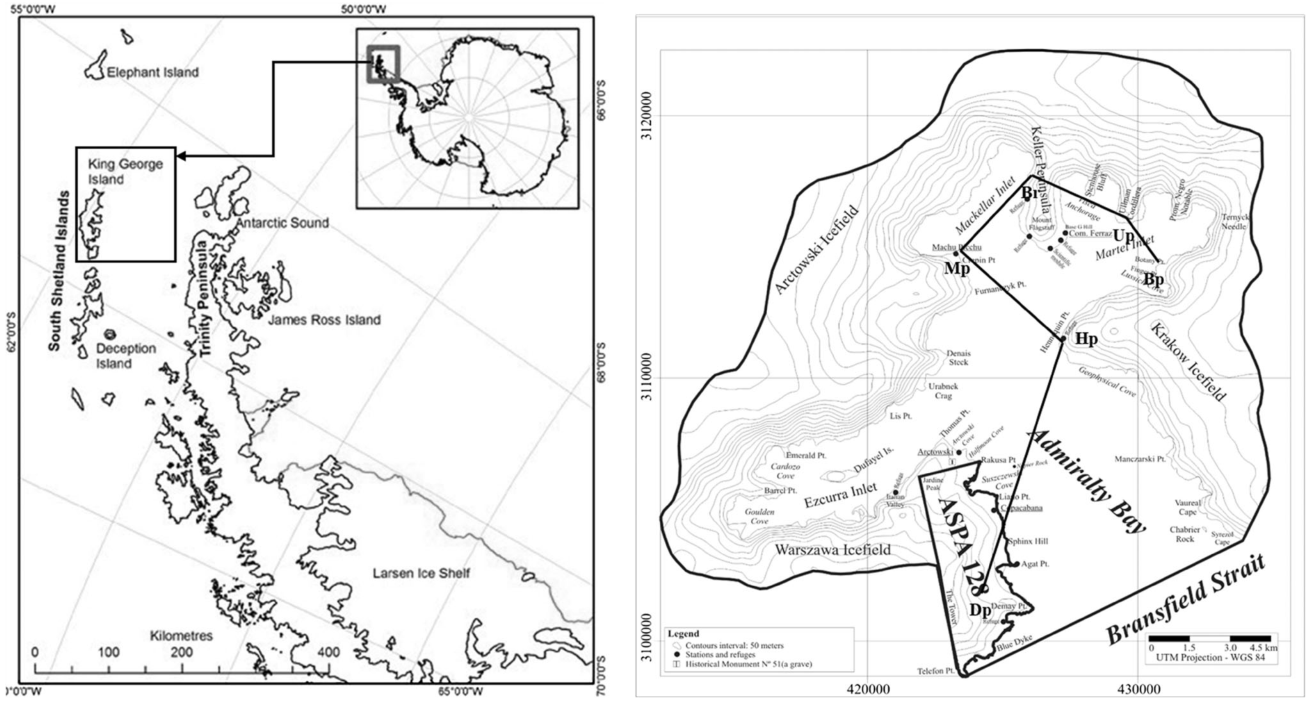

Fig. 1 Map of Admiralty Bay at King George Island, in Antarctica showing the sites and the transect where samples were collected for this study (Simões et al. 2004). Bp = Botany point (62°05′S, 58°19′W); Up = Ullman point (62°05′S, 58°20′W); Br = Brazilian Refuge II (62°04′S, 58°25′W); Mp = Macchu Picchu station (62°07′S, 58°23′W); Hp = Hennequin point (62°05′S, 58°24′W); and Dp = Demay point (62°12′S, 58°19′W). The distance among the sites was 2 km apart (Bp to Up), 4 km apart (Up to Br), 4 km apart (Br to Mp), 5 km apart (Mp to Hp) and 10.5 km apart (Hp to Dp)

Table 1 Molecular identification of endophytic yeasts associated with the Antarctic angiosperms *Deschampsia antarctica* and *Colobanthus quitensis*

Host plant	UFMGANT[a]	No. of isolates	Top BLAST search results (GenBank accession number)[b]	Query cover (%)	Identity (%)	No. of bp analyzed	Proposed taxa (GenBank acc. no.)
Deschampsia antarctica	257	21	*Cryptococcus victoriae* (AF363647)	100	99	560	*Cr. victoriae* (KT363897)[c]
	351	7	*Cystobasidium laryngis* (AF189937)	99	99	600	*C. laryngis* (KT363898)[c]
Colobanthus quitensis	250	56	*Cr. victoriae* (AF363647)	100	99	562	*Cr. victoriae* (KT363899)[c]
	303	19	*Rhodotorula mucilaginosa* (AF070432)	100	99	537	*Rh. mucilaginosa* (KT363900)[c]
	295	5	*Sporidiobolus ruineniae* (AF070434)	100	99	370	*S. ruineniae* (KT363901)[c]
	273	4	*Leucosporidium golubevii* (AY212997)	100	97	413	*L.* aff. *golubevii* (KT363902)[c]

Identification conducted using BLAST searches of the D1/D2 domain

[a] UFMGCB = culture of microorganisms and cells from the Federal University of Minas Gerais

[b] Taxa subjected to phylogenetic analysis based on the D1/D2 regions for elucidation of taxonomic positions

[c] D1/D2 sequences deposited

phylogenetic tree of the D1/D2 sequences was obtained by using the neighbor-joining method and the Kimura 2-P algorithm with 1,000 bootstrap replications according to Felsenstein (1985) performed with the program MEGA version 6.0 (Tamura et al. 2013).

Results

One hundred and twelve endophytic yeast isolates were obtained. Twenty-eight isolates originated from the leaves of 56 specimens of *D. antarctica*, and 80 isolates were from leaves of 60 specimens of *C. quitensis*. The endophytic yeasts were identified as *Cryptococcus victoriae*, *Cystobasidium laryngies*, *Leucosporidium* aff. *golubevii*, *Rhodotorula mucilaginosa* and *Sporidiobolus ruineniae* using the sequencing of D1/D2 rRNA (Table 1). The psychrophilic yeast *C. victoriae* was the most abundant species isolated from the two angiosperms. In contrast, *C. laryngies* was detected only in *D. antarctica*, and *R. mucilaginosa*, *S. ruineniae* and *L.* aff. *golubevii* were found only in *C. quitensis*. The phylogenetic analysis showed that the Antarctic endophytic yeasts and their closest relatives formed four clades (Fig. 2). The endophytic yeasts showed sequences with high similarity with taxa obtained from substrates located in different habitats of the world, including tropical, temperate and polar environments. Clade 4, formed by the sequences of *C. victoriae* UFMGANT 205 and 257 obtained from *C. quitensis* and *D. antarctica*, respectively, was closely related to taxa isolated from Antarctica, but also from the Arctic, Alpine and Himalayan environments. The species *R. mucilaginosa* UFMGANT 303 (endophyte of *C. quitensis*) and *C. laryngies* (endophyte of *D. antarctica*) sequences formed a clade (Clade 3) with sequences of taxa obtained from different habitats, environments and regions, which included leaves and fruits, sewage sludge, high-altitude freshwater lakes and alpine glaciers. The sequence of *S. ruineniae* UFMGANT 295 from *C. quitensis* formed Clade 2 and displayed similarities with related to taxa obtained from banana nectar in the tropical environment and from ant nests in temperate regions of the USA. The *L. golubevii* UFMGANT 273 sequence, obtained from leaves of *C. quitensis*, formed Clade 1 with sequences of *Leucosporidiella*, *Rhodotorula* and *Leucosporidium* taxa obtained from snow, glacial meltwater, soil and macroalgae present in different extreme habitats of the world.

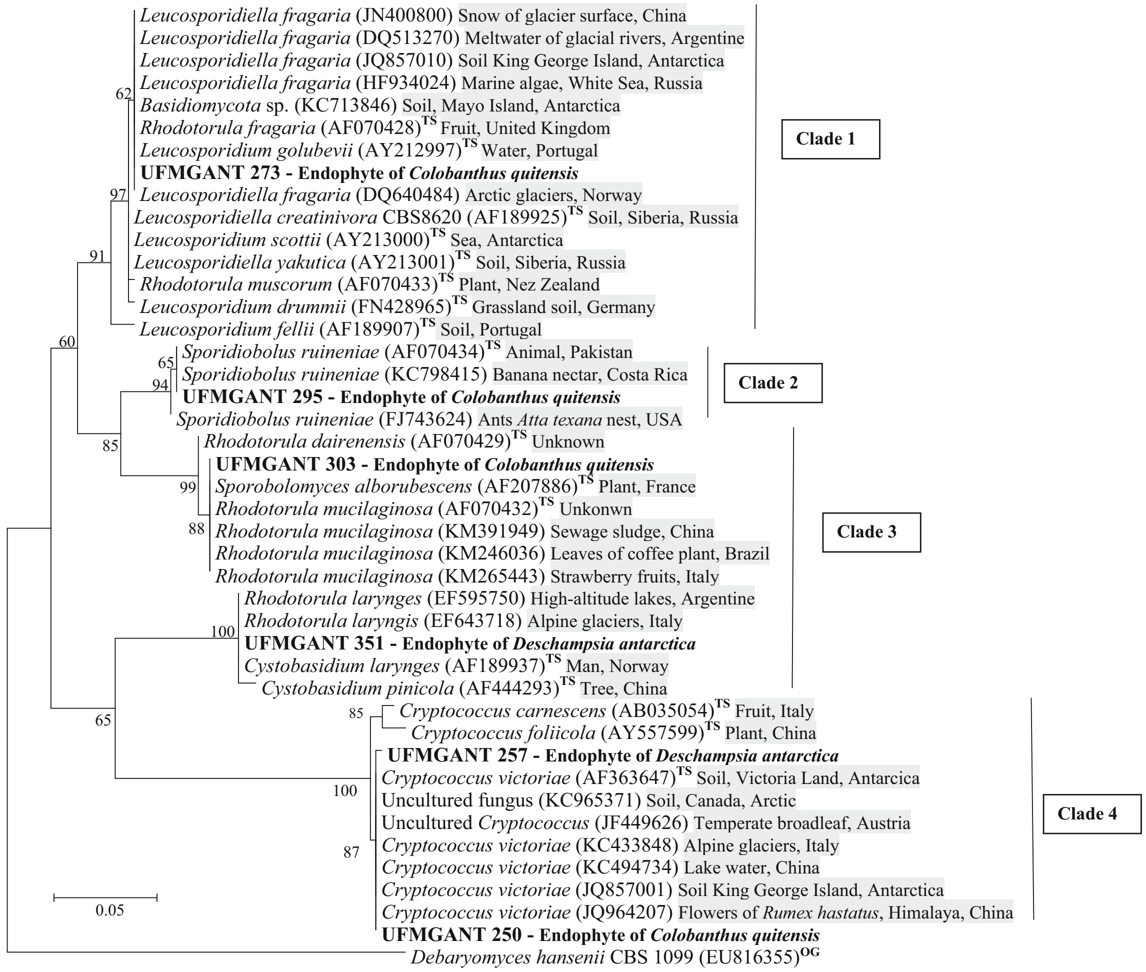

Fig. 2 Phylogenetic tree showing the nearest relatives and its origin (in *gray*) of endophytic yeasts (in *bold*) as well as sequences of type species (TS). The tree was constructed based on the rRNA gene sequences (D1/D2) using the maximum composite likelihood model. The tree was rooted with *Debaryomyces hansenii* CBS 1099 (EU816355) as out-group (OG). For detailed information about the origin and distribution of sequences, please access their GenBank codes

Discussion

Multiple studies have shown a high diversity of endophytic fungal communities associated with plants living in tropical, temperate, Arctic and Antarctic ecosystems (Higgins et al. 2007; Rosa et al. 2009). Few studies have reported the presence of endophytic yeasts associated with plants around the world (Doty 2013); even rarer reported is their association with polar plants (Zhang and Yao 2015). However, the increasing reports of endophytes from the next-generation sequencing studies seem to suggest that endophytic yeasts may not actually be rare, but instead overlooked, likely due to historic biases in culture methods that focus on filamentous fungi. In contrast, the molecular methods used here can not identify the uncultivable and/or slow endophyte communities. Our results corroborate Doty (2013), who states that yeasts are common endophytes, particularly the genera *Cryptococcus*, *Debaromyces*, *Sporobolomyces* and *Rhodotorula*.

The endophytic yeasts obtained from the Antarctic angiosperms were isolated at 15 °C after 60 days. For this reason, these yeasts can be classified as psychrotolerant fungi. According to Robinson (2001) and Ruisi et al. (2007), several fungi obtained from Antarctic environments appear to be psychrotolerant taxa when compared with those classified as psychrophilic. The frequent recovery of psychrotolerant microorganisms in Antarctica may be caused by local microclimate conditions of the Antarctic summer season, when the samples were obtained, as well as with the ability of the fungi to tolerate large variations in temperature (Vaca et al. 2013).

The yeast *C. laryngies* was detected as an endophyte only in *D. antarctica* (a monocot), and *R. mucilaginosa*, *S. ruineniae* and *L.* aff. *golubevii* were found only in *C. quitensis* (a dicot). The host specificity among endophytes and their hosts remains unknown. May (1991) suggests that strong host affinity is rare in communities containing a high diversity of host plants. However, Arnold and Lutzoni (2007) observed a lower host affinity among endophytes of angiosperms in tropical versus boreal sites. Our data provide additional preliminary evidence that polar endophytes may be specific to species or classes of plant hosts.

Cryptococcus victoriae was the most frequently isolated endophytic species of *D. antarctica* and *C. quitensis*. *Cryptococcus* (Basidiomycota) species have been found frequently in various Antarctic substrates. *C. victoriae* was originally described from Antarctica (Vishniac 2006) and was already described in penguin guano, soil, sediment, freshwater samples, the rhizosphere of *D. antarctica* (Vaz et al. 2011), macroalgae (Furbino et al. 2014), lichens (Santiago et al. 2015). However, *C. victoriae* has been characterized in environments outside of Antarctica, including soil and rhizosphere soil in Korea (Hong et al. 2002), sea water in Portugal (Gadanho et al. 2003), the gut of the insect *Chrysoperla rufilabris* in the USA (Woolfolk and Inglis 2004), an industrial malting area and indoor air in Finland (Laitila et al. 2006; Pitkäranta et al. 2008), in glacial ice from the Arctic (Butinar et al. 2007), in a dry meat processing factory in Norway (Asefa et al. 2009) and from the Italian Alps (Turchetti et al. 2008; Branda et al. 2010). According to Garcia et al. (2012), *C. victoriae* can be considered as a generalist species able to tolerate different stressful environments but not the most extreme conditions, which show strains with high physiology, morphology and molecular plasticity. Additionally, *C. victoriae* has been described in association with plants. Renker et al. (2004) and Wuczkowski and Prillinger (2004) reported *C. victoriae* in the roots, rhizosphere and seeds of different plants in Germany and Austria, and Zhang and Yao (2015) showed its presence as an endophyte of Arctic plants.

The genus *Rhodotorula* includes pigmented yeast species with a worldwide distribution. *Rhodotorula mucilaginosa* is a ubiquitous basidiomycetous yeast, which occurs in different habitats and substrates, including cold, extreme environments (Sampaio 2011a). In Antarctica, *Rhodotorula* has been isolated from terrestrial and marine substrates (Vaz et al. 2011; Godinho et al. 2013). Additionally, *C. laryngis*, also reported as *R. laryngis*, was isolated from natural environments in seawater and ice cores (Sampaio 2011a). However, *R. mucilaginosa* was reported as inhabiting the phylloplane and stems of living and dead parts of plants (Glushakova et al. 2015), as well as an endophyte of *Citrus sinensis* (Gai et al. 2009).

Although *S. ruineniae* has been isolated from foliage, rotten wood, soil, dung and air, its original habitat seems to be the phylloplane (Sampaio 2011b). *L.* aff. *golubevii*, obtained as an endophyte of *C. quitensis*, was isolated from the water of the river in the north of Portugal (Sampaio et al. 2003). To the best of our knowledge, our detection of *S. ruineniae* and *L.* aff. *golubevii* represents the first reports of these two species in Antarctica. The fact that we detected two species new to Antarctica in a relatively small and geographically limited study suggests that the Antarctic fungal diversity may be more extensive than is currently reported.

Conclusion

Endophytic fungi have been reported as able to increase the fitness of their host plants by conferring abiotic and biotic stress tolerance. Fracchia et al. (2003) showed the growth-promoting effects of *R. mucilaginosa*, a soil yeast, on the arbuscular mycorrhizal fungi (AMF) *Glomus mosseae* and *Gigasora rosea*. Those authors proposed that *R. mucilaginosa* produce exudates that stimulated the hyphal growth of AMF spores, increasing the chance of contact between AMF hyphae and plant roots and consequently increasing mycorrhizal establishment. Despite the yeasts' occurrence in other substrates in Antarctica, their abundance in an endophytic association with the Antarctic angiosperms suggests a possible symbiotic relationship with their plant hosts, which may provide shelter and growing conditions suitable for the yeasts' survival, dispersal and colonization of other Antarctic environments. In contrast, the endophytic yeasts might directly or indirectly promote the fitness of their host plants by producing metabolites beneficial for plant survival in the extreme environments of Antarctica, such as hormones, pigments, natural products and polysaccharides. However, our study only allows speculating on the nature of the interaction between the endophytic yeasts and their hosts. To elucidate details of the symbiosis between the endophytic yeasts and its hosts, further mesocosm experiments will be necessary in situ in Antarctica.

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Compliance with ethical standards

Conflict of interest We declare no conflict of interest among the authors.

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