Received: 25 April 2023 | Revised: 5 October 2023 | Accepted: 9 October 2023

DOI: 10.1002/yea.3903

Yeast WILEY

REVIEW ARTICLE

EcoYeast

Yeasts from tropical forests: Biodiversity, ecological interactions, and as sources of bioinnovation

Carlos A. Rosa[1] | **Marc-André Lachance**[2] | **Savitree Limtong**[3,4,5] | **Ana R. O. Santos**[1] | **Melissa F. Landell**[6] | **Andreas K. Gombert**[7] | **Paula B. Morais**[8] | **José P. Sampaio**[9] | **Carla Gonçalves**[9] | **Paula Gonçalves**[9] | **Aristóteles Góes-Neto**[1] | **Rosângela Santa-Brígida**[10] | **Marlúcia B. Martins**[10] | **Daniel H. Janzen**[11] | **Winnie Hallwachs**[11]

[1]Departamento de Microbiologia, ICB, C.P. 486, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

[2]Department of Biology, University of Western Ontario, London, Ontario, Canada

[3]Department of Microbiology, Faculty of Science, Kasetsart University, Bangkok, Thailand

[4]Biodiversity Center Kasetsart University, Kasetsart University, Bangkok, Thailand

[5]Academy of Science, Royal Society of Thailand, Bangkok, Thailand

[6]Setor de Genética, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Maceió, Alagoas, Brazil

[7]Department of Engineering and Food Technology, School of Food Engineering, University of Campinas, Campinas, São Paulo, Brazil

[8]Laboratório de Microbiologia Ambiental e Biotecnologia, Campus de Palmas, Universidade Federal do Tocantins, Palmas, Tocantins, Brazil

[9]UCIBIO-i4HB, Departamento de Ciências da Vida, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Caparica, Portugal

[10]Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

[11]Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania, USA

Correspondence

Carlos A. Rosa, Departamento de Microbiologia, ICB, C.P. 486, Universidade Federal de Minas Gerais, Belo Horizonte, MG 31270-901, Brazil.

Email: carlrosa@icb.ufmg.br

Funding information

FCT/MCTES; Natural Science and Engineering Research Council of Canada; Fundação do Amparo a Pesquisa do EStado de Minas Gerais; Conselho Nacional de Desenvolvimento Científico e Tecnológico

Abstract

Tropical rainforests and related biomes are found in Asia, Australia, Africa, Central and South America, Mexico, and many Pacific Islands. These biomes encompass less than 20% of Earth's terrestrial area, may contain about 50% of the planet's biodiversity, and are endangered regions vulnerable to deforestation. Tropical rainforests have a great diversity of substrates that can be colonized by yeasts. These unicellular fungi contribute to the recycling of organic matter, may serve as a food source for other organisms, or have ecological interactions that benefit or harm plants, animals, and other fungi. In this review, we summarize the most important studies of yeast biodiversity carried out in these biomes, as well as new data, and discuss the ecology of yeast genera frequently isolated from tropical forests and the potential of these microorganisms as a source of bioinnovation. We show that tropical forest biomes represent a tremendous source of new yeast species. Although many studies, most using culture-dependent methods, have already been carried out in Central America, South America, and Asia, the tropical forest biomes of Africa and Australasia remain an underexplored source of novel yeasts. We hope that this review will encourage new researchers to study yeasts in unexplored tropical forest habitats.

KEYWORDS
biotechnological innovation, insects, plants, tropical forests, yeast biodiversity

Take-away

- Tropical rainforests and related biomes are tremendous sources of novel yeasts.
- Tropical yeasts participate in several ecological interactions that contribute to the health of these ecosystems.
- Most studies of yeast diversity in tropical forests were carried out using culture-dependent methods.
- Yeasts from tropical rainforests are rich sources for bioinnovation.

1 | INTRODUCTION

Tropical forests encompass less than 20% of Earth's terrestrial area and are home to an enormous diversity of organisms (Dinerstein et al., 2017; Pillay et al., 2022). These ecosystems occur between the tropics of Cancer and Capricorn (23.5° N and S of the equator, respectively) and are characterized by dense, relatively tall, closed canopies with trees making up the dominant life form in structurally complex arrangements (Banin et al., 2015). Differently from temperate and boreal forests, there is no dominance of any one particular tree species in tropical forests (Lüttge, 2008). These forests are found in Asia, Australia, Africa, Central and South America, Mexico, and many Pacific Islands. Currently, the largest contiguous tracts occur in South America (the Amazon basin), Central Africa (the Congo basin), and Papua New Guinea (Figure 1).

Some works estimate that more than 50% of the known terrestrial biodiversity is found in tropical forests (Banin et al., 2015; Dinerstein et al., 2017). For example, Pillay et al. (2022) determined that tropical forests harbor 62% of global terrestrial vertebrate species, more than twice the number found in any other terrestrial biome on Earth. However, tropical forests are possibly the most endangered habitat on Earth and are very vulnerable to deforestation (Hoang & Kanemoto, 2021). Therefore, forest degradation and deforestation in tropical countries represent an inestimable loss for both the already known and the still uncovered biodiversity.

Tropical forests provide an extraordinary diversity of habitats for microorganisms. These habitats include floral and extrafloral nectar, fruits, leaves, tree bark, tree exudates, soil and the rhizosphere, water, plant and animal debris, insects, and other

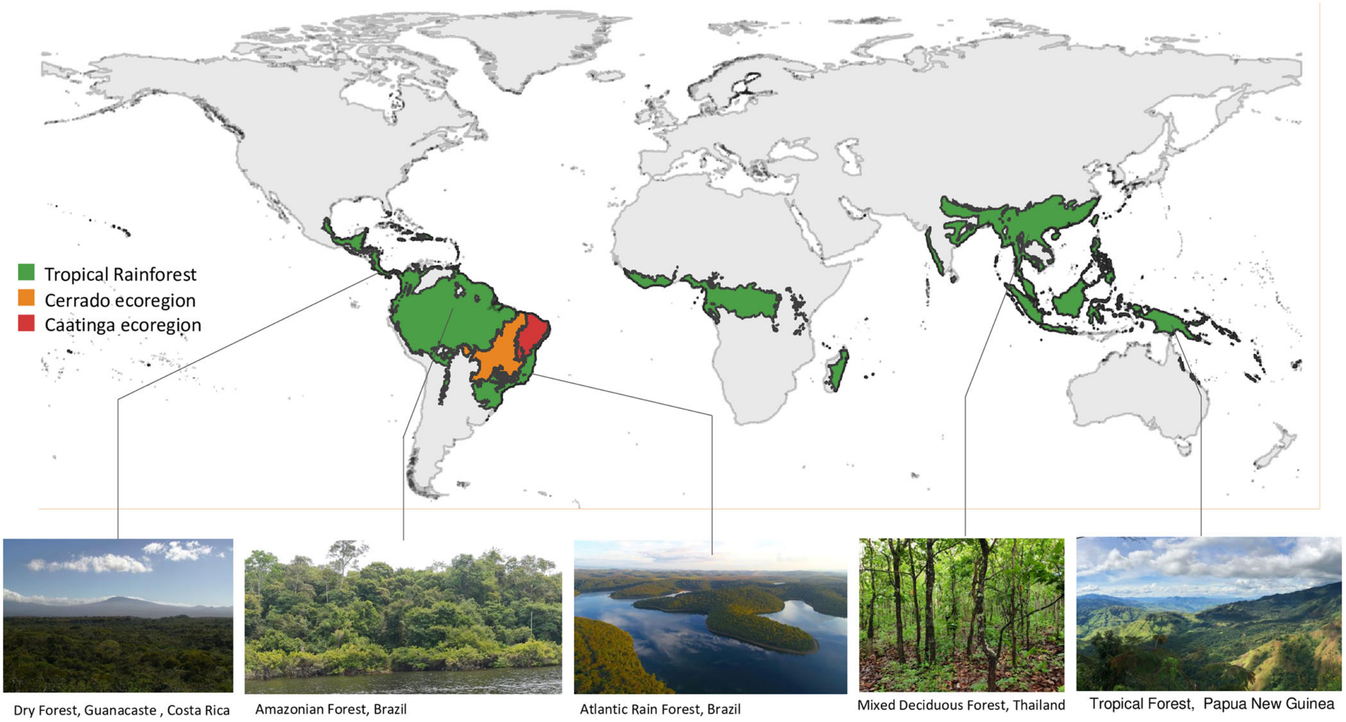


FIGURE 1 Geographic distribution of the tropical rainforest, Cerrado, and Caatinga biomes. This figure was delineated using the World Wildlife Fund terrestrial ecoregions map. The map was modified to exclude mountain and coastal forest mosaic ecoregions in Africa. For the purpose of the sampling analysis, the biome was partitioned into a sampling frame consisting of square blocks 18.5 km per side. The shapefile contains the sampling frame boundary for the humid tropical biomes (photography of the Eastern Highlands Province, Papua New Guinea is authored by Vika Jordanov and available for free in Unsplash. The other photographs are authored by the authors of this paper).

FIGURE 2 Substrates of tropical rainforest biomes where a high number of yeast species were isolated. (a) Morning-glory flowers (*Ipomoea* sp.); (b) rotting wood; (c) *Datura* sp. flower with drosophilids; (d) *Drosophila* spp. flies; (e) Bromeliad; (f) Tree exudates in a Cerrado biome; and (f) Agaricales mushrooms.

organisms (Figure 2). These habitats are colonized by a huge diversity of microbial communities, most of them still unknown. Yeasts are a component of these microbial communities. These unicellular fungi participate in the mineralization of organic matter in forest biomes and may produce plant growth promoters. Many species are opportunistic pathogens of plants and animals. Yeasts can have many kinds of ecological interactions with other fungi, plants, and animals, or can be sources of food for many organisms (Blackwell, 2017; Ganter et al., 2017). In tropical forest biomes, it is important to determine the composition of yeast species in a habitat, to distinguish prevalent from transient species, to identify the physiological traits that allow the colonization of each habitat, and to characterize the ecological interactions that contribute to ecosystem functioning. Yeast surveys have revealed that many species are specialists in some habitats, such as the surface and guts of insects and other animals, rotting plant materials, the phylloplane, flowers, soil, and water (Barros et al., 2023; Gomes et al., 2015; Lachance, Klemens, et al., 2001; Morais et al., 2017; Santos et al., 2018; Sapsirisuk et al., 2022; de Vega et al., 2017). Tropical forests provide an abundance of substrates for yeast colonization, and studies of these ecosystems are essential to understand the genetic diversity of yeasts, their biogeography, their interactions with other organisms, and their ecological role, as well as their biotechnological potential.

In this review, we present data on the yeast diversity of forest ecosystems of South America, Central America, and Asia, where these studies are more extensive. Australasia and African tropical forests will be focused as hotspots to study yeast biodiversity areas where studies need to be encouraged. Studies on yeast biodiversity in Central American forests are presented through those carried out in the dry forest of the Area de Conservación Guanacaste, Costa Rica, where a series of expeditions were conducted by some co-authors of this review, and utilized to inventory the diversity of yeasts and their association with plants and insects. We hope that reading the article can induce new researchers to study yeasts in unexplored habitats, focusing on the discovery of new species and their role in ecosystems, the factors that influence the structure of yeast communities, and the exploration of these microorganisms for bioinnovation purposes. Mozzachiodi et al. (2022) have published an excellent review on yeast biodiversity and abundance in temperate

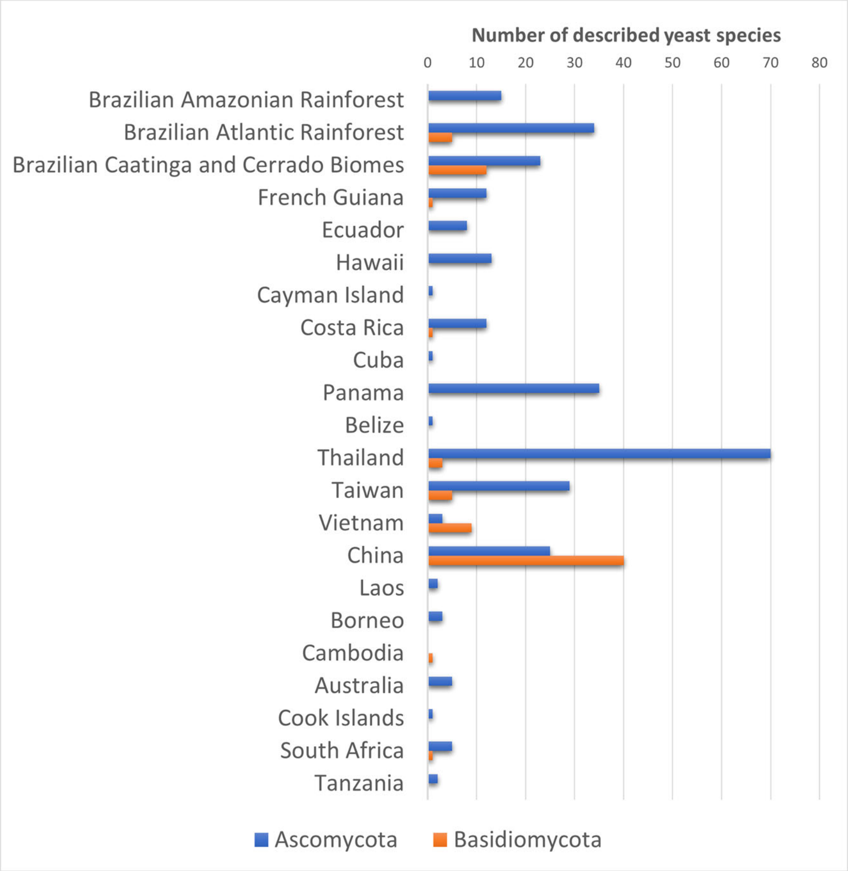


FIGURE 3 Overview of the number of yeast species described in the last 30 years from samples collected in tropical rainforest biomes worldwide.

forests. Those authors presented several sampling and isolation strategies to study yeasts in forest biomes, and to avoid repetition of this subject in the present review, we strongly recommend their review. Here, we present the state of the art of studies on yeast biodiversity in tropical forest biomes, based on published works and unpublished data. An overview of the species described from tropical rainforests in the last 30 years is given in Figure 3 and Supporting Information: Table S1.

2 | YEAST DIVERSITY IN TROPICAL FORESTS AND RELATED FOREST BIOMES IN SOUTH AMERICA

2.1 | Amazonian rainforests

The Amazonian rainforest biome covers approximately 40% of South America, including parts of nine countries: Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname, and French Guiana. In Brazil, the Amazonian biome represents 40% of the country (Figure 1). The region features different types of vegetation, ranging from dense forests to savannahs and mountain refuges. Several works have been published on the yeast diversity in Amazonian rainforest biomes (Barriga et al., 2014; Barros et al., 2023; Cadete et al., 2012; Guamán-Burneo et al., 2015; Jacques & Casaregola, 2019; James et al., 2009, 2013; Lopes et al., 2018; Matos et al., 2021; Mok et al., 1984; Morais, Rosa, et al., 1995; Neves et al., 2006; Vital et al., 2001). Most of these works show that the Amazonian rainforest biome is a vast source of novel yeasts.

One of the first works focusing on the yeast diversity of Amazonian biomes was performed by Mok et al. (1984). The authors collected 1949 soil samples from diverse geographical and ecological settings in the Brazilian Amazon Basin and investigated these samples for the presence of opportunistic pathogenic yeasts using the indirect mouse inoculation procedure. From 12% of the soil samples, 241 yeast and yeast-like isolates were assigned to six genera, and 82 species were recovered. Nine yeasts with known pathogenic potential were encountered: *C. glabrata* (= *Nakaseomyces glabratus*), *C. guilliermondii* (= *Meyerozyma guilliermondii*), *C. albicans*, *C. pseudotropicalis* (= *Kluyveromyces marxianus*), *C. tropicalis*, *Rhodotorula rubra* (= *Rh. mucilaginosa*), and *Wangiella dermatitidis*. The composition and distribution of the yeast species in soil differed from those of the yeasts harbored by bats, suggesting that the Amazonian external environment and internal bat organs act as independent natural habitats for yeasts.

Morais, Martins et al. (1995) studied the yeast succession in fallen ripe amapa fruit (*Parahancornia amapa*). The amapa is an endemic tree distributed in the upland and seasonally flooded forests of the Amazon Region. The fruits are edible and are known to serve as food to animals. They are visited by insects, including *Drosophila* flies that feed and breed on deteriorating fruits on the ground. The samples were taken at the Mocambo Forest Reserve site and Salvaterra Ecological Reserve in the Brazilian state of Pará. The yeast community associated with this Amazon fruit differed from those isolated from other fruits (*Anacardium giganteum*, *Clusia grandiflora*, *Helycostis* sp., and *Platonia insignis*) in the same forest. The authors reported that the occupation of the substrate depended on both the competitive interactions of yeast species, such as the production of killer toxins, and the selective dispersion by the drosophilid guild of the amapa fruit. Common fruit-associated species of *Kloeckera/Hanseniaspora*, *Me. guilliermondii*, and *Pichia kudriavzevii* colonized fruits during the first 3 days after the fruit had fallen. These yeasts were dispersed by the invader *Drosophila malerkotliana* and served as food for them. Resident flies of the *D. willistoni* group fed selectively on patches of yeasts colonizing fruits 3–10 days after the fruit fell. *Kleckera apiculata*, *Kl. apis*, *Saccharomycopsis* (*Candida*) *amapae*, *P. kudriavzevii*, *C. sorbosa*-like complex, *C. fructus*, *C. sorboxylosa*-like complex, and *P. kluyveri* were the prevalent species in the fruit, representing 50% of the total isolates. The authors also reported the isolation of 14 candidates for novel species. However, yeast identification in these previous studies was carried out by morphology and growth tests, and the identity of these yeasts was not verified by DNA sequencing.

The first work that utilized sequencing of the D1/D2 region for the identification of yeast communities isolated from Amazonian forest biomes was done by Cadete et al. (2012). The authors collected rotting wood in two sites of Amazonian rainforest in the state of Roraima, in Northern Brazil, to identify new D-xylose-fermenting yeasts that might potentially be used in the production of bioethanol from sugarcane bagasse hemicellulosic hydrolysates. A total of 224 yeast isolates, cultured in yeast nitrogen base (YNB)-D-xylose or YNB-xylan media, were obtained from rotting wood samples. *Candida tropicalis*, *Vanrija humicola*, *C. boidinii*, and *D. hansenii* were the most frequently isolated species. Six isolates of *Spathaspora passalidarum*, two of *Scheffersomyces stipitis*, and representatives of five new species were identified among D-xylose-fermenting isolates (Supporting Information: Table S1). Of the 33 yeast species identified, 26 were previously known and 7 represented candidates for novel species. Lopes et al. (2018) collected yeasts from rotting wood in the same region with the objective of isolating cellobiose-fermenting strains. The authors obtained 46 yeast species, with 11 representing candidates for novel species. *C. boidinii* (*Ogataea* clade), *Me. guilliermondii*, *Cyberlindnera subsufficiens*, *C. blattae*, *C. orthopsilosis*, and *P. manshurica* were the most frequently isolated species.

Similar results were obtained by Barros et al. (2023) studying yeast communities associated with rotting wood in other biomes of the Amazonian Forest in the state of Amazonas. The authors obtained a total of 569 yeast isolates from rotting wood samples collected in three Amazonian sites, representing 83 species, of which 53 were previously known, and 30 (36%) were candidates for novel species. Among the possible novel species, yeasts belonging to *Spathaspora*, *Scheffersomyces*, and *Sugiyamaella* were found, which are genera that contain species recognized as natural xylose fermenters, a trait of biotechnological interest. Other unpublished studies in the same biome showed that approximately 50% of the yeast species isolated from soil and passalid beetles represented candidates for novel species (A. R. O. Santos & C. A. Rosa, unpublished results; Souza et al., 2023).

During recent studies in two Brazilian Amazonian rainforest biomes, we obtained 647 isolates from different substrates. A total of 157 yeast species were identified, with 54 (34%) representing candidates for novel species (Supporting Information: Table S2). *C. orthopsilosis*, *Spencermartinsiella* sp., *Schw. polymorphus*, and *Apiotrichum mycotoxinivorans* were most frequent in rotting wood, *Nakaseomyces* sp. and *Starmerella apicola* in flowers, *P. manshurica* and *Limtongozyma cylindracea* in fruits, *Wickerhamomyces sydowiorum* in tree barks, and three species of *Moniliella* in tree saps, with two representing candidates for novel species. These results show the high diversity of yeast species in these Amazonian rainforest biomes.

Other studies were done in Amazonian rainforest biomes, namely, in Ecuador and French Guiana. James et al. (2009, 2011, 2013, 2014, 2015) described *C. carvajalis*, *Saturnispora quitensis*, *C. ecuadorensis*, *W. arborarius*, and *Kazachstania yasuniensis* from different tropical forest biomes in Ecuador. Guamán-Burneo et al. (2015) studied D-xylose-assimilating yeasts associated with rotting wood from the Galápagos Archipelago, Ecuador. A total of 140 yeast isolates were obtained, and the most frequently isolated species belonged to the *Yamadazyma*, *Kazachstania*, *Kurtzmaniella*, *Lodderomyces*/*C. albicans*, *Metschnikowia*, and *Saturnispora* clades. Barriga et al. (2014) reported on the yeast biodiversity associated with different substrates collected in four islands of the Galápagos Archipelago and compared it with the yeast diversity of biomes of mainland Ecuador. A total of 881 yeast isolates were obtained and identified by DNA sequencing. The yeast species shared between Galápagos and mainland biomes were mostly generalists and grew on a wide variety of substrates. In contrast, most species found exclusively in a region utilized a narrow range of substrates.

Some species described based on isolates obtained in mainland Ecuador and the Galápagos were also isolated in other regions, including Asia and Australia. Specifically, *S'copsis fodiens*, *Kodamaea transpacifica*, *W. arborarius*, and *C. theae* were isolated from different substrates, mainly flowers, including *Ipomoea* spp., and associated insects. Freitas et al. (2013) suggested a human-mediated dispersion of these species by transpacific contacts in ancient times between South American and Polynesian populations.

Jacques and Casaregola (2019) reported on the yeast diversity of tropical rainforest biomes and other environments in French Guiana. A total of 365 samples were collected from various substrates such as plants, fruits, and insects, at 13 locations, yielding 276 yeast isolates. Identification based on DNA sequencing showed that 210 isolates out of 276 belonged to 82 described species (67 Saccharomycotina, 14 Basidiomycota, and 1 Pezizomycotina), and 54 Saccharomycotina isolates could not be assigned to a known species. In addition, among the 43 Basidiomycotina isolates found, 12 could not be assigned to a known species. The authors concluded that French Guiana forest biomes constitute a largely unexplored reservoir for yeast diversity. These authors described 10 new yeast species based on isolates obtained in this study (Supporting Information: Table S1).

2.2 | Atlantic Rain Forests

The Brazilian Atlantic Rain Forest is composed of two major vegetation types: the coastal forest, which covers mostly low to medium elevations, and the tropical seasonal forest, which extends across the plateau (usually >600 rn elev.) in the center and southeastern interior of the country (Figure 1) (Morellato & Haddad, 2000). The Atlantic Rain Forest is the most altered Brazilian biome with less than 28% of its original forest cover remaining, and is considered a hotspot of biodiversity (Barros et al., 2021; Myers et al., 2000; Rezende et al., 2018). This complex biome contains a species diversity higher than most of the Amazon Forest and also has high levels of endemism (Morellato & Haddad, 2000). The first study of yeasts in the Atlantic Rain Forest in Brazil was done by da Cunha et al. (1957). The authors reported the diets and nutritional preferences of tropical species of *Drosophila* in Atlantic Rain Forest sites in the state of São Paulo. The genera *Pichia* and *Hanseniaspora/Kloeckera* predominated among yeasts associated with the flies. The next important study of yeasts from Atlantic Rain Forests was performed by Morais et al. (1992). These authors reported the distribution and diversity of yeasts vectored by and from the crop of eight species groups of *Drosophila* in two Atlantic Rain Forest fragments and an urban wooded area in the state of Rio de Janeiro. Typical forest *Drosophila* groups showed a higher diversity of yeasts than the cosmopolitan melanogaster species group, suggesting different strategies of utilization of substrates by the flies. Apiculate yeasts, including *Kl. apis*, *Kl. javanica*, and *Kl. japonica*, were the prevalent species. Most of the yeasts were strong glucose fermenters and assimilated few carbon compounds, suggesting that the flies preferred fruit as food sources. Morais, Rosa et al. (1995) studied the yeast communities associated with four species of the *Drosophila fasciola* subgroup (*repleta* group) in sites of the Atlantic Rain Forest in Rio de Janeiro. This *Drosophila* prefers the humid areas of the neotropical region and is the dominant section of the *D. repleta* (cactophilic *Drosophila*) group in the rainforests. The physiological abilities and species composition of *D. fasciola* yeast communities differed from those of other forest-inhabiting *Drosophila*, and the narrow feeding niches of these flies suggested the use of only part of the substrates available to the flies as food in the forest environment. Pimenta et al. (2009) studied the yeast communities associated with fruits, mushrooms, tree exudates, and flies of the genus *Drosophila*, in two Atlantic Rain Forest fragments. A total of 608 yeast isolates were obtained, belonging to 71 species. Distinct yeast communities were observed in *Drosophila* flies, fruits, mushrooms, and tree exudates. The studies of yeasts associated with *Drosophila* in these forest biomes supported the view that habitat is a strong determinant of yeast community identity (Morais et al., 1992).

Other studies of yeasts from Atlantic Rainforests were carried out focusing on the search for species able to ferment D-xylose or xylanase producers (Lopes et al., 2018; Morais et al., 2013, 2020; Sena et al., 2017). Morais et al. (2013) investigated the yeast species associated with rotting wood in two Atlantic Rain Forest areas. The authors used YNB-D-xylose and YNB-xylan media to culture the yeasts. A total of 321 isolates were obtained, with *Schw. polymorphus*, *Sc. queiroziae*, *B. californica*, and *C.* (*Ogataea*) *boidinii* as the most frequently isolated species. Sixty-nine species were identified, 12 were found in both areas sampled, and 15 were candidates for new species. *Sugiyamaella* sp. 1 and *Su. xylanicola* showed the ability to ferment D-xylose into ethanol, and *Spencermartinsiella* sp. 1, *Su. xylanicola*, and *Tremella* sp. were able to produce extracellular xylanases. Lopes et al. (2018) investigated the yeast species associated with rotting wood samples obtained from Atlantic Rain Forest and Amazonian forest biomes, with a special focus on cellobiose-fermenting species. About 647 yeast strains were isolated from rotting wood samples, representing 86 known species and 47 candidates for novel species. Eighty-six known species and 47 novel species of yeasts were isolated. *Candida boidinii*, *Cy. subsufficiens*, *Me. guilliermondii*, *Schw. polymorphus*, *C. natalensis*, and *D. hansenii* were the most frequently isolated species. Among the cellobiose-fermenting yeasts, 14 known and 3 novel yeast species were identified. Morais et al. (2020) studied the yeasts associated with rotting wood from four Atlantic Rainforest sites. The yeasts were isolated using a culture medium based on sugarcane bagasse hydrolysate. A total of 330 yeast strains were isolated, representing 51 species; the most frequent were *P. manshurica*, *C. pseudolambica*, and *Wickerhamomyces* sp. 3. Fourteen candidates for novel species were obtained in this study (Table S1).

Monteiro Moreira and Martins do Vale (2020) studied the soil yeast communities in a postmining site with revegetated and native areas along Savannah (Cerrado) and Atlantic Rain Forest biomes. A higher species richness was observed for yeast communities in the revegetated areas, with ascomycetous species dominating over basidiomycetous species. *Candida maltosa* was the most frequent species in the two biomes. The authors suggested that the elevated species richness in a revegetated area points to a possible ecological role of yeasts in environmental recovery. Moreira et al. (2020) reported on soil fungal diversity in a postmining area, comparing natural and modified environments by metabarcoding of the ITS2 region. The authors compared the soil fungal communities of biomes with different vegetation types and levels of human intervention, ranging from none to high environmental impact (Atlantic Rain Forest, iron outcrops, *Eucalyptus*, and grass). Sequence data were compared with culture data obtained from previous studies. Yeasts represented a proportion of fungal communities ranging from 1.7% to 17% of fungal sequences in soil. Basidiomycetous species had a higher proportion in relation to ascomycetous species, except for grass environments, where a higher proportion of ascomycetous yeasts was detected. The yeast communities responded to the environmental stress caused by mining activity, resulting in changes in species composition, with a notable increase in the abundance of black yeasts.

The number of studies of yeast biodiversity in the Atlantic Rain Forest biome of South America remains limited. Whereas initial studies were restricted to yeasts associated with *Drosophila* flies, studies performed since the beginning of the 1990s started to focus on other sources such as soil, leaves, and rotting wood.

2.3 | Other tropical forest biomes in South America

The Cerrado ecosystem is characterized by forest, savannah, and rupestrian (altitudinal) grassland formations. It covers 23% of the Brazilian territory, as well as areas of Guiana, Suriname, Colombia, and Venezuela (known as "Llanos"). This ecosystem is considered a hotspot of biodiversity and is the largest tropical savannah in South America with a high degree of endemism (Myers et al., 2000). The Cerrado biome also includes forests, from moist forests in the river plains, namely, the Araguaia River Plains, to seasonally dry forests on mountain slopes that cross Central Brazil from North to South.

The yeast species described based on isolates collected in the Cerrado biome are shown in Supporting Information: Table S1. Six ecological studies on the yeast diversity of this biome are noteworthy. Carvalho et al. (2013) obtained 307 yeast isolates from native Cerrado soils collected during rainy and dry seasons. Twenty-three species were isolated, and most were abundant only during the dry season. Among the various genera isolated, the relative abundance of the Ascomycota and Basidiomycota phyla was 80% and 20%, respectively. Various yeast isolates were able to produce carboxymethyl cellulase, xylanase, esterases, glycosyl hydrolases, and leucine arylamidases, suggesting a contribution of these yeasts in the recycling of organic matter in the soil. Sperandio et al. (2015) determined the composition and diversity of yeasts on leaves and fruits of *Byrsonima crassifolia* and *Eugenia dysenterica*, two plants of the Brazilian Cerrado biome. The isolates were identified as *Aureobasidium pullulans*, *Meyerozyma* sp., *C. oleophila*, *C. railenensis*, *Ps. sydowiorum*, *Ps. hubeiensis*, *Cr. nemorosus*, *Meira argovae*, and *Rh. mucilaginosa*. Three isolates identified as the yeast-like fungus *A. pullulans* exhibited potential for the control of the citrus green mold *P. digitatum* in both in vitro and in vivo tests. Morais et al. (2020) reported on the yeast communities in bromeliad tanks in two rupestrian savannah (Cerrado) biomes in Brazil. The yeast diversity comprised 90 species of which 60% were basidiomycetous yeasts usually associated with phylloplane, soils, and aquatic habitats. *Papiliotrema laurentii*, *Rh. mucilaginosa*, *Pa. nemorosus*, and *Ps. hubeiensis* were the most frequent species associated with bromeliads. Eighteen yeast species, two ascomycetous and 16 basidiomycetous, were consistently isolated from these substrates in both areas and may represent a core community in bromeliads in rupestrian fields. Vale et al. (2015) surveyed, using yeast extract-malt extract agar (YMA), the yeasts in nuts of *Attalea speciosa*, a palm tree that occurs in forests in the transition zone between Cerrado and Amazon forest biomes, and found 86 species dominated by oleaginous yeasts. Those yeasts presented dissimilar species composition to yeasts associated with *Acrocomia aculeata*, *Attalea dubia* and *Mauritia flexuosa* palm tree species in the same ecotonal areas. Januário da Costa Neto and Benevides de Morais (2020) studied the distribution of yeasts associated with the stingless bees *Frieseomelitta varia*, *Scaptotrigona aff. postica*, *S. polysticta*, *Tetragonisca angustula*, *Melipona compressipes manaosensis*, and *M. scutellaris* in the Cerrado and the importance of these microorganisms for resource partitioning in bees. Fifty-four species were identified, with *T. delbrueckii* as the most frequent, followed by *P. membranifaciens*, *St. apicola*, *P. kluyveri*, *St. meliponinorum*, and *St. bombicola*. The diversity of *Starmerella* species suggested a strong association with stingless bees. The authors concluded that although stingless bees are generalists, the prevalence of some yeast species in only one bee species is indicative of differences in niche breadth that may point to a role of these microorganisms in resource partitioning of bees in Brazilian forest savannahs. Melo et al. (2021) examined the yeast community of the leaf-cutter ant *Acromyrmex balzani* in the Cerrado biome. A total of 720 yeasts were isolated, comprising 52 species distributed in 20 genera. The isolates produced a wide range of carbon polymer-degrading enzymes and were able to assimilate the carbon sources present in plant materials. The predominant species in the ant nests were *Pa. laurentii* (18%), *Ap. mycotoxinovorans* (8%), *Me. caribbica* (7%), *A. pullulans* (6%), *Tr. asahii* (6%), and *Rh. paludigena* (5%). Together, these species represented 53% of the total number of isolates. Figueiredo et al. (2023) reported, using metagenomic approaches, that Saitozyma podzolica was the third fungal species with the highest relative abundance in a preserved area of Cerrado biome, whereas in a site of the same biome degraded by bauxite mining, this species was the 28th species in order of relative abundance. These authors suggested that Sa. podzolica can be used as a bioindicator of environmental quality and in the restoration of mined areas. These studies show the importance of studying yeasts found in the Cerrado biome, which contains more than 7000 plant species, 44% of which are endemic, thus being considered the most biodiverse tropical savannah worldwide (dos Reis et al., 2022).

The Caatinga dry forest is an exclusively Brazilian biome that covers approximately 70% of the Brazilian Northeastern region and 10% of the country's territory (Souza et al., 2020). The region features different types of vegetation, ranging from small to medium-sized plant species resistant to the high annual variability in rainfall and the high temperatures. Despite this, the Caatinga is still considered the most diverse and largest Seasonally Dry Tropical Forest and Woodland in the tropics (Silva et al., 2017, 2019; Teixeira et al., 2021).

Studies of the diversity and taxonomy of yeasts in this biome are still at their early stage, but have shown great promise. Barbosa et al. (2016) examined the richness of the yeasts associated with honey obtained from stingless bees of the Caatinga. Based on growth characteristics, they found 12 species belonging to the phylum Ascomycota, with a prevalence of *Candida* species, but also *D. hansenii*, *Dekkera bruxellensis*, *Kl. africana*, and *P. anomala* (= *W. anomalus*). Four yeast species were described based on isolates obtained from bromeliads collected in the Caatinga biome (Supporting Information: Table S1). An unpublished study in the same dry region sampled by Félix et al. (2020) shows a high frequency and abundance of *V. alagoana* and *T. ananatis* on bromeliads, confirming that these two species are widespread in this biome. Species of *Aureobasidium* were also common, with *A. melanogenum* and *A. thailandense* being more frequently found. Members of the phylum Basidiomycota increased in frequency and abundance in the dry period, especially *Occultifur brasiliensis*, *Pa. laurentii*, and *T. ananatis*. On the other hand, members of the phylum Ascomycota that stood out in the rainy season included *Candida* species and others such as *A. thailandense* and *C. blankii*. Approximately 15%–20% of the yeast species isolated from bromeliads were candidates for novel species. Despite being a promising region, the Caatinga biome is not well characterized in terms of yeast diversity, as studies have been limited to a small part of the biome, with sampling of only a few substrates, mainly bromeliads. Due to the unique ecological characteristics of the Caatinga forest, extensive studies using culture-based and culture-independent metagenomic approaches would be important to assess the diversity of the yeasts in this environment as well as their biotechnological potential.

3 | YEAST DIVERSITY OF THE DRY FOREST OF THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

3.1 | Yeasts of the Area de Conservación Guanacaste, Costa Rica

Our knowledge of the yeast diversity of the Area de Conservación Guanacaste comes from a series of explorations conducted from 1999 to 2003, prompted by the CRUSA-OTS-NSF workshop on Lepidopteran gut microbiology, held in Costa Rica in 1999. One objective was to examine the microbiota of the gut content of Lepidopteran caterpillars, following years of intense study of these insects (Janzen & Hallwachs, 2009). A large inventory of caterpillars and the plants upon which they feed allowed the elicitation of their adult stage in rearing barns situated in Santa Rosa National Park and the San Gerardo Biological Station. This provided access to a broad array of material to explore for the presence of yeasts. The forest of Guanacaste and adjoining regions of the province of Alajuela is classified primarily as a dry forest, although areas located at higher elevations of the Cordillera Guanacaste may qualify as rainforest. We also explored the yeast communities of sap fluxes of trees such as *H. courbaril* (Fabaceae), *Maclura tinctoria* (Moraceae), and a few representatives of other species. Our study sites were not restricted to uninterrupted forests. Areas that have experienced disturbance due to human activity are likely to serve as habitat for yeast-rich plants of the morning glory family (Convolvulaceae), which were of particular interest following the identification of species, many new to science. These species have affinities to the yeast genera *Metschnikowia*, *Wickerhamiella*, *Starmerella*, and *Kodamaea*, and were associated with insects of these flowers in various parts of the world (Lachance, Klemens, et al., 2001). Convolvulaceae flowers of Guanacaste serve as a source of nectar and shelter for a variety of insects, the most conspicuous of which are *Conotelus* spp. (Coleoptera: Nitidulidae), *Trigona* spp. and other meliponine bees, halictid and anthophorid bees, as well as drosophilids and other small dipters. Similar insect communities have been observed also in flowers of *Tabebuia rosea*, *Tecoma stans*, and other bignoniaceous trees, all of which have the potential also to carry yeasts.

3.2 | Ephemeral flowers and their insects

One of the most abundant and most diverse yeast clades associated with Convolvulaceae (*Ipomoea*, *Merremia*, *Operculina*) flowers and their insects is known as the large-spored *Metschnikowia* clade. Because of its global distribution, the clade will be discussed in greater detail in a later section. Suffice it to say that *Metschnikowia* (formerly *Candida*) *ipomoeae* was the most abundant species in the Guanacaste morning glory insect community (Supporting Information: Table S3), followed by *M. lochheadii*. Also noteworthy is that *M. similis* and two undescribed species provisionally designated as “cos” and “mer” are so far known only from Costa Rican collections.

Next in abundance (Supporting Information: Table S2) came *W. parazyma*, an asexual form first reported as *C.* (now *Wickerhamiella*) *azyma* (Lachance, Starmer, et al., 2001), from which it is hardly distinguishable except by barcode sequencing (Lachance et al., 2010). Growth on galactose is more rapid in *Wick. azyma* and growth in the presence of 2-deoxycholic acid (0.5% in YNB-glucose) is more vigorous in *Wick. parazyma*. The two do not seem to co-occur but their habitats are similar. The former is known from isolates in Hawai'i and the Paleotropics, whereas the latter appears to be Pantropical. In Guanacaste, *Wick. parazyma* abounded not only in the predominant inland morning glories but also in flowers and insects of other plants that often contained few, if any, other yeasts typically associated with this ecosystem. Such sources include insects or flowers of *Cassia* sp., *T. stans*, *Merremia umbellata*, and *Ipomoea pes-caprae*. *Wickerhamiella occidentalis* is one of four closely related, sexually reproducing species that differ in host and distribution, but are thought to be vectored primarily by drosophilids and other dipterans (Lachance, Klemens, et al., 2001). The species was named for its presence in the New World (Lachance et al., 1998). Of the other two species, one is known only from Brazil and the other from Australia and Malaysia. *Wickerhamiella lipophila*, isolated once in Guanacaste from a specimen of *Conotelus* sp. in *I. batatas*, was previously known only from Hawai'i (Lachance et al., 2000), as is the case for *Wick.* (formerly *Candida*) *drosophilae*, isolated in Guanacaste from a small fly in a roadside purple morning glory flower (Lachance et al., 1998). A single isolate from *Conotelus* sp. in a *T. rosea* flower represents a new *Wickerhamiella* species whose closest known relative is a single isolate from a banana flower in China (Wang et al., 2008).

As expected for flowers that experience frequent visits by bees, the yeast community of ephemeral flowers of Guanacaste exhibits a wide diversity of *Starmerella* species (Supporting Information: Table S2), dominated by *St. apicola*, and complemented by mostly new species, some of which have been reported also in Brazil (Rosa et al., 2007; Santos et al., 2018). *Starmerella apicola* has been recovered from bees, often those of the tribe Meliponini, in Europe, Asia, and the New World, and exhibits considerable polymorphism in barcode sequences (Lachance et al., 2010), which is consistent with the extensive species diversification observed in the genus as a whole (Santos et al., 2018). Roadside purple morning glories are the source of several isolates recently identified as *St. camargoi*, which was described (Santos et al., 2018) based on isolates from flowers of a morning glory and a *Gossypium* species in two Brazilian localities. Bees of *M. quinquefolia* flowers yielded isolates of *St. floris*, described together with morning glory isolates in Brazil's Mato Grosso do Sul state (Rosa et al., 2007), as well as the ascogenous *St. meliponinorum*, described along with several isolates from meliponine bees of Minas Gerais state in Brazil (Teixeira et al., 2003). Single isolates of three potentially new *Starmerella* species were also recovered.

Ephemeral flowers and their insects also yielded a small number of yeast species that were identified only by microscopy, for reasons of logistics. Noteworthy among these are *M. reuukaufii*, recognizable on the presence of characteristic bacilliform chlamydospores sometimes referred to as reukaufii cells, along with other *Metschnikowia* isolates that feature ovoid chlamydospores characteristic of species such as *M. peoriensis* (Kurtzman et al., 2018), *M. pulcherrima* (including several synonyms; Sipiczki, 2022), and a few others.

3.3 | Caterpillar frass

Yeasts are not a dominant component of the microbiota of caterpillar frass pellets, which abound in bacteria and molds. A total of 62 specimens yielded only 47 ascomycetous yeast isolates, nearly half of which ($n = 20$) were the ubiquitous, halotolerant *D. hansenii* (Supporting Information: Table S4), and a third of which ($n = 17$) were basidiomycetous species typical of those commonly found on plant surfaces (data not shown). The next most abundant ($n = 3$) species, *Me. guilliermondii* and *C. intermedia*, are also widespread in a broad variety of habitats, including not only plants, but also food and clinical specimens (Corte et al., 2015; Lachance et al., 2011). Of greater interest are two isolates with a perfect barcode match to strain UFMG-CM-Y3128, labeled *Clavispora* sp. and recovered in Brazil from rotten wood (Lopes et al., 2018). The remaining isolates were singletons representing a broad array of species known from eclectic substrates, including clinical sources. Among these is an isolate with a perfect sequence match with strain CLIB 1737, isolated from fruit in French Guiana, and strain F14-10-8 recovered from a cocoa flower in Cuba, which placed phylogenetically in the vicinity of *M. torresii*, itself known from a single seawater sample. The single isolate of *Yam. riverae* went unnoticed in the description of the species (Lopes et al., 2015), which was based on cultures recovered from various substrates that included rotting wood, tree bark, and ant nests in various Brazilian locations. Negligeable overlap existed between the caterpillar frass community and others examined in the region. One exception was *M. reukaufii*, a common nectar yeast, which was also recovered from flowers and insects of a roadside *Tecoma stans*. Another shared species was an undescribed Metschnikowiaceae outlier repeatedly recovered in fluxes of *H. courbaril*, to be discussed next. It is worth noting that the caterpillars, their food plants, containers, and frass are not handled under any kind of asepsis at rearing barns, and given the need for an enrichment step, the idea of a specific yeast community of caterpillar frass remains an open matter.

3.4 | Sap fluxes

Also known as guapinol or stinking toe, *H. courbaril* is a prevalent tree of the lowland forest of Central and parts of South America (Janzen, 1983). The tree often produces sap flows, some of which are extensive. This creates a rich habitat in which various insects may feed, oviposit, and maintain a characteristic yeast community, dominated by *P. chibodasensis* (Supporting Information: Table S4). A close relative of *P. membranifaciens*, the species shares a similar growth profile characterized by strictly oxidative assimilation of ethanol and simple organic acids, as well as the frequent formation of a hydrophobic pellicle on the surface of liquid substrates. The yeast was present in most sap samples examined, including those of four other tree species, and has been recovered in other localities and substrates, including rotting wood in the Brazilian Amazon (GenBank KT377036; Lopes et al., 2018) and oak sap fluxes in the Canadian Great Lakes region. Growth responses vary somewhat, but none of the isolates assimilated carbohydrates other than xylose, weakly, which is somewhat at variance with the species description (Kobayashi et al., 2017), which reports, inter alia, weak growth on trehalose and starch for isolates from soil and rotten wood in Indonesia. Over a third of the samples yielded a yet-to-be-described *Sporopachydermia* species (Lachance, 2011a) closely related or even possibly conspecific with an isolate recovered from the sap flux of *a koa* (*Acacia koa*, Fabaceae) tree, and moderately related to an isolate from an ohia (*Metrosideros polymorpha*, Myrtaceae), both in Hawai'i. Next comes the yeast-like, achlorophyllous alga, *Prototheca* spp., shared by many decaying tree materials worldwide, followed by lesser numbers of several species, some yet to be described. One is a peripheral member of the Metschnikowiacaeae that appears conspecific to two isolates from the Brazilian Amazon basin, of which one came from rotten wood and the other from a passionfruit flower (GenBank MH348143 and OP113841, respectively). These are followed by a handful of isolates that nearly match *Groenewaldozyma auringiensis* in their barcode sequence and others that were described as *O. falcaomoraisii* (Morais et al. 2005) based on these isolates along with others from sap flows of carvoeiro trees (*Sclerobium* sp., Fabaceae) in Tocantins state, Brazil. The latter yeast is a close relative of *O. ortonii*, a significant component of the yeast community of *M. tinctoria*, to be discussed next. It is of interest that two such sister yeast species be associated with sympatric trees of different families. A singleton isolate shared with *M. tinctoria* represents a sister species to *O. trehaloabstinens* that has yet to be reported elsewhere. Most *Ogataea* species assimilate methanol, which probably accounts for their presence in decomposing wood, be it in the form of sap fluxes or woody debris. The sequestration of methanol may serve to detoxify decaying wood in favor of insects that participate in the decomposition process. The remaining yeast species of *H. courbaril* sap are unremarkable except for representatives of two undescribed species. One is a moderately close relative of *W. quercuum* that also predominates in samples of other trees in Guanacaste as well as those of a wide miscellany of substrates from other continents, as evidenced by the several entries elicited by a BLAST search of GenBank. The other is a single isolate of a moderate relative of *Limtongiella siamensis*. Although unique among yeasts recovered in Costa Rica, the strain has an identical barcode sequence to an isolate from the sap flux of a breadfruit tree (*Artocarpus altilis*, Moraceae) in Maui. Two bees sampled near a flux of *H. courbaril* yielded isolates of *St. roubikii*. These, together with several isolates from meliponine bees of water lilies in Belize were the basis for the species description (Santos et al., 2018). The presence of a nearly pure culture of a *Starmerella* species in these samples makes it unlikely that the bees were feeding off the sap.

The yeast community of the moraceous tree *M. tinctoria* was discussed in some detail by Lachance, Starmer et al. (2001), with the description of *C. galis* and *C.* (iter. nom. *Ogataea*) *ortonii*. The study encompassed isolates obtained in the year 2000. We now add to these data those of a 2001 collection (Supporting Information: Table S4). What has not changed is that all but a single yeast species found were at the time new to science. The above two species remain the principal members of the yeast community of *M. tinctoria* sap, having been found in over half and over a third of the samples, respectively. The phylogenetic position of *C. galis* remains ill-defined, with possible affinities to the genus *Cyberlindnera* and a clear, but moderate connection to three GenBank entries for isolates recovered from the mycetangium of a lucanid beetle in Japan, oak bark in Colombia, and an undisclosed substrate in China (GenBank LC661392, ON264698, and JN936886, respectively). As mentioned already, two species are shared with the community of *H. courbaril*. Among species that are unique to *M. tinctoria*, two *Wickerhamomyces* species have no known close relative. A sister species to *Myxozyma geophila* was also recovered the same year from a breadfruit flux on Maui. An *Ambrosiozyma* species is related to *A. vanderkliftii*, which itself is known from three isolates of oak bark beetles in Japan. An isolate would appear to represent a sister species to *C.* (inter. nom. *Yamadazyma*) *temnochilae*, which is known from two isolates from trogossitid and passalid beetles collected in Panama (Suh et al., 2005). Shared with the community of *Gliricidia sepium* were representatives of a sister species to a strain of *Ogataea* (Af116-2-2; GenBank LC661398), isolated in Japan from the same source as the nearest relative to *C. galis*, namely, the mycangium of a lucanid beetle.

Other trees sampled included *Gliricidia sepium*, a species that has been transplanted pantropically for use in building live fences, *Enterolobium cyclocarpum*, *Samanea* (a.k.a. *Pithecellobium*) *saman*, *Ficus* sp., and *Quercus oleoides* (Supporting Information: Table S4). Although the small sample sizes preclude inferring potential yeast communities, some observations are appropriate. The first tree species shared with *H. courbaril* and *M. tinctoria* the presence of *P. chibodasensis*, identifying the yeast as a generalist of sap fluxes and possibly spread by a common vector. A study of rapidly evolving genetic markers would be required to shed light on this question. Most samples of *G. sepium* featured the *W. quercuum* sister species found in *H. courbaril*, which was also found in a flux of *S. saman*. The yeast has a worldwide distribution in a variety of substrates, including rotten wood in Brazil, but an adaptation to the leguminous sap flux community is likely in view of our having also isolated it from fluxes of *Acacia koa* in both Hawai'i and Rarotonga and *Prosopis juliflora* (mesquite) in Arizona. Such generalizations are clouded by differences in sampling approaches of various laboratories, some of which focus on materials that contain large yeast populations, as is the case for many plant–insect interfaces, while others examine substrates where yeasts are transient and require enrichment procedures for their isolation. The single yeast specimen (*Metschnikowiaceae*; GenBank access number AF530620, Supporting Information: Table S4) recovered from *Q. oleoides* represents an undescribed metschnikowiaceous species with a strong affinity to the Brazilian isolates *Candida* sp. strains UFMG-CM-6917 and UFMG-CM-Y2876, obtained from soil and rotten wood, respectively, with a moderate relatedness to *C. bentonensis*.

Ficus sp. yielded fewer than one isolate per sample, but the yeast species composition distinguished itself by the presence of a unique *Wickerhamomyces* species whose nearest relative is the undescribed species encountered in *M. tinctoria*, raising the possibility that these yeasts are endemic and have co-radiated with the two moraceous tree species (Supporting Information: Table S4). Another unique species is a sister to an undescribed *Sporopachydermia* recovered in a beetle of an *Aconita* sp. flower in Rarotonga (Lachance, 2011a). One isolate of *Cl. opuntiae* was shared with a necrotic tissue sample from *Hylocereus* sp., where the presence of this yeast species is not completely unexpected, as it has been isolated from many cactus species across the Neotropics. The occurrence of this yeast in a *Ficus* sp. exudate is surprising but might suggest local vectoring by lepidopteran species, which abound in the Guanacaste forest. A worldwide association with cactus-boring moths has been suggested for *Cl. opuntiae* (Lachance, 2011b). A *Hylocereus* flower and various insects collected from it yielded yeasts typical of cactus flowers and their insects, including *Ko. restingae*, which have been found on this substrate worldwide. Necrotic tissue of both *Hylocereus* and *Stenocereus aragonii*, a Costa Rican endemic columnar cactus, also yielded *P. cactophila*, regarded as ubiquitous in cactus necroses (Ganter, 2011). A single sample of the columnar cactus in a state of advanced decay yielded a remarkable diversity of yeasts, including a unique *Wickerhamomyces* species and a novel *Tortispora* species, *Tor. cuajiniquilana*, whose nearest known relative is an isolate of another novel species, *Tor. sangerardonensis*, isolated from an unidentified tree in the foothills of the Cordiliera (Lachance & Kurtzman, 2013).

Other substrates sampled at a low frequency yielded a similar pattern of rare or new yeast species (Supporting Information: Table S4). Noteworthy is the isolation, from a single *Trigona* species collected on an unidentified Asteraceae, of two novel species, namely, *St. vitae*, also found in flowers of two Brazilian trees (Santos et al., 2018), and *Wick. dianesei*, of which the only other known isolate came from a leaf of a rubiaceous vine in Brazil (Lachance et al., 2018). Not listed in Supporting Information: Table S4 are individual samples of tree materials that yielded only molds or no growth at all. These include *Bursera simarouba* (Burseraceae), gumbo limbo, which is utilized by wasps and meliponine bees (Stevens, 1983), and adequately sampled, should be host to interesting yeasts species. Two samples of resin collected from the bark of gumbo limbo only yielded molds, as did a sap flux of *Licania arborea* (Chrysobalanaceae).

Our knowledge of the yeast diversity of the Guanacaste forest is far from complete. Yeasts of basidiomycetous affinity have been neglected due to the need to concentrate efforts. Among ascomycetous species, the proportion of isolates that were or remain new to science is extraordinarily high, such that one can expect that our sampling effort is far from approaching a saturation point. It is certain, for example, that an extensive survey of the hundreds of bee species known in the region would yield many more *Starmerella* species, and that isolations from nectar or soil, neither of which has been examined, would uncover a vast array of diversity.

4 | YEAST DIVERSITY IN TROPICAL FORESTS OF ASIA

Tropical forests of Asia are located mainly in Southeast Asian countries, and some regions of Taiwan, the People's Republic of China, India, and Japan. Although the forests in tropical regions of Asia, especially Southeast Asia, are rich in biodiversity, the investigation of yeasts is only carried out in some countries. In this section, we review yeasts in some habitats, for example, soil, water, and plants in some tropical forest types such as mangrove forests, peat swamp forests, tropical rain forests, dipterocarp forests, and lower montane coniferous forests in some countries where investigations were performed and reports published.

4.1 | Yeast diversity in tropical forests of Thailand

In Thailand, the study on yeasts in forests was started in 1987 when Dr. Takashi Nakase of the Japan Collection of Microorganisms conducted collaborative research with scientists of the Thailand Institute of Scientific and Technological Research. He and his colleagues together with Thai scientists investigated ballistoconidium-forming yeasts (phylum Basidiomycota) from plants in natural environments, namely, forests, rice fields, and grasslands in Thailand in 1987, 1990, and 1996. The results of these studies were summarized in the book chapter, yeast biodiversity in tropical forests of Asia, by Nakase et al. (2006). Ballistoconidium-forming yeasts associated with plant leaves constitute a community that is rich in biodiversity where both known and new yeast species were found (Nakase et al., 2006). New yeast species were discovered from plant leaves collected in tropical forests (dry evergreen and dry dipterocarp forests) of the Sakearat Environmental Research Station in Nakhon Ratchasima province (Fungsin et al., 2001, 2006; Fungsin, Hamamoto, et al., 2002; Fungsin, Takashima, et al., 2002; Fungsin, Takashima, Artjariyasripong, & Nakase, 2003; Fungsin, Takashima, Artjariyasripong, Potacharoen, et al., 2003).

Mangrove forests (intertidal forests) are plant communities in saline coastal habitats distributed in tropical and subtropical regions of various geographical areas (Aksornkoae, 1999; Allard et al., 2020). The mangrove ecosystem provides carbon storage and coastline stabilization, both important sources of ecological benefits and ecosystem services (Allard et al., 2020). In mangrove forests, yeasts play an important role in the detrital food web in that they may be a food source for some marine invertebrates and zooplankton (Nagahama, 2006). Yeast diversity in water, sediment/soil, and plant materials in mangrove forests in Thailand have been intensively investigated since 2007. These investigations have shown a high yeast diversity in mangrove forests. Yeasts in both phyla *Ascomycota* and *Basidiomycota* were detected, although the dominant species were *Ascomycota*. Various new yeast species were discovered. In addition to the new species shown in Supporting Information: Table S1, other new species were proposed from strains isolated from brackish water samples collected in other mangrove forests in Thailand. *Torulaspora maleeae* was described based on many strains, one of which came from sediment in the mangrove forest of the Laem Son National Park, Ranong Province (Limtong et al., 2008). New species discovered in decaying plant materials floating in water in mangrove forests consist of *C. chanthaburiensis* and *N.* (*Candida*) *kungkrabaensis* found in Chanthaburi province and *C. suratensis* found in Suratthani province (Limtong & Yongmanitchai, 2010).

An investigation of yeasts in soils of mixed deciduous forest in Amphoe Wang Nam Khiao, Nakhon Ratchasima province yielded 19 known yeast species in the phylum *Ascomycota*. They were *C. amphixiae*, *C. glabrata*, *C. natalensis*, *C. nivariensis*, *C. orthopsilosis*, *C. parapsilosis*, *D. nepalensis*, *D. pseudopolymorphus*, *D. vanrijiae* var. *vanrijiae*, *H. occidentalis*, *P. caribbica*, *P. galeiformis*, *P. kudriavzevii*, *P. terricola*, *Ko. ohmeri*, *W. anomalus*, *W. mucosus*, *W. sydowiorum*, and *S'copsis crataegensis* (Limtong et al., 2009). In addition, three new species, *Kazachstania siamensis* (Limtong et al., 2007), *P. jaroonii*, and *W. edaphicus* (Limtong et al., 2009), were discovered and described. The finding of only *Ascomycota* could be the result of using an enrichment technique for yeast isolation. In another investigation, *C. tropicalis*, *D. albidus*, and *Tr. asahii* were reported in soils in the Khaoploung forest area (mixed deciduous forest located in the Lopburi province) following an enrichment technique (Khamweera et al., 2022). In an effort to obtain oleaginous yeasts with better lipid-producing abilities, 11 yeast species were isolated from soils collected from lower montane coniferous forests in three mountains in Chiang Rai province. The samples were inoculated on plates with two different nitrogen-depleted media. The isolates consisted of five ascomycetous species namely, *Cy. saturnus*, *Lipomyces mesembrius*, *L. starkeyi*, *L. tetrasporus*, and *Me. guilliermondii*, and six basidiomycetous species, namely, *Rh. mucilaginosa*, *Cystobasidium slooffiae*, *Naganishia diffluens*, *Pa. flavescens*, *Pa. terrestris*, and *Sa. podzolica* (Sapsirisuk et al., 2022). In some forest types, the yeasts of other forest habitats were also studied. These included mushrooms, flowers, fruits, tree barks, and insect frass collected from the mixed deciduous forest areas of the Phujong Nayoy National Park, Ubon Ratchathani province. Ascomycetous yeasts found in this national park consisted of *C. glabrata*, *C. litsaeae*, *C. orthopsilosis*, *C. parapsilosis*, *C. tropicalis*, *C. zeylanoides*, *D. vanrijiae* var. *yarrowii*, *Ko. ohmeri*, *Magnusiomyces* (*Dipodascus*) *magnusii*, *P. fabianii*, *P. kudriavzevii*, *P. pijperi*, *Me. guilliermondii*, *Sa.* (*Candida*) *sekii*, and *T. globosa*, while the basidiomycetous species comprised *A. pullulans*, *Blastobotrys mokoenaii*, *Rhodosporidiobolus* (*Sporidiobolus*) *ruineniae*, *Tr. asahii*, *Tr. mycotoxinivorans*, and *Va.* (*Asterotremella*) *humicola* (Thongekkaew et al., 2012). Collections from habitats in various forest types also led to the discovery of several new yeast species (Supporting Information: Table S5).

The peat swamp forest is a unique ecosystem, where plant debris does not undergo complete decomposition due to a waterlogged condition. In this forest type, a thick layer of peat is derived from the accumulation of partially degraded organic matter (Chimner & Ewel, 2005; Dedysh et al., 2006). The yeast diversity in peat swamp forests of both the primary and secondary types in Thailand have been intensively investigated during the last decade. A collection was performed in the Princes Sirindhorn (Pru To Daeng) Wildlife Sanctuary in Narathiwat province, which is the largest primary peat swamp forest in Thailand (Jaiboon et al., 2016), the Khanthuli forest, which consists of primary and secondary types of peat swamp forest in Surat Thani province (Boonmak et al., 2020; Nasanit et al., 2020), the Khuankreng peat swamp forest of Nakhon Si Thammarat province (Nasanit et al., 2020; Satianpakiranakorn et al., 2020), and the Rayong Botanical Garden peat swamp forest, which is a secondary peat swamp forest in Rayong province (Satianpakiranakorn et al., 2020). Yeasts in both phyla *Ascomycota* and *Basidiomycota* were found. These included new species, namely, *N. todaengensis* (Polburee et al., 2017), *C. kantuleensis* (Nitiyon et al., 2018), *Cryptotrichosporon siamensis* (Kaewwichian et al., 2018), *Sa. kantuleensis* (Khunnamwong and Limtong, 2018), and *Teunia siamensis* (Khunnamwong et al., 2020).

4.2 | Yeast diversity in tropical forests of Vietnam

In Vietnam, ballistoconidium-forming yeasts from plant leaves in a tropical rain forest of the Cuc Phuong National Park of Ninh Binh province were reported in 1999. They belonged to the genera *Bullera*, *Kockovaella*, *Sporobolomyces*, and *Tilletiopsis* (Nakase et al., 2006). In this investigation, four new *Kockovaella* species, *Ko. calophylli*, *Ko. cucphuongensis*, *Ko. litseae*, and *Ko. vietnamensis* were proposed (Luong et al., 2000). Later, another new species, *Cr. cellulolyticus*, was discovered from the same forest (Luong et al., 2005). *Lipomyces orientalis* was proposed as a new species based on strains isolated from mixed forest soil samples taken near Bai San Island, Nha Trang (Thanh, 2006). An investigation of yeasts in soils of Cát Tiên National Park, South Vietnam detected the species *C. akabanensis*, *Filobasidium chernovii*, *Sa. podzolica*, *Hannaella* sp., *Schw. polymorphus*, and *A. pullulans* (Glushakova et al. (2019).

4.3 | Yeast diversity in tropical forests of Indonesia

Yeasts were isolated from leaf and leaf litter samples collected from the Papalia Protected Forest, a tropical lowland monsoon wet forest, and Mekongga Protected Forest, which covers lowland and upland rain forests, in Southeast Sulawesi (Kanti, 2015). They belonged to *Ascomycota*, namely, *C. azyma*, *C. albicans*, *C. catenulata*, *C. insectorum*, *C. intermedia*, *C. lessepsii* and *C. tropicalis*, and *Basidiomycota*, namely, *Va. humicola*, *Cr. humicola*, *Pa. flavescens*, *Ps. aphidis*, *Ps. rugulosa*, *Sporidiobolus pararoseus*, and *Spor. ruineniae*. Unidentified species of the genera *Candida* and *Yamadazyma* were also found. Moreover, *Z. mellis* showed high lipase production among the yeast strains isolated from wild forest honey in Central Sulawesi (Palilu et al., 2019).

4.4 | Yeast diversity in tropical forests of China

Tropical forests in China are extremely scarce, being distributed only in Hainan province, southern Yunnan province, southern Guangxi province, and river valleys in southeast Tibet province (Zong, 2020). Investigations of yeasts have been carried out mainly in the Xishuangbanna Tropical Rainforest, Yunnan province. In 2002, 584 yeast strains were isolated from the soils of this forest and 539 strains were identified in the genera *Cryptococcus*, *Debaryomyces*, *Candida*, *Saccharomyces*, *Pichia*, *Torulaspora*, *Trichosporon*, *Rhodotorula*, *Geotrichum*, *Sporidiobolous*, *Williopsis*, and *Zygosaccharomyces*, while 45 strains could not be identified at the genus level (Li et al., 2002). Later, a number of new species were described from strains isolated from rotting wood samples collected from the Xishuangbanna Tropical Rainforest and the other forests. They include *C. yunnanensis* and *C. parablackwelliae* (Zhai et al., 2019), *Deakozyma yunnanensis* (Zheng et al., 2017), *Kaz. jinghongensis* (Ke et al., 2019), *Sa. galanensis* (Huang et al., 2019), *Su. xiaguanensis* (Huang et al., 2018), and *W. menglaensis* (Chai et al., 2019). Five *Spathaspora* species, *Sp. elongata*, *Sp. mengyangensis*, *Sp. jiuxiensis*, *Sp. parajiuxiensis*, and *Sp. rosae* were discovered in the Xishuangbanna Primeval Forest Park of Jinghong and the Jiuxi Mountain Forest Park of Honghe in Yunnan province (Lv et al., 2020). The new species *Ko. hongheensis*, *Ko. ovata*, and *Ko. yamadae* were proposed based on strains from the Xishuangbanna Primeval Forest Park, Yunnan province, and the Baotianman Nature Reserve, Henan province (Chai, Gao, Li, et al., 2022). *Naumovozyma baii* was proposed from two strains obtained from the Bawangling National Park, Hainan province (Liu et al., 2012), and *T. jiuxiensis* found from the Jiuxi Mountain Forest Park, Yunnan province (Chu et al., 2022). Moreover, an investigation of the ascomycetous yeasts isolated from plant materials collected from tropical forests in Yunnan and Hainan provinces revealed three new species from flowers, namely, *C. alocasiicola*, *C. hainanensis*, and *C. musiphila*, and one new species from tree sap, namely, *C. heveicola* (Wang et al., 2008).

5 | TROPICAL FORESTS OF AFRICA AND AUSTRALASIA: UNEXPLORED BIOMES FOR YEASTS

5.1 | African tropical forests

The moist forests of the African tropical region can be divided into three major blocks: the Central and West African area, the East African coastal region, and Madagascar. These regions have distinctive floral and faunal characteristics, particularly Madagascar, which possesses a unique biota with very high levels of endemism (Sayer et al., 1992).

One interesting work on yeast ecology associated with flies of the family Drosophilidae was done by Pignal and Lachaise (1979) in the Lamto savannahs (Ivory Coast). These authors isolated yeasts from 154 flies belonging to 22 species, and obtained 150 isolates, with *Hanseniaspora* spp. and *P. membranifaciens* as the most frequently isolated species. The drosophilids fed on a large variety of yeasts. Some crops contained up to 100,000 cells, and the yeasts fermented and assimilated few carbon compounds. The largest studies of African yeasts were conducted by Johannes P. van der Walt, a South-African yeast taxonomist. He and his colleagues studied samples collected from grassland soils, arboricolous beetle infestions and other similar niches, applying a wide range of enrichment techniques, and describing 109 new species (Smith and Groenewald, 2012). Information about the ecology of the species described by van der Walt and colleagues is missing in most works. South Africa has regions with a subtropical climate, and studies on the yeast biodiversity in these biomes could yield novel species and ecological information about these microorganisms. Recently, de Vega et al., (2012, 2014, 2017) described *M. proteae*, *M. drakensbergensis*, *M. caudada*, *W. nectarea*, and *W. natalensis* based on isolates obtained from nectar of flowers of *Protea* spp. and and associated insects in South Africa. de Vega et al. (2017) reported the presence of nearly monospecific populations of *M. koreensis*, *M. reukaufii* or *C. rancensis* in more than 40 plant species pollinated mainly by bees and butterflies. The nectars of plant species pollinated by beetles were dominated by *M. proteae*, *M. drakensbergensis*, *M. caudada*, and *Wickerhamiella* species.

Grondin et al. (2015) studied the epiphytic yeasts isolated from the skins of tropical fruits collected at several locations in Madagascar and Reunion Island. Twenty-six species were identified, and the most representative were *C. jaroonii*, *C. oleophila*, *C. pararugosa*, *C. quercitrusa*, *C. railenensis*, four *Pichia* species, and *A. leucospermi*. Probably, the low diversity of yeast species associated with the fruits could be related to the enrichment methodology used for yeast isolation, and the low number (three) of each fruit collected. The fruits collected were apple, persimmon, avocado, passion fruit, rose apple, pear, pineapple, Cape gooseberry, dragon fruit, peach, and cocoa. The authors did not collect indigenous fruits of these regions, whose yeast biodiversity might be more representative of these biomes.

Koricha et al. (2019) determined the occurrence and frequency of wild yeasts associated with domestic and wild edible tree barks, fruits, and rhizosphere soil samples collected over two seasons (i.e., spring and summer) in South West Ethiopia. A hundred and eighty-two isolates were obtained from 120 samples analyzed. Sixteen genera and 27 species were identified. *C. blattae*, *P. kudriavzevii*, *Me. guilliermondii*, *C. humilis*, and *S. cerevisiae* were the most frequently isolated yeasts. Nwaefuna et al. (2023) reported the yeast communities associated with dung beetles inhabiting pristine environments in Botswana. The authors obtained a total of 97 phylogenetically diverse yeast isolates, representing 19 species belonging to 11 genera. Approximately 60% of the isolates were potentially new species because of their low internal transcribed spacer (ITS) sequence similarity when compared to the most recent optimal species delineation threshold. Based on the studies of yeast biodiversity in tropical forests of Central America, South America, and Asia, we can expect that further studies of the yeast biodiversity of African tropical forests are likely to represent a vast reservoir of novel yeast species.

5.2 | Australasia

Tropical and subtropical rainforests are found in northern and eastern Australia in wet coastal areas, notably on the Cape York Peninsula. Dry rainforests occur in subcoastal and inland areas of northern and eastern Australia and northern Western Australia. Monsoon rainforests occur in northern Australia in seasonally dry coastal and subcoastal regions. Therefore, most of the tropical rainforests in this region reside on the world's second-largest island of New Guinea. The biodiversity and ecology of yeasts associated with natural habitats have attracted little systematic research in Australasia, and most studies concern yeasts from foods and beverages, such as wine, fruit juices, soft drinks, dairy products, high-sugar products, and processed meats (Fleet 2001). Studies on the ecological interactions between yeasts, plants, and insects were carried out by Lachance, Klemens et al. (2001) in Australia and some Pacific Islands. These studies led to the description of several yeast species such as *C. tolerans* (*Metschnikowia* clade), *W. australiensis*, *M. hibisci*, *Ko. antophila*, *Ko. kadauensis*, and *S'copsis fodiens* (Lachance, Klemens, et al., 2001; Lachance et al., 2012). *Kodamaea anthophila* was the most frequently isolated species from the 400 flower and insect samples collected in the New South Wales and Queensland regions (Lachance, Klemens, et al., 2001). Lachance, Klemens et al. (2001) reported that the yeast communities of the Australian region exhibited little heterogeneity in species composition, whether at the geographic, plant species, or insect species level. According to these authors, intraspecific variation was higher in samples from

Australia compared to those from Pacific Islands. For example, both mating types of *Wick. australiensis* were well represented in Australia; they were imbalanced (8:1) in Fiji, and only one mating type was recovered on Rarotonga. Likewise, Australian *K. anthophila* formed four highly distinct colony morphologies on YM agar, compared to strains for Fiji, Rarotonga, or Hawaii, which produced only one morph. The yeast communities studied in these regions were focused on insects and flowers of morning glories and *Hibiscus* species (Lachance, Klemens, et al., 2001). Soil, bark, or rotting wood were not examined, such that tropical forests of the Australasia region still contain many unexplored yeast habitats.

6 | YEAST ECOLOGY IN TROPICAL FORESTS

Several ascomycetous and basidiomycetous yeasts are frequently isolated from tropical forest biomes, notably the large-spored *Metschnikowia* species, *Carlosrosaea*, *S. cerevisiae*, *Spathaspora*, *Sugiyamaella*, *Starmerella*, and *Wickerhamiella* species as well as others that occur at lower frequencies (Barbosa et al., 2018; de Vega et al., 2014; Lachance et al., 2020; Morais et al., 2020; Santos et al., 2015, 2018, 2023; Souza et al., 2023). Below we will review the most important works done with these yeasts, discussing their distribution and interactions with other organisms.

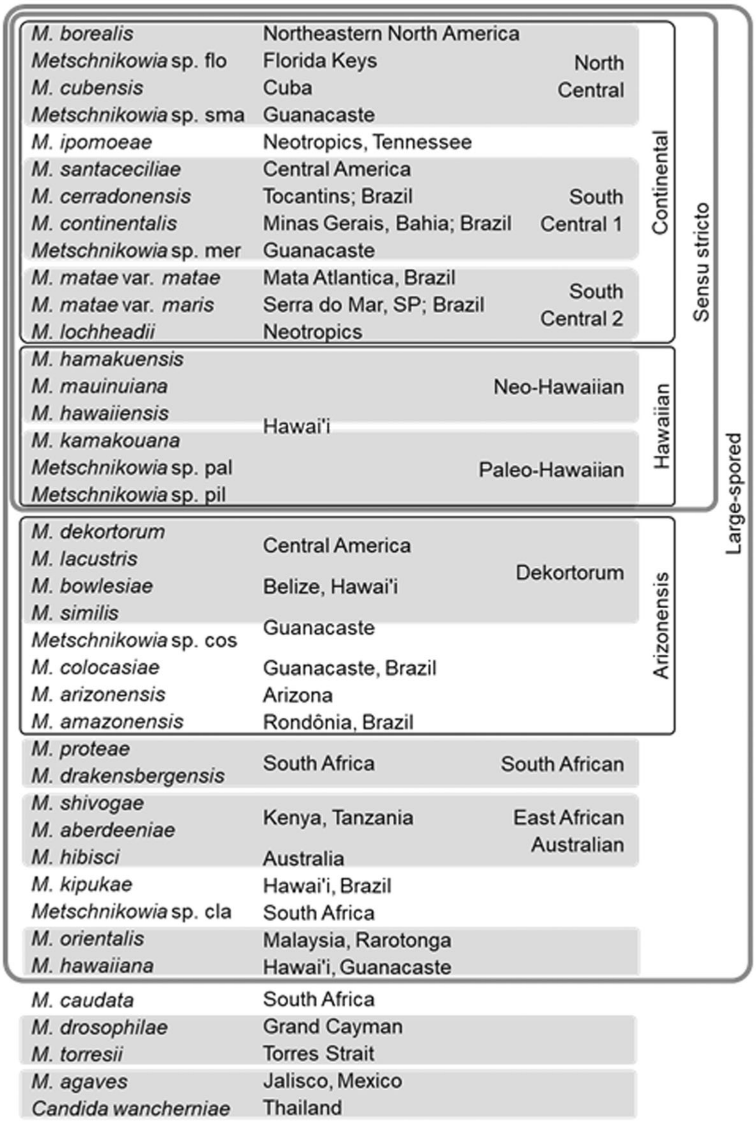
6.1 | Large-spored and other haplontic *Metschnikowia* species

Before the discovery of *M. hawaiiensis* in 1987 (Lachance et al., 1990), the genus was known from seven diplontic species, four of which occurred in marine substrates, two in association with plants, and one whose ecology remains elusive (Lachance, 2011c). In addition, two asexual species with clear affinities with *Metschnikowia* were assigned to the genus *Candida*, as was the practice at the time. Of the two, *M. rancensis*, is probably diplontic also, but we now know that *M. torresii* is a haplontic species (Lee et al., 2020), as are *M. hawaiiensis* and 29 of the other species described after 1990. These form a clade that has been referred to as “the haplontic, heterothallic *Metschnikowia* species” (Lachance et al., 2020), detailed in Figure 4. A defining characteristic of the genus as a whole is the formation of two (rarely one) needle-shaped ascospores. In haplontic species, compatible mating types conjugate to form asci and ascospores that in many cases are 10–50 times larger than the haploid parent cells, and for this reason they are termed the “large-spored *Metschnikowia* species.” Seven of these await formal description as they are known in the literature each from a single isolate (Lee et al., 2018; Santos et al., 2015), precluding the observation of the sexual cycle.

Except for *M. borealis*, which is found northward of Tennessee into eastern Canada, large-spored *Metschnikowia* species are tropical to subtropical. Whereas these species cannot be regarded as strictly forestial, their distribution often follows that of forests, because they inhabit flowers and insects often found in clearings in or near forests. The same anthropogenic pressures responsible for the loss of forest cover also threaten these flowers and their insects. Large-spored and other haplontic *Metschnikowia* species stand out by their pronounced biogeography (Figure 4), which is thought to reflect strong associations with their vector insects. The nature of the relationship is unknown; there is no direct evidence of pathogenicity, although several species exhibit some extracellular protease or lipase activities, or have the ability to form biofilms through the production of very long germ tubes (Lachance et al., 1990) reminiscent of those of *C. albicans* (Sudbery, 2011). The correlation between phylogeny and geographic distribution is most pronounced in the recently emerged “sensu stricto” subclade (Figure 4), which is further divided into two subclades, one that is endemic to Hawai'i and the other to the continental Americas. Members of the Hawaiian subclade are associated with endemic nitidulid beetles, and their distribution follows a trend where more recently emerged species tend to inhabit the younger parts of the archipelago, suggesting a succession of peripatric speciation events (Lachance et al., 2005) reminiscent of those observed in other Hawaiian endemic species (Colvin, 2018). All species of the continental subclade have been found in association with the Pan-American nitidulid genus *Conotelus*, whose phylogenetic classification remains elusive and morphological identification to species challenging at best (Murray, 1864). The beetle genus is represented by eight sequences in GenBank, only four of which are mutual orthologs. The continental large-spored *Metschnikowia* species consist of three subclades, one of which has a more northern tendency, while the other two share a Central and South American distribution. *Metschnikowia ipomoeae* occupies a lineage of its own that differs from the rest by its wider distribution, having been recovered from Tennessee to São Paulo state in Brazil. It was introduced to Hawai'i together with *Conotelus mexicanus*, as was *M. lochheadii* (Lachance et al., 2008). The species is genetically homogeneous across its range except for strains recovered from inland sites in Costa Rica, which differed from the rest at all of 12 loci examined (Wardlaw et al., 2009). Originally assigned to the asexual genus *Candida*, *M. ipomoeae* grows in a dry, hydrophobic form that reduces the propensity of complementary mating types to conjugate, which explains why the sexual cycle was not reported until somewhat recently (Santos et al., 2015). Long germ tubes are not formed. The unusual growth habit of *M. ipomoeae* may affect its vagility and account for its wider range as well as its isolation in ovules of cotton plants (Sachs et al. 2006). Although the report does not mention the presence of *Conotelus* sp. on the plants, the beetle is known to occur on cotton blossoms (Glover, 1878). All species of the sensu stricto subclade hybridize, although interspecies crosses lead to the formation of sterile asci (Lee et al., 2018).

The more ancient Arizonensis subclade is strictly Neotropical, with the exception of the eponymous species, which is known from only a single locality of the Sonoran Desert in association with *Carpophilus* sp. (Nitidulidae) of prickly pear flowers (Lachance, 2011c). Other species appear to be vectored by *Conotelus* spp. for the most part. Despite their considerable genetic distance (average nucleotide

FIGURE 4 Clade structure of haplontic *Metschnikowia* species, along with their known geographic distribution.



M. borealis	Northeastern North America	North Central	Continental	Sensu stricto	Large-spored
Metschnikowia sp. flo	Florida Keys				
M. cubensis	Cuba				
Metschnikowia sp. sma	Guanacaste				
M. ipomoeae	Neotropics, Tennessee				
M. santaceciliae	Central America	South Central 1			
M. cerradonensis	Tocantins; Brazil				
M. continentalis	Minas Gerais, Bahia; Brazil				
Metschnikowia sp. mer	Guanacaste				
M. matae var. *matae*	Mata Atlantica, Brazil	South Central 2			
M. matae var. *maris*	Serra do Mar, SP; Brazil				
M. lochheadii	Neotropics				
M. hamakuensis	Hawai'i	Neo-Hawaiian	Hawaiian		
M. mauinuiana					
M. hawaiiensis					
M. kamakouana		Paleo-Hawaiian			
Metschnikowia sp. pal					
Metschnikowia sp. pil					
M. dekortorum	Central America	Dekortorum	Arizonensis		
M. lacustris					
M. bowlesiae	Belize, Hawai'i				
M. similis	Guanacaste				
Metschnikowia sp. cos					
M. colocasiae	Guanacaste, Brazil				
M. arizonensis	Arizona				
M. amazonensis	Rondônia, Brazil				
M. proteae	South Africa	South African			
M. drakensbergensis					
M. shivogae	Kenya, Tanzania	East African			
M. aberdeeniae					
M. hibisci	Australia	Australian			
M. kipukae	Hawai'i, Brazil				
Metschnikowia sp. cla	South Africa				
M. orientalis	Malaysia, Rarotonga				
M. hawaiiana	Hawai'i, Guanacaste				
M. caudata	South Africa				
M. drosophilae	Grand Cayman				
M. torresii	Torres Strait				
M. agaves	Jalisco, Mexico				
Candida wancherniae	Thailand				

identity = 83%; Lachance et al., 2020), *M. amazonensis* and *M. arizonensis* mate profusely, the hybrids giving rise to abundant sterile asci (Santos et al., 2020). Mating reactions between these and other subclade members are poor. *M. colocasiae* forms convoluted colonies reminiscent of those of *M. ipomoeae*. Interfertility patterns among the four species of a late-emerging subclade are less sharply defined, such that assignment of the isolates to species based on both reproductive isolation and phylogenetic patterns was not without some difficulty (Lee et al., 2020). The distribution of the subclade is Mesoamerican except for *M. bowlesiae*, for which one mating type was recovered in Hawai'i from a *Conotelus* specimen and a native (*Prosopeus subaeneus*) nitidulid, the two from the same patch of morning glories. The other mating type was isolated from four *Conotelus* specimens in various flowers in a Belizean locality.

Isolates of *M. drakensbergensis* and *M. proteae* came from nectar or insects of *Protea* spp. flowers in the KwaZulu-Natal province of South Africa (de Vega et al., 2012, 2014). The insects were primarily scarab beetles, bees, and drosophilids. East African species came from meloid and buprestid beetles as well as drosophilids of native morning glories (Lachance, 2011c). They form a clade with *M. hibisci*, which is known from nitidulid beetles of the genus *Aethina* found in flowers of morning glories and *Hibiscus* spp. in a broad range of eastern Australian localities.

Metschnikowia kipukae is known from many isolates from Hawai'i Island as well as Brazilian localities. All isolates have the mating type α and do not mate with mating type *a* of other species. Similarly, several isolates of *M. hawaiiana*, isolated in Hawai'i and Costa Rica, have mating type *a* but do not hybridize—a strain reported as mating type α by Lee et al. (2018) had been misidentified and has been reassigned to *M. kipukae*. *Metschnikowia orientalis* is known from two mating types *a* strains from Rarotonga and a single α strain from the Cameron Highlands of Malaysia, all from nitidulid beetles.

Although not considered members of the large-spored clade, a few other haplontic *Metschnikowia* species are worth mentioning. South African *M. caudata*, found in the nectar of *Protea* species (de Vega et al., 2014), forms long, thin, flexuous asci containing a single tapered ascospore with a swollen end, a morphology that is unique among ascomycete yeasts. It shares habitats with *M. drakensbergensis*. The two mating types of *M. drosophilae* were isolated from morning glories flowers and drosophilids on Grand Cayman Island (Lachance, 2011c). Mating is sparse and attempts at hybridization with *M. torresii*, a related marine isolate, did not succeed. The two mating types of *M. agaves* remain known exclusively from Mexican blue agave, and no information is available on its interfertility with *C. wancherniae*, known from three strains recovered from leaves and frass in Thailand (Nakase et al., 2009), or the intriguing *Metschnikowia* cf. *typographici*, regrettably known only from low magnification photomicrographs and electron micrographs of cross-sections (Kleespies et al., 2017). The kinship of this yet-to-be-cultured species was inferred by sequencing DNA amplified directly from the unpurified gut content of bark beetles in Austria.

6.2 | Genus *Saccharomyces*

Although several species of the genus *Saccharomyces* are mostly known from their application in human-driven fermentations, it is now well-established that most *Saccharomyces* species have a natural ecology and are distributed in natural settings (Alsammar & Delneri, 2020; Boynton & Greig, 2014; Liti, 2015; Sampaio & Gonçalves, 2017). Because the more detailed studies on the natural distribution and ecology of *Saccharomyces*—that is, those combining comprehensive sampling strategies with accurate molecular identifications—were focused on temperate regions of the Northern Hemisphere (e.g., Sampaio & Gonçalves, 2008; Sniegowski et al., 2002), knowledge is more advanced for those climates. These studies revealed the widespread association of *Saccharomyces* spp. with the bark of trees of the Fagaceae family (or soil underneath these trees), with relevance to oaks (*Quercus* spp.) (Sampaio & Gonçalves, 2017). Given that Fagaceae are mostly distributed in temperate regions, the ecological preferences of *Saccharomyces* spp. in tropical regions remained mostly unknown despite anecdotal reports of isolation of individual strains (Morais et al., 2006; Nakase et al., 2006; Naumov et al., 1995).

In one of the few more structured studies carried out in tropical forests, Barbosa et al. (2016) collected 545 samples, preferentially from tree barks of various native trees in Brazil (71% of the samples), but also including soil, moss, mushrooms, plant inflorescences, and fruits. They surveyed the Atlantic rainforest biome, which in some cases included contact zones with "Cerrado" (savannah) and "Caatinga," and the Amazonian Forest biome. Among the native trees sampled, *Tapirira guianensis* (Anacardiaceae), a common tree in Brazil especially in riparian areas, emerged as a possible tropical habitat of *Saccharomyces* with a frequency of isolation of 13%. All 34 strains isolated from this tree were found to belong to *S. cerevisiae* and the reported success rate of isolation was comparable to what had been reported in other studies involving this species in the Northern Hemisphere (Wang et al., 2012). The reason why only *S. cerevisiae* was isolated might reside in the temperature preferences of the various species in the genus, being *S. cerevisiae* and *S. paradoxus* the more heat tolerant (Gonçalves et al., 2011). These are, therefore, the species more likely to be found in tropical regions. Indeed, besides *S. cerevisiae*, rare strains of *S. paradoxus* were isolated in Brazil, originally under the name *S. cariocanus*, today a synonym of *S. paradoxus* (Naumov et al., 2000). The predominance of *S. cerevisiae* over *S. paradoxus* in tropical environments might also reside on temperature preferences, since laboratory experiments have shown that wild *S. cerevisiae* strains grow optimally at temperatures that are approximately 7°C higher than those preferred by *S. paradoxus* (Sweeney et al., 2004). Moreover, a statistical model predicted that the potential geographical range for *S. cerevisiae* is mostly subtropical or tropical, contrary to a predicted temperate distribution for *S. paradoxus* (Robinson et al., 2016).

Besides South America, *S. cerevisiae* has also been isolated in tropical forests in Asia. A *Saccharomyces* survey conducted in China reported the isolation of *S. cerevisiae* from rotten wood and tree bark in subtropical and tropical regions in southern China (Wang et al., 2012), and a more recent publication reported also the occurrence of *S. paradoxus* in Chinese subtropical forests (He et al., 2022). Rainforest *S. cerevisiae* isolates from Hainan, a tropical island in southern China, belonged to distinct wild populations, some of them very diverged from the bulk of *S. cerevisiae* lineages known worldwide and showing considerable levels of reproductive isolation (Wang et al., 2012). This increased genetic diversity of *S. cerevisiae* in tropical and subtropical regions in Eastern Asia was further expanded with the discovery of novel highly diverged lineages in Taiwan (Lee et al., 2022). The distribution of *S. cerevisiae* in tropical regions also includes Southeast Asia, with reports referring to its occurrence in inflorescences of bertam palms (*Eugeissona tristis*) in Malaysia (Wiens et al., 2008). In Thailand, *S. cerevisiae* has been isolated from the sap of several palms, namely, coconut (*Cocos nucifera*), palmyra (*Borassus flabellifer*), and nipa (*Nypa fruticanspalms*) (Limtong et al., 2020). Given that the isolation procedures were done on sap collected by humans on natural or cultivated palms, these are not typical forest isolates. Nevertheless, the finding of *S. cerevisiae* and not of other species in the genus might be an indication that the tropics might harbor mostly, if not only, this species. Similarly, a study conducted in Africa reported the isolation of a few strains of *S. cerevisiae* from native trees or their fruits in South Africa (Han et al., 2021). In fact, reports on the isolation of *Saccharomyces* species other that *S. cerevisiae* in tropical or subtropical forests are scarce and might correspond to exceptional situations. For example, Naumov et al. (2013) reported the isolation of *S. arboricola* and *S. kudriavzevii* in Taiwan, but the isolates were obtained in a mountainous region and therefore in cooler habitats.

6.3 | Genus *Spathaspora*

The genus *Spathaspora* contains species that ferment ᴅ-xylose to ethanol or convert this pentose to xylitol, traits with biotechnological potential for obtaining bioproducts through the fermentation of lignocellulosic materials (Cadete & Rosa, 2018; Santos et al., 2023). Most species were isolated from rotting wood samples or associated passalid beetles in tropical forest biomes in Brazil and China, except by *Sp. passalidarum* whose holotype was obtained from the gut of *Odontotaenius disjunctus*, a passalid wood-boring collected in state of Louisiana, United States, in a region that could be considered of subtropical climate. This yeast was also isolated from rotting wood in the Boatianman Nature Reserve in Central China, characterized by a typical warm-temperate natural landscape and typical climate features of the transition zone (Ren et al., 2014). However, most isolates of this species were obtained in the Brazilian Amazonian rainforest biome (Cadete et al., 2012; Souza et al. 2017). This species occurs in the Amazonian rainforest in rotting wood or passalid beetles associated with this substrate. Another 20 species of *Spathaspora* are known (Souza et al., 2023), with 13 species obtained from Brazilian ecosystems, six from China, and one from Panamá. Interestingly, among the Brazilian species, *Sp. passalidarum*, *Sp. roraimensis*, *Sp. suhii*, *Sp. boniae*, *Sp. brunopereirae*, *Sp. domphillipsii*, *Sp. xylofermentans*, and *Sp. brasiliensis* were obtained exclusively from Amazonian biomes. By contrast, *Sp. arborariae*, *Sp. boniae*, *Sp. girioi*, *Sp. gorwae*, *Sp. haegerdaliae*, *Sp. piracicabensis*, and *Sp. materiae* were isolated from the Atlantic Rain Forest or ecotone zones between Cerrado and Atlantic Rain Forest biomes (Cadete & Rosa, 2018; Souza et al., 2023). This geographical distribution may be related to the presence of different insect vectors, probably passalid beetles, in each region.

6.4 | The *Wickerhamiella/Starmerella* (W/S) clade

The genera *Starmerella* and *Wickerhamiella* form a clade (W/S clade) that branches close to the genus *Yarrowia* in the Saccharomycotina species tree. Most species are associated with flowers and floricolous insects (Gonçalves et al., 2020). Although some species exhibit a cosmopolitan distribution, most *Starmerella* and *Wickerhamiella* species appear to be endemic to specific regions or have a restricted distribution (Gonçalves et al., 2020; Santos et al., 2018; de Vega et al., 2017). Most species have been isolated in the tropical and subtropical biomes in South and Central America, Asia, Australia, and Africa. While the W/S clade is generally associated with the floral niche, *Starmerella* and *Wickerhamiella* species show some degree of niche partitioning, some species being mostly associated with either flowers, bees, or other floricolous insects. To which extent niche portioning is reflective of the multiple phylogenetic subclades observed within this clade (Gonçalves et al., 2020) remains an open question.

The genus *Starmerella* includes approximately 50 species and the majority were isolated from bees and substrates visited by these insects, suggesting an ecological relationship between the yeasts and the insect (Figure 5). Indeed, the potential benefits of the yeasts to the bees have been recently proposed (Pozo et al., 2020). Many *Starmerella* species are found primarily in the neotropical biomes, and most species seem to be restricted to certain regions possibly following the geographic distribution of their insect vectors (de Paula et al., 2021; Januário da Costa Neto & Benevides de Morais, 2020). Only two ascoporogenous species are known, *St. bombicola* and *St. meliponinorum*. The others are known only from their asexual stages. Some species, namely, *St. batistae*, *St. cellae*, and *St. riodocensis*, were described as associated with solitary bees. Female solitary bees are mass-provisioning, and all the floral resources for larval development are placed within a brood cell. Once the cell is closed, the female has no further contact with her developing offspring (Danforth et al., 2019). Yeasts appear to be an important component of the provisioned pollen and nectar, and may be an important element of the bee's larval nutrition (Danforth et al., 2019; Rosa et al., 1999). There are approximately 20,000 solitary bee species, and most occur in tropical forest biomes. Investigation of the interaction between *Starmerella* species and solitary bees is promising and it is hoped to lead to the elucidation of the role of these microorganisms in the bee nests.

Species such as *St. meliponinorum*, *St. apicola*, *St. neotropicalis*, *St. etchellsii*, and *St. bombicola* have been isolated from stingless bees (Meliponini). These bees are represented by approximately 550 species and 61 genera, and are found in all tropical and subtropical regions of the world (de Paula et al., 2021). Paludo et al. (2018, 2019) reported an interesting interaction among two possible new species of the genera *Zygosacharomyces* (*Zygosacharomyces* sp.; GenBank KY766262) and *Starmerella* (*Candida* sp. strain SDCP2; GenBank KX999555) in nests of the stingless bee *Scaptotrigona depilis*. The *Starmerella* species produces ethanol and isoamyl alcohol, which stimulate the growth of *Zygosaccharomyces* sp. Ingestion of *Zygosaccharomyces* sp. by the larvae of *S. depilis* is essential for the survival and metamorphosis of these bees. This yeast provides essential steroid precursors to the developing bee. Insect pupation requires ecdysteroid hormones, and as larvae of this stingless bee cannot synthesize sterols *de novo*, the bee obtains steroids in its diet by ingesting *Zygosaccharomyces* sp. cells (Paludo et al., 2019). The co-occurrence of *Starmerella* and *Zygosaccharomyces* species in bee nests suggests an important role of these yeasts for larval bee development. Interestingly, *Starmerella* and *Zygosaccharomyces* species encompass mostly fructophilic species, which prefer fructose over glucose when both sugars are present at high concentrations. Fructophily is thought to have evolved in yeasts through the horizontal acquisition of a high-capacity fructose transporter (Ffz1) from a species related to *Monascus* (Pezizomycotina) by the ancestor of the W/S clade (Gonçalves et al., 2016). A subsequent horizontal transfer of Ffz1 from the W/S clade to the *Zygosaccharomyces* ancestor apparently introduced fructophily into the latter clade (Gonçalves et al., 2016). Ffz1-associated fructophily is thought to be an adaptation to the floral niche, a hypothesis that is in line with the finding of all three taxa involved in the horizontal dissemination of Ffz1 (*Monascus*, *Starmerella*, and *Zygosaccharomyces*) in association with stingless bee pollen and bee bread (Paludo et al., 2019). Other horizontal gene transfer events into the W/S clade have been reported that may affect multiple aspects of their adaptation to the floral environment (Gonçalves et al., 2020; Kominek et al., 2019).

FIGURE 5 Stingless and solitary bees, and Passalid beetles. Entrance of the nest of the stingless bee *Lestrimelitta* sp. (a); entrance of the nest of the stingless bee *Nannotrigona* sp. (b); view of the nest of the stingless bee *Tetragosnica angustula* (c); collection of honey in a nest of *Scaptotrigona* sp. (d); nests on the ground of the solitary bee *Diadasina distincta* (e); larva of Passalid beetle (f); and adult of Passalid beetle (g).

Exploring the association between these events and the ecology of these yeasts is therefore an interesting aspect for future research. Several species of *Starmerella* have been described in recent years, mostly from flowers collected in Central and South America and Asia. These studies show the wide distribution of the genus in tropical forest ecosystems, but the true ecological niches of many of these species remain to be determined.

Yeast species of the genus *Wickerhamiella* also exhibit nutritional specialization. Most are associated with flowers, fruits, leaves, insects, and mushrooms. The first species described, *W. domercqiae*, was based on two isolates, one from a wine vat in South Africa and the other from a sugar cane factory in Brazil. Lachance et al. (1998) described five additional species. *Wickerhamiella australiensis* was isolated from flowers and floricolous insects of Australian *Hibiscus* trees and *Ipomoea* sp. in tropical areas of Australia. *Wickerhamiella cacticola* has been isolated in cactus flowers in all regions of Brazil where they were sampled (Freitas et al. 2020). This species is vectored by a nitidulid beetle and other insects among the cactus flowers. *Wickerhamiella occidentalis* was found in *Ipomoea* spp. flowers collected in Hawaii, Central and South America, as well as Tennessee. This yeast is also vectored by nitidulid beetles (mainly *Conotelus* spp.) among morning glory flowers. *Wickerhamiella drosophilae* was isolated from flowers of *I. indica* and from *D. floricola* that congregate on the flowers in Hawaii. The yeast was also isolated from flowers collected in Brazil and in Costa Rica. *Wickerhamiella lipophila* was likewise isolated from flowers of *I. indica* and their associated insects in Hawaii. These species produce strong extracellular lipases (Lachance et al., 1998). The species descriptions were followed by many more, such that the genus now accommodates approximately 45 species. Although some exhibit a cosmopolitan distribution, most appear to be endemic to specific regions, mainly in the Neotropics and in Asia. Some species, for example, *W. versatilis*, have been isolated also from hives of stingless bees (Tiago et al., 2022) or from floral nectar of tropical plants (Canto et al., 2017). They have also been frequently used as starter cultures for soy sauce fermentation (van der Sluis et al., 2001; Wang et al., 2022). The most recent species described was *Wick. nakhonpathomensis* and *Wick. bidentis*. The first was isolated from the fruiting body of a *Coprinus* species and from the inflorescence of a *Coffea* species collected in Thailand, and the second from flowers and insects collected in Japan (Khunnamwong et al., 2022; Seike et al., 2023).

6.5 | Genus *Sugiyamaella*

Wood-ingesting passalid beetles and rotting wood have been suggested as habitats for many species of the genus *Sugiyamaella* (Souza et al., 2023; Urbina et al., 2013). Passalids are commonly found in fallen tree trunks, and in these habitats, the beetles find food, shelter, and conditions for breeding (Figure 5). Many species of *Sugiyamaella* are xylanase producers, an ability that could confer an adaptative advantage in the colonization of the gut of beetles inhabiting rotting wood (Sena et al., 2017). The genus accommodates 35 species, most of which have been isolated from insects that inhabit rotting wood, rotten lignocellulosic materials, soil, mushrooms, or peat (Souza et al., 2023). Urbina et al. (2013) reported the isolation of 771 yeast cultures from the gut of 16 passalid species collected in nine localities in Guatemala. Seventy-nine isolates belonged to species of the *Sugiyamaella* clade, representing 10% of the isolated yeasts, with several undescribed species. Chai, Gao, Yan et al. (2022) described *Su. cylindrica* and *Su. robnettiae* obtained from rotting wood collected in the Tianchi Mountain National Forest Park located near Luoyang City, Henan Province, China. Souza et al. (2023) described the species *Su. beilyi* and *Su. amazoniana* from guts of Amazonian passalids and their habitats, and reported the occurrence of other 21 candidates for possible novel *Sugiyamaella* species associated with these beetles in this region. These results show that the characterization of the ecological niches of *Sugiyamaella* species may yield new insights into the ecological relationships of these yeasts with passalid beetles and their associated substrates in tropical and subtropical forest biomes.

6.6 | Other ascomycetous yeasts from tropical forests

Metahyphopichia, with the single species *M. laotica*, was a genus proposed by Sipiczki et al. (2016) to accommodate six strains isolated in Laos and Brazil. These strains alternate between yeast and filamentous growth morphologies and were isolated from flowers in Laos and tree barks in Brazil. Later, Khunnamwong et al. (2022) described *M. suwanaadthiae* based on isolates obtained from mushrooms, insects, and soil in Thailand. These authors transferred *C. silvanorum* to the genus *Metahyphopichia* as a new combination, *M'pichia silvanorum*. This yeast was isolated from the gut of a hansome fungus beetle (*Amphix laevigatus*) in Barro Colorado Island, Panama, and from cerambycid larvae on a rotting log in Louisiana, USA (Lachance et al., 2011). The geographic distribution of these species suggests that the genus *Metahyphopichia* is associated with substrates, possibly insects, of tropical biomes. Another genus that could be associated with tropical regions is *Savitreea*, as *Sav. pentosicarens*, the single species of the genus, was isolated in Thailand and French Guiana. The same could be suggested to *Hagleromyces aurorensis*, as this species was isolated from bromeliads in a Cerrado biome in Brazil. Species of the genera *Suhomyces* and *Teunomyces* have been preferentially isolated from mushrooms and fungus-feeding insects in tropical forests (Jadhav et al., 2020; Kurtzman et al., 2016). Several other ascomycetous genera have species isolated from tropical and temperate forests, for instance, *Hanseniaspora*, *Kazachstania*, *Kluyveromyces*, and *Starmera*. Some species of these genera were only isolated from tropical biomes: *Hanseniaspora nectarophila*, *Kaz. jinghongensis*, *Kaz. menglunensis*, *Kaz. rupicola*, *Kaz. serrabonitensis*, *K. starmeri*, and *Starmera ilhagrandensis*.

6.7 | Basidiomycetous species

Some basidiomycetous genera such as *Dioszegia*, *Kockovaella*, and *Phaffia* were only recently reported as occurring in tropical biomes (Gomes et al., 2015, 2016; Li et al., 2020; Santos et al., 2021). These yeasts have been isolated from plant leaves and tree bark in temperate forest biomes or cold aquatic environments (Trochine et al., 2017; David-Palma et al., 2020; Li et al., 2020). Other basidiomycetous genera have been only reported from substrates of different tropical ecosystems (Felix et al., 2017; Li et al., 2020). Species of the genus *Carlosrosaea* were described as associated with bromeliads in Brazil (Felix et al., 2017). Two species, *Ca. hohenbergiae* and *Ca. vrieseae*, were obtained from bromeliads collected in Atlantic Forest fragments in Northeastern Brazil. *Ca. aechmeae* was isolated from phytotelmata of the bromeliad *Vriesea minarum* in a tropical rupestrian field site (altitudinal fields) in Southeastern Brazil, and from leaves of bromeliads collected in a subtropical biome in South Brazil. Li et al. (2020) described two additional species of *Carlosrosaea*, *Ca. foliicola* and *Ca. simaoensis*, isolated from leaves in tropical and subtropical zones, respectively, in China. Marques et al. (2021) reported that *Ca. vrieseae* was able to produce indole-3-acetic acid (IAA) and siderophores, and had the ability to solubilize phosphate. Filtrate containing IAA-like compounds produced by this yeast improves development and photosynthetic performance in *V. minarum* seedlings, causing them to grow as well as when treated with commercial IAA, suggesting a potential use of the yeast as biofertilizer agent.

Phaffia brasiliana is a basidiomycetous yeast recently described from the soil in a Cerrado-Atlantic Rain Forest ecotone in Brazil (Santos et al., 2021). The genus *Phaffia* is of practical importance as it is the only yeast genus that produces the biotechnologically relevant pigment astaxanthin. Until the description of *P. brasiliana*, the distribution of the other four species in the genus encompassed solely environments with temperate climates (David-Palma et al., 2020). Therefore, it was assumed that the range of *Phaffia* does not include tropical regions. Likewise, the moderate temperatures of the region where *P. brasiliana* was found and the maximum growth temperature of this species around 30–32°C, suggest that this species is specifically adapted to the ecosystem where it was found and not to tropical climates in general (Santos et al., 2021).

Species of the genera *Occultifur*, *Hannaella*, *Jaminaea*, and *Tremella* are frequently isolated from leaves, bromeliads, flowers, and soil in different tropical biomes (Gomes et al., 2015; Surussawadee et al., 2015; Navarro et al., 2022). However, these basidiomycetous genera are cosmopolitan, with species occurring in tropical and temperate forests. Except for a few genera, for example, *Phaffia*, the biogeography of basidiomycetous yeasts has been little studied, and should be considered in further ecological studies, especially in tropical biomes.

7 | TROPICAL FORESTS AS A SOURCE OF YEASTS FOR BIOINNOVATION

In this section, we will consider the studies that aimed at discovering species with biotechnological interest. Buzzini and Martini (2002) screened 196 strains of ascomycetes (representative of 23 species of 8 genera), 155 of basidiomycetes (representative of 10 species of 3 genera), and 46 yeast-like organisms (*A. pullulans*) with the aim of investigating the extracellular enzymatic activity profile of yeasts. These yeasts were isolated from the three sites of Brazilian Atlantic Rain Forest biome, and yeasts were obtained from 120 samples of water, insect, soil, and plant materials. The isolates were tested for amylase, esterase, lipase, protease, pectinase, chitinase and cellulase activities using agar plate-based methods. Although the work employed taxonomic identification using classical morphological and biochemical methods, meaning that the number of species might differ from the current consensus, it also demonstrated the huge potential of tropical yeasts as a source mainly of esterase, lipase, and protease activities. Later, the same research group took advantage of a subset of these strains, namely, 98 ascomycetes (representative of 40 species belonging to 12 genera) and characterized them in terms of volatile organic compounds (VOC), such as alcohols, aldehydes, and esters, which can potentially be used in the food, beverage, cosmetics, or pharmaceutical industries, mainly as flavoring agents (Buzzini et al., 2003). The study demonstrated the potential of such yeasts as VOC producers, since all but two of the strains produced the 11 analyzed VOCs to at least some extent. Also using the same yeast collection, these authors evaluated the capacity of the strains to produce killer toxins, which could be explored for their antimicrobial activity (Buzzini et al., 2004).

In the search for enzymes with transfructosylating activity, Maugeri and Hernalsteens (2007) isolated yeast strains from Brazilian biomes, namely, Pantanal, Cerrado, Atlantic, and Amazon Forests. From the 495 strains initially isolated, 130 presented some activity over sucrose, from which 4 were selected as potential producers of fructooligosaccharides (FOS), which can be used as prebiotics in human and animal nutrition. One strain of *Rhodotorula* was capable of producing FOS at high levels (>100 g/L), without hydrolyzing the product.

Cadete et al. (2009) collected 25 samples of rotting wood in Atlantic Forest biomes of Brazil (two different locations) and inoculated each into a defined xylose- or xylan-containing medium, with antibiotics, to allow for yeast growth. After isolation and characterization procedures, the new species, *Sp. arborariae*, was found to be capable of fermenting xylose into ethanol at high rates (specific growth rates of ~0.35 1/h) and yields (~0.50 g ethanol/g xylose). This species might provide a source of new genes, enzymes or transporters, to engineer industrial strains for efficient ethanol production from lignocellulosic feedstocks. Indeed, in a later work, it was shown that a gene taken from a strain of *Sp. passalidarum* isolated in Louisiana (United States) was key to enable anaerobic growth and ethanol production from xylose in an engineered *S. cerevisiae* strain (Cadete et al., 2016).

Other initiatives include the isolation of a strain of *Pa. flavescens* from the phylloplane of a tree in Karnataka (India) which produces exopolysaccharides (Aravind et al., 2014), which in turn can be used in the food, cosmetics, and pharmaceutical industries (Rahbar Saadat et al., 2021). The isolation of 101 yeast strains (belonging to 26 species) from the skin of tropical fruits collected in Madagascar and the Reunion islands and the characterization of their VOC-producing profiles (52 different molecules were identified, acids, alcohols, ketones, aldehydes, or esters) (Grondin et al., 2015). Another was the isolation of yeasts from peat in Southern Thailand and subsequent screening for the production of ethanol (from glucose and xylose), indole-3-acetic acid (a plant growth promoter), and some extracellular enzymes (cellulases, xylanases, pectinases, amylases, proteases, and lipases) (Jaiboon et al., 2016). Yet another example is the bioremediation potential of pyrene (a polycyclic aromatic hydrocarbon) of a strain of *Candida* sp. isolated from a tropical forest in Malaysia (Hadibarata et al., 2017).

Given the small number of studies targeting the exploration of tropical yeast biodiversity for potential biotechnological applications, there is an urgent need to intensify targeted studies, particularly considering the climate emergency and the necessity to replace fossil feedstocks and traditional chemical processes for renewable feedstocks and biotechnological processes. Yeasts or yeast products have applications in areas as diverse as fermented food and beverages, pharmaceuticals, enzymes, vitamins, carotenoids, lipids, steroids, polysaccharides, glucans, nucleotides, flavors, biofuels, platform chemicals (sometimes called building blocks), and even biocontrol and bioremediation (Deak, 2009). Another strategy that could be adopted is to include high-throughput screening methods to detect different biotechnological traits in yeast strains isolated both in large- and small-scale studies on yeast, fungal, or even microbial biodiversity in tropical forest environments.

8 | CONCLUDING REMARKS

Most studies carried out on yeast diversity in tropical forest biomes were performed using culture-based methods, and almost always using only one culture medium and one incubation temperature, which only allow the growth of selected microorganisms. This may be a factor that negatively affects the yeast diversity indices found in the studies presented in this review. The use of different culture media and incubation temperatures for yeast isolation has shown that many species are only isolated in a certain culture medium and a certain temperature. Another limitation is the possible occurrence of nonculturable species. A better view of the yeast diversity in forest biomes could arise from the use of DNA metabarcoding approaches, as they provide detailed access to the diversity of microorganisms. Culture-independent techniques could give a more precise picture of the yeast diversity of tropical forest biomes and show whether the diversity in these environments is higher than that found in temperate forest ecosystems. However, fewer studies are published on yeast biodiversity in tropical forest ecosystems when one takes into account the complexity of available habitats and the ecological interactions involved. Most of the work was carried out in the search for new yeast species, and many important aspects of their ecological niche remained unexplored. Compared to studies performed in temperate forests, we are still beginning to understand the diversity of yeasts in tropical forest environments. Thus, more studies are necessary, including works using metagenomic approaches, to gain a better understanding of the ecological role of yeasts in these biomes.

As described in this review, recent studies in Brazilian Amazon rainforest biomes have shown the occurrence of about 30%–50% of candidates for new species. Studies need to be carried out urgently in the tropical forest biomes of Africa, Australia, and the Pacific Islands with high biological diversity. There are several gaps in our knowledge of the occurrence, geographical distribution, and role in the ecosystem functioning of the yeast communities in tropical forests. Topics for investigation are diverse and should include: (i) estimation of the diversity of yeast communities of tropical forests in comparison to temperate forests and other biomes; (ii) assessments of the geographical distribution of the yeast species in tropical forest ecosystems across latitudinal gradients, using culture-based and culture-independent techniques; (iii) identification of which species are truly indigenous for tropical forest biomes; (iv) understanding of how the tropical yeast species contribute to the ecosystem functioning; (v) identification of tropical yeast species to be used for assisting future conservation and forest restoration programs; (vi) use of high-throughput screening to survey metabolites and other products of tropical yeasts for bioinnovation proposals.

Most of the tropical forests are in the process of deforestation due to human activity. Thus, the discovery of new microorganisms with potential applications in bioinnovation may be outrun by the loss of microbial diversity. As developing countries are where most tropical forests are located, they have the most to gain economically from an invigorated microbial biodiversity exploration program.

AUTHOR CONTRIBUTIONS

All authors participated in manuscript planning and review of the final draft. Carlos A. Rosa, Marc-André Lachance, Savitree Limtong, Melissa F. Landell, Paula B. Morais, Carla Gonçalves, and Paula Gonçalves conceptualized the manuscript and edited the final draft for submission. Ana R. O. Santos, Aristóteles Góes-Neto, Rosângela Santa-Brígida, Marlúcia B. Martins, Daniel H. Janzen, and Winnie Hallwachs participated of sample collection, yeast identification, and data analyses. Carlos A. Rosa, Paula B. Morais, and Melissa F. Landell wrote the introduction and the section on yeasts in South America. Marc-André Lachance wrote the section on yeasts from Costa Rica and large-spored *Metschnikowia* species. Savitree Limtong wrote the section on yeasts from Asian forests. José P. Sampaio wrote the section on the genus *Saccharomyces*. Carlos A. Rosa wrote the section on the genera *Spathaspora* and *Sugiyamaella*. Carlos A. Rosa, Paula Gonçalves, and Carla Gonçalves wrote the section of the clade *Wickerhamiella/Starmerella*. Carlos A. Rosa and José P. Sampaio wrote the section on basidiomycetous yeasts. Andreas K. Gombert wrote the section on yeasts as sources for bioinnovation.

ACKNOWLEDGMENTS

The authors would like to thank three anonymous reviewers for their feedback, which has helped improve this manuscript. This work is a part of the project "INCT Yeasts: Biodiversity, preservation, and biotechnological innovation," funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brasília, Brazil, Grant #406564/2022-1. This work was also funded by CNPq Grants Numbers 457499/2014-1, 311553/2018-4, 312889/2021-6, and 408733/2021-7, Fundação do Amparo a Pesquisa do Estado de Minas Gerais (FAPEMIG, process number APQ-01525-14), and the Natural Science and Engineering Research Council of Canada (Marc-André Lachance). Paula Gonçalves was supported by Grant PTDC/BIA-EVL/1100/2020 and Carla Gonçalves by Grant PTDC/BIA-EVL/0604/2021, both from FCT/MCTES, Portugal.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Carlos A. Rosa http://orcid.org/0000-0002-0056-9075
Marc-André Lachance http://orcid.org/0000-0001-9139-3935
Melissa F. Landell http://orcid.org/0000-0001-6848-0803
Andreas K. Gombert http://orcid.org/0000-0001-9557-3773
Paula B. Morais http://orcid.org/0000-0002-5050-5766
Paula Gonçalves http://orcid.org/0000-0003-2103-1060

REFERENCES

Aksornkoae, S. (1999). *Mangrove: Ecology and Management*. Kasetsart University Press.

Allard, S. M., Costa, M. T., Bulseco, A. N., Helfer, V., Wilkins, L. G. E., Hassenrück, C., Zengler, K., Zimmer, M., Erazo, N., Mazza Rodrigues, J. L., Duke, N., Melo, V. M. M., Vanwonterghem, I., Junca, H., Makonde, H. M., Jiménez, D. J., Tavares, T. C. L., Fusi, M., Daffonchio, D., … Bowman, J. (2020). Introducing the mangrove microbiome initiative: Identifying microbial research priorities and approaches to better understand, protect, and rehabilitate mangrove ecosystems. *mSystems*, *5*(5):e00658-20. https://doi.org/10.1128/mSystems.00658-20

Alsammar, H., & Delneri, D. (2020). An update on the diversity, ecology and biogeography of the *Saccharomyces* genus. *FEMS Yeast Research*, *20*, foaa013. https://doi.org/10.1093/femsyr/foaa013

Aravind, K., Naik, T. P., & Krishnaswamy, K. (2014). Exopolysaccharide production potential of yeast *Cryptococcus flavescens* SK01 strain from the phylloplane of *Semecarpus kathalekanensis*. *Journal of Pure and Applied Microbiology*, *8*(4), 3339–3343.

Banin, L. F., Phillips, O. L., & Lewis, S. L. (2015). Tropical forests. In S. H. Kelvin, R. T. Corlett, & Y. Bergeron (Eds.), *Routledge handbook of forest ecology* (pp. 56–75). Routledge.

Barbosa, R., Almeida, P., Safar, S. V. B., Santos, R. O., Morais, P. B., Nielly-Thibault, L., Leducq, J.-B., Landry, C. R., Gonçalves, P., Rosa, C. A., & Sampaio, J. P. (2016). Evidence of natural hybridization in Brazilian wild lineages of *Saccharomyces cerevisiae*. *Genome Biology and Evolution*, *8*, 317–329. https://doi.org/10.1093/gbe/evv263

Barbosa, R., Pontes, A., Santos, R. O., Montandon, G. G., de Ponzzes-Gomes, C. M., Morais, P. B., Gonçalves, P., Rosa, C. A., & Sampaio, J. P. (2018). Multiple rounds of artificial selection promote microbe secondary domestication—The case of Cachaça yeasts. *Genome Biology and Evolution*, *10*(8), 1939–1955. https://doi.org/10.1093/gbe/evy132

Barriga, E. J. C., Barahona, P. P., Tufino, C., Bastidas, B., Guaman-Burneo, C., Freitas, L. F., & Rosa, C. A. (2014). An overview of the yeast biodiversity in the Galapagos islands and other Ecuadorian regions. In O. Grillo (Ed.), *Biodiversity—The dynamic balance* (pp. 193–232). IntechOpen. https://doi.org/10.5772/58303

Barros, K. O., Alvarenga, F. B. M., Magni, G., Souza, G. F. L., Abegg, M. A., Palladino, F., da Silva, S. S., Rodrigues, R. C. L. B., Sato, T. K., Hittinger, C. T., & Rosa, C. A. (2023). The Brazilian Amazonian rainforest harbors a high diversity of yeasts associated with rotting wood, including many candidates for new yeast species. *Yeast*, *40*(2), 84–101. https://doi.org/10.1002/yea.3837

Barros, L. A., Mendonça, B. A. F., Sothe, C., Fernandes-Filho, E. I., & Elkin, C. (2021). Fire in the Atlantic Rainforest: An analysis of 20 years of fire foci distribution and their social-ecological drivers, *Geocarto International* 37(16), pp. 4737–4761. https://doi.org/10.1080/10106049.2021.1899301

Blackwell, M. (2017). Made for each other: Ascomycete yeasts and insects. *Microbiology Spectrum*, *5*(3), FUNK-0081-2016. https://doi.org/10.1128/microbiolspec.FUNK-0081-2016

Boonmak, C., Khunnamwong, P., & Limtong, S. (2020). Yeast communities of primary and secondary peat swamp forests in Southern Thailand. *Antonie Van Leeuwenhoek*, *113*, 55–69. https://doi.org/10.1007/s10482-019-01317-0

Boynton, P. J., Greig, D. (2014). The ecology and evolution of non-domesticated *Saccharomyces* species. *Yeast*, *31*(12), 449–462. https://doi.org/10.1002/yea.3040

Buzzini, P., & Martini, A. (2002). Extracellular enzymatic activity profiles in yeast and yeast-like strains isolated from tropical environments. *Journal of Applied Microbiology*, *93*(6), 1020–1025. https://doi.org/10.1046/j.1365-2672.2002.01783.x

Buzzini, P., Martini, A., Cappelli, F., Pagnoni, U. M., & Davoli, P. (2003). A study on volatile organic compounds (VOCs) produced by tropical ascomycetous yeasts. *Antonie Van Leeuwenhoek*, *84*(4), 301–311. https://doi.org/10.1023/a:1026064527932

Buzzini, P., Vaughan, A. E., Turchetti, B., & Martini, A. (2004). La biodiversità dei lieviti isolati da ambienti tropicali: una fonte potenziale di molecole di interesse biotecnologico. *Informatore Botanico Italiano*, *36*(1), 286–292.

Cadete, R. M., de Las Heras, A. M., Sandström, A. G., Ferreira, C., Gírio, F., Gorwa-Grauslund, M. F., Rosa, C. A., & Fonseca, C. (2016). Exploring xylose metabolism in *Spathaspora* species: XYL1.2 from *Spathaspora passalidarum* as the key for efficient anaerobic xylose fermentation in metabolic engineered *Saccharomyces cerevisiae*. *Biotechnology for Biofuels*, *9*, 167. https://doi.org/10.1186/s13068-016-0570-6

Cadete, R. M., Melo, M. A., Dussán, K. J., Rodrigues, R. C. L. B., Silva, S. S., Zilli, J. E., Vital, M. J. S., Gomes, F. C. O., Lachance, M. A., & Rosa, C. A. (2012). Diversity and physiological characterization of D-xylose-fermenting yeasts isolated from the Brazilian Amazonian Forest. *PLoS One*, *7*(8), e43135. https://doi.org/10.1371/journal.pone.0043135

Cadete, R. M., & Rosa, C. A. (2018). The yeasts of the genus *Spathaspora*: Potential candidates for second-generation biofuel production. *Yeast*, *35*(2), 191–199. https://doi.org/10.1002/yea.3279

Cadete, R. M., Santos, R. O., Melo, M. A., Mouro, A., GonÃ§alves, D. L., Stambuk, B. U., Gomes, C. O., Lachance, M., & Rosa, C. A. (2009). *Spathaspora arborariae* sp. nov., a D-xylose-fermenting yeast species isolated from rotting wood in Brazil. *FEMS Yeast Research*, *9*(8), 1338–1342. https://doi.org/10.1111/j.1567-1364.2009.00582.x

Canto, A., Herrera, C. M., & Rodriguez, R. (2017). Nectar living yeasts of a tropical host plant community: Diversity and effects on community wide floral nectar traits. *PeerJ*, *5*, e3517. https://doi.org/10.7717/peerj.3517

Carvalho, F. P., de Souza, A. C., Magalhães-Guedes, K. T., Dias, D. R., Silva, C. F., & Schwan, R. F. (2013). Yeasts diversity in Brazilian Cerrado soils: Study of the enzymatic activities. African. *Journal of Microbiology Research*, *7*(32), 4176–4190.

Chai, C. Y., Gao, W. L., Li, Y., Yan, Z. L., & Hui, F. L. (2022). *Kodamaea hongheensis* f.a., sp. nov., *Kodamaea ovate* f.a., sp. nov. and *Kodamaea yamadae* f.a., sp. nov., three new yeast species of *Kodamaea* (Saccharomycetales, Debaryomycetacae) from China. *MycoKeys*, *89*, 89–137. https://doi.org/10.3897/mycokeys.89.81119

Chai, C.-Y., Gao, W.-L., Yan, Z.-L., & Hui, F.-L. (2022). Four new species of Trichomonascaceae (Saccharomycetales, Saccharomycetes) from Central China. *MycoKeys*, *90*, 1–18.

Chai, C.-Y., Huang, L.-N., Cheng, H., Liu, W.-J., & Hui, F.-L. (2019). *Wickerhamomyces menglaensis* f.a., sp. nov., a yeast species isolated from rotten wood. *International Journal of Systematic and Evolutionary Microbiology*, *69*, 1509–1514. https://doi.org/10.1099/ijsem.0.003350

Chimner, R. A., & Ewel, K. C. (2005). A tropical freshwater wetland: II. Production, decomposition, and peat formation. *Wetlands Ecology and Management*, *13*, 671–684. https://doi.org/10.1007/s11273-005-0965-9

Chu, S.-B., Hu, W. T., & Hui, F. L. (2022). *Torulaspora jiuxiensis* sp. nov., a novel yeast species isolated from rotting wood. *International Journal of Systematic and Evolutionary Microbiology*, *72*(12), 005629. https://doi.org/10.1099/ijsem.0.005629

Colvin, A. Z. (2018). Peripatric speciation. *WikiJournal of Science*, *1*(2), 008.

Corte, L., Di Cagno, R., Groenewald, M., Roscini, L., Colabella, C., Gobbetti, M., & Cardinali, G. (2015). Phenotypic and molecular diversity of *Meyerozyma guilliermondii* strains isolated from food and other environmental niches, hints for an incipient speciation. *Food Microbiology*, *48*, 206–215.

da Cunha, A. B., Shehata, A. M. E. T., & de Oliveira, W. (1957). A study of the diets and nutritional preferences of tropical species of *Drosophila*. *Ecology*, *38*, 98–106.

Danforth, B. N., Minckley, R., & Neff, J. L. (2019). *The solitary bees—Biology, evolution, conservation* (p. 472). Princeton University Press.

David-Palma, M., Libkind, D., Brito, P. H., Silva, M., Bellora, N., Coelho, M. A., Heitman, J., Gonçalves, P., & Sampaio, J. P. (2020). The untapped Australasian diversity of astaxanthin-producing yeasts with biotechnological potential—*Phaffia australis* sp. nov. and *Phaffia tasmanica* sp. nov. *Microorganisms*, *8*(11), 1651. https://doi.org/10.3390/microorganisms8111651

Deak, T. (2009). Ecology and biodiversity of yeasts with potential value in biotechnology. In T. Satyanarayna & G. Kunze (Eds.), *Yeast biotechnology: Diversity and applications* (pp. 151–168). Springer. https://doi.org/10.1007/978-1-4020-8292-4_8

Dedysh, S. N., Pankratov, T. A., Belova, S. E., Kulichevskaya, I. S., & Liesack, W. (2006). Phylogenetic analysis and in situ identification of bacteria community composition in an acidic *Sphagnum* peat bog. *Applied and Environmental Microbiology*, *72*, 2110–2117. https://doi.org/10.1128/AEM.72.3.2110-2117.2006

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., … Saleem, M. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, *67*, 534–545.

Félix, C. R., Andrade, D. A., Almeida, J. H., Navarro, H. M. C., Fell, J. W., & Landell, M. F. (2020). *Vishniacozyma alagoana* sp. nov. a tremellomycetes yeast associated with plants from dry and rainfall tropical forests. *International Journal of Systematic and Evolutionary Microbiology*, *70*(5), 3449–3454. https://doi.org/10.1099/ijsem.0.004193

Felix, C. R., Navarro, H. M. C., Paulino, G. V. B., Broetto, L., & Landell, M. F. (2017). *Carlosrosaea hohenbergiae* sp. nov. and *Carlosrosaea aechmeae* sp. nov., two tremellaceous yeasts isolated from bromeliads in north-eastern Brazil. *International Journal of Systematic and Evolutionary Microbiology*, *67*(6), 1752–1757. https://doi.org/10.1099/ijsem.0.001856

Figueiredo, M. A., da Silva, T. H., Pinto, O. H. B., Leite, M. G. P., de Oliveira, F. S., Messias, M. C. T. B., Rosa, L. H., Câmara, P. E. A. S., Lopes, F. A. C., & Kozovits, A. R. (2023). Metabarcoding of soil fungal communities in rupestrian grassland areas preserved and degraded by mining: implications for restoration. *Microbial Ecology*, *85*, 1045–1055. https://doi.org/10.1007/s00248-023-02177-y

Fleet, G. H. (2001). Biodiversity and ecology of Australasian yeasts (fungi). *Australian Systematic Botany*, *14*(3), 501–511. https://doi.org/10.1071/SB00017

Freitas, L. F. D., Barriga, E. J. C., Barahona, P. P., Lachance, M. A., & Rosa, C. A. (2013). *Kodamaea transpacifica* f.a., sp. nov., a yeast species isolated from ephemeral flowers and insects in the Galápagos Islands and Malaysia: Further evidence for ancient human transpacific contacts. *International Journal of Systematic and Evolutionary Microbiology*, *63*(11), 4324–4329. https://doi.org/10.1099/ijs.0.052282-0

Freitas, L. F. D., Batista, T. M., Santos, A. R. O., Hilário, H. O., Moreira, R. G., Franco, G. R., Morais, P. B., Lachance, M. A., & Rosa, C. A. (2020). Yeast communities associated with cacti in Brazil and the description of *Kluyveromyces starmeri* sp. nov. based on phylogenomic analyses. *Yeast*, *37*(12): 625–637. https://doi.org/10.1002/yea.3528

Fungsin, B., Hamamoto, M., Arunpairojana, V., Sukhumavasi, J., Atthasampunna, P., & Nakase, T. (2001). *Bensingtonia thailandica* sp. nov., a novel basidiomycetous yeast species isolated from plant leaves in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *51*, 1209–1213. https://doi.org/10.1099/00207713-51-3-1209

Fungsin, B., Hamamoto, M., Arunpairojana, V., Sukhumavasi, J., Atthasampunna, P., & Nakase, T. (2002). *Kockovaella barringtoniae* sp. nov., a new basidiomycetous yeast species isolated from a plant leaf collected in a tropical rain forest in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *52*, 281–284. https://doi.org/10.1099/00207713-52-1-281

Fungsin, B., Takashima, M., Artjariyasripong, S., Arunpairojana, V., Hamamoto, M., & Nakase, T. (2002). *Bullera arundinariae* sp. nov., a new species of ballistoconidium-forming yeast isolated from a plant in Thailand. *Microbiology and Culture Collections*, *18*(2), 83–90.

Fungsin, B., Takashima, M., Artjariyasripong, S., & Nakase, T. (2003). *Bullera panici* sp. nov. and *Bullera siamensis* sp. nov., two new yeasts in the *Bullera variabilis* cluster isolated in Thailand. *Microbiology and Culture Collections*, *19*, 23–32.

Fungsin, B., Takashima, M., Artjariyasripong, S., Potacharoen, W., & Nakase, T. (2003). *Bullera sakaeratica* sp. nov., a new species of ballistoconidium-forming yeast found in Thailand. *Microbiology and Culture Collections*, *19*, 33–39.

Fungsin, B., Takashima, M., Sugita, T., Artjariyasripong, S., Potacharoen, W., Tanticharoen, M., & Nakase, T. (2006). *Bullera koratensis* sp. nov. and *Bullera lagerstroemiae* sp. nov., two new ballistoconidium-forming yeast species in the Trichosporonales clade isolated from plant leaves in Thailand. *The Journal of General and Applied Microbiology*, *52*(2), 73–81. https://doi.org/10.2323/jgam.52.73

Ganter, P. F. (2011). Everything is not everywhere: The distribution of cactophilic yeast. In D. Fontaneto (Ed.), *Biogeography of microscopic organisms* (pp. 130–176). Cambridge University Press. https://doi.org/10.1017/CBO9780511974878

Ganter, P. F., Morais, P. B., & Rosa, C. A. (2017). Yeasts in cacti and tropical fruit. In P. Buzzini, M. A. Lachance, & A. Yurkov (Eds.), *Yeasts in natural ecosystems: Diversity*. Springer. https://doi.org/10.1007/978-3-319-62683-3_8

Glover, T. (1878). *Manuscript notes from my journal: Cotton, and the principal insects, &c., frequenting or injuring the plant, in the United States*. U.S. Department of Agriculture, National Agricultural Library. https://doi.org/10.5962/t.171490

Glushakova, A., Maksimova, I., Morozova, A., & Kachalkin, A. (2019). Distribution features of yeasts in soils of South Vietnam (case study of the biogeocenoses of the National Park Cát Tiên). *IOP Conference Series: Earth and Environmental Science*, *368*, 012012. https://doi.org/10.1088/1755-1315/368/1/012012

Gomes, F. C. O., Safar, S. V. B., Marques, A. R., Medeiros, A. O., Santos, A. R. O., Carvalho, C., Lachance, M. A., Sampaio, J. P., & Rosa, C. A. (2015). The diversity and extracellular enzymatic activities of yeasts isolated from water tanks of *Vriesea* minarum, an endangered bromeliad species in Brazil, and the description of *Occultifur brasiliensis* f.a., sp. nov. *Antonie Van Leeuwenhoek*, *107*(2), 597–611. https://doi.org/10.1007/s10482-014-0356-4

Gomes, F. C. O., Safar, S. V. B., Santos, A. R. O., Lachance, M. A., & Rosa, C. A. (2016). *Kockovaella libkindii* sp. nov., a yeast species isolated from water tanks of bromeliad. *International Journal of Systematic and Evolutionary Microbiology*, *66*(12), 5066–5069. https://doi.org/10.1099/ijsem.0.001471.t

Gonçalves, C., Coelho, M. A., Salema-Oom, M., & Gonçalves, P. (2016). Stepwise functional evolution in a fungal sugar transporter family. *Molecular Biology and Evolution*, *33*(2), 352–366. https://doi.org/10.1093/molbev/msv220

Gonçalves, C., & Gonçalves, P. (2019). Multilayered horizontal operon transfers from bacteria reconstruct a thiamine salvage pathway in yeasts. Proceedings of the National Academy of Sciences of the United States of America,*116*(44), 22219–22228. https://doi.org/10.1073/pnas.1909844116.

Gonçalves, P., Gonçalves, C., Brito, P. H., & Sampaio, J. P. (2020). The *Wickerhamiella/Starmerella* clade—A treasure trove for the study of the evolution of yeast metabolism. *Yeast*, *37*(4), 313–320. https://doi.org/10.1002/yea.3463

Gonçalves, P., Valério, E., Correia, C., de Almeida, J. M. G. C. F., & Sampaio, J. P. (2011). Evidence for divergent evolution of growth temperature preference in sympatric *Saccharomyces* species. *PLoS One*, *6*, e20739. https://doi.org/10.1371/journal.pone.0020739

Gonçalves, C., Wisecaver, J. H., Kominek, J., Oom, M. S., Leandro, M. J., Shen, X. X., Opulente, D. A., Zhou, X., Peris, D., Kurtzman, C. P., Hittinger, C. T., Rokas, A., & Gonçalves, P. (2018). Evidence for loss and reacquisition of alcoholic fermentation in a fructophilic yeast lineage. *eLife*, *7*, e33034. https://doi.org/10.7554/eLife.33034

Grondin, E., Shum Cheong Sing, A., Caro, Y., Raherimandimby, M., Randrianierenana, A. L., James, S., Nueno-Palop, C., François, J. M., & Petit, T. (2015). A comparative study on the potential of epiphytic yeasts isolated from tropical fruits to produce flavoring compounds. *International Journal of Food Microbiology*, *203*, 101–108. https://doi.org/10.1016/j.ijfoodmicro.2015.02.032

Guamán-Burneo, M. C., Dussán, K. J., Cadete, R. M., Cheab, M. A. M., Portero, P., Carvajal-Barriga, E. J., da Silva, S. S., & Rosa, C. A. (2015). Xylitol production by yeasts isolated from rotting wood in the Galápagos Islands, Ecuador, and description of *Cyberlindnera galapagoensis* f.a., sp. nov. *Antonie Van Leeuwenhoek*, *108*(4), 919–931. https://doi.org/10.1007/s10482-015-0546-8

Hadibarata, T., Khudhair, A. B., Kristanti, R. A., & Kamyab, H. (2017). Biodegradation of pyrene by Candida sp. S1 under high salinity conditions. *Bioprocess and Biosystems Engineering*, *40*, 1411–1418. https://doi.org/10.1007/s00449-017-1798-7

Han, D. Y., Han, P. J., Rumbold, K., Koricha, A. D., Duan, S. F., Song, L., Shi, J. Y., Li, K., Wang, Q. M., & Bai, F. Y. (2021). Adaptive gene content and allele distribution variations in the wild and domesticated populations of *Saccharomyces cerevisiae*. *Frontiers in Microbiology*, *12*, 247. https://doi.org/10.3389/FMICB.2021.631250/BIBTEX

He, P. Y., Shao, X. Q., Duan, S. F., Han, D. Y., Li, K., Shi, J. Y., Zhang, R. P., Han, P. J., Wang, Q. M., & Bai, F. Y. (2022). Highly diverged lineages of *Saccharomyces paradoxus* in temperate to subtropical climate zones in China. *Yeast*, *39*, 69–82. https://doi.org/10.1002/YEA.3688

Hoang, N. T., & Kanemoto, K. (2021). Mapping the deforestation footprint of nations reveals growing threat to tropical forests. *Nature Ecology & Evolution*, *5*(6), 845–853. https://doi.org/10.1038/s41559-021-01417-z.

Huang, L. N., Xi, Z. W., Li, Y., & Hui, F. L. (2018). *Sugiyamaella xiaguanensis* f.a., sp. nov., a yeast species isolated from rotting wood. *International Journal of Systematic and Evolutionary Microbiology*, *68*(10), 3307–3310. https://doi.org/10.1099/ijsem.0.002988

Huang, L. N., Xi, Z. W., Zhai, Y. C., Chai, C. Y., & Hui, F. L. (2019). *Saturnispora galanensis* sp. nov., a yeast species isolated from rotting wood. *International Journal of Systematic and Evolutionary Microbiology*, *69*(9), 2658–2661. https://doi.org/10.1099/ijsem.0.003501

Jacques, N., & Casaregola, S. (2019). Large biodiversity of yeasts in French Guiana and the description of *Suhomyces coccinellae* f.a. sp. nov. and *Suhomyces faveliae* f.a. sp. nov. *International Journal of Systematic and Evolutionary Microbiology*, *69*(6), 1634–1649. https://doi.org/10.1099/ijsem.0.003369

Jadhav, R., Tiwari, S., Avchar, R., Groenewald, M., & Baghela, A. (2020). Suhomyces drosophilae sp. nov., isolated from *Drosophila* flies feeding on a stinkhorn mushroom. *International Journal of Systematic and Evolutionary Microbiology*, *70*(9), 4908–4913. https://doi.org/10.1099/ijsem.0.004358

Jaiboon, K., Lertwattanasakul, N., Limtong, P., & Limtong, S. (2016). Yeasts from peat in a tropical peat swamp forest in Thailand and their ability to produce ethanol, indole-3-acetic acid and extracellular enzymes. *Mycological Progress*, *15*, 755–770. https://doi.org/10.1007/s11557-016-1205-9

James, S. A., Barriga, E. J. C., Barahona, P. P., Harrington, T. C., Lee, C. F., Bond, C. J., & Roberts, I. N. (2014). *Wickerhamomyces arborarius* f.a., sp. nov., an ascomycetous yeast species found in arboreal habitats on three different continents. *International Journal of Systematic and Evolutionary Microbiology*, *64*(Pt 3), 1057–1061. https://doi.org/10.1099/ijs.0.059162-0

James, S. A., Cadet, G. M., Carvajal Barriga, E. J., Barahona, P. P., Cross, K., Bond, C. J., & Roberts, I. N. (2011). *Saturnispora quitensis* sp. nov., a yeast species isolated from the Maquipucuna cloud forest reserve in Ecuador. *International Journal of Systematic and Evolutionary Microbiology*, *61*(12), 3072–3076. https://doi.org/10.1099/ijs.0.030759-0

James, S. A., Carvajal Barriga, E. J., Barahona, P. P., Cross, K., Bond, C. J., & Roberts, I. N. (2013). *Candida ecuadorensis* sp. nov., an ascomycetous yeast species found in two separate regions of Ecuador. *International Journal of Systematic and Evolutionary Microbiology*, *63*(Pt 1), 393–397. https://doi.org/10.1099/ijs.0.047555-0

James, S. A., Carvajal Barriga, E. J., Bond, C. J., Cross, K., NÃºÃ±ez, N. C., Portero, P. B., & Roberts, I. N. (2009). *Candida carvajalis* sp. nov., an ascomycetous yeast species from the Ecuadorian Amazon jungle. *FEMS Yeast Research*, *9*(5), 784–788. https://doi.org/10.1111/j.1567-1364.2009.00518.x

James, S. A., Carvajal Barriga, E. J., Portero Barahona, P., Nueno-Palop, C., Cross, K., Bond, C. J., & Roberts, I. N. (2015). *Kazachstania yasuniensis* sp. nov., an ascomycetous yeast species found in mainland Ecuador and on the Galápagos. *International Journal of Systematic and Evolutionary Microbiology*, *65*(4), 1304–1309. https://doi.org/10.1099/ijs.0.000102

Januário da Costa Neto, D., & Benevides de Morais, P. (2020). The vectoring of *Starmerella* species and other yeasts by stingless bees in a Neotropical savanna. *Fungal Ecology*, *47*, 100973. https://doi.org/10.1016/j.funeco.2020.100973

Janzen, D. H. (1983). *Hymenaea courbaril* (Guapinol, Stinking Toe). In D. H. Janzen (Ed.), *Costa Rican natural history* (pp. 253–256). University of Chicago Press.

Janzen, D. H., & Hallwachs, W. (2009). Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (nn-SRNP-nnnnn voucher codes). http://janzen.sas.upenn.edu

Kaewwichian, R., Khunnamwong, P., Jindamorakot, S., Lertwattanasakul, N., & Limtong, S. (2018). *Cryptotrichosporon siamense* sp. nov., a ballistoconidium-forming yeast species in Trichosporonales isolated in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *68*, 2473–2477. https://doi.org/10.1099/ijsem.0.002858

Kanti, A. (2015). Carboxymethyl cellulose hydrolyzing yeast isolated from South East Sulawesi. *Indonesia. Jurnal Biologi Indonesia*, *11*(2), 285–294.

Ke, T., Zhai, Y. C., Yan, Z. L., Hui, F. L. (2019). *Kazachstania jinghongensis* sp. nov. and *Kazachstania menglunensis* f.a., sp. nov., two yeast species isolated from rotting wood. *International Journal of Systematic and Evolutionary Microbiology*, *69*(11): 3623–3628. https://doi.org/10.1099/ijsem.0.003670

Khamweera, P., Bamrong, N., & Pookmak, S. (2022). Identification of yeasts isolated from Khaoploung forest by comparative ITS and D1/D2 sequence analysis. *Phranakhon Rajabhat Research Journal (Science and Technology)*, *17*(1), 61–74.

Khunnamwong, P., Kingphadung, K., Lomthong, T., Kanpiengjai, A., Khanongnuch, C., & Limtong, S. (2022). *Wickerhamiella nakhonpathomensis* f.a. sp. nov., a novel ascomycetous yeast species isolated from a mushroom and a flower in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *72*(1), 005191. https://doi.org/10.1099/ijsem.0.005191

Khunnamwong, P., Lertwattanasakul, N., & Limtong, S. (2020). *Teunia siamensis* f.a., sp. nov., a novel tremellaceous yeast species isolated from soil in a secondary peat swamp forest area. *International Journal of Systematic and Evolutionary Microbiology*, *70*(6), 3673–3678. https://doi.org/10.1099/ijsem.0.004219

Khunnamwong, P., & Limtong, S. (2018). *Saturnispora kantuleensis* f.a., sp. nov., a novel yeast species isolated from peat in a tropical peat swamp forest in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *68*(4), 1160–1164. https://doi.org/10.1099/ijsem.0.002641

Kleespies, R. G., Lim, Y. W., Tkaczuk, C., Wrzosek, M., Steinwender, B. M., & Wegensteiner, R. (2017). *Metschnikowia* cf. *typographi* and other pathogens from the bark beetle *Ips sexdentatus*—Prevalence, histological and ultrastructural evidence, and molecular characterization. *Journal of Invertebrate Pathology*, *143*, 69–78.

Kobayashi, R., Kanti, A., & Kawasaki, H. (2017). *Pichia chibodasensis* sp. nov., isolated in Indonesia. *International Journal of Systematic and Evolutionary Microbiology*, *67*(4), 1024–1027.

Kominek, J., Doering, D. T., Opulente, D. A., Shen, X. X., Zhou, X., DeVirgilio, J., Hulfachor, A. B., Groenewald, M., Mcgee, M. A., Karlen, S. D., Kurtzman, C. P., Rokas, A., & Hittinger, C. T. (2019). Eukaryotic acquisition of a bacterial operon. *Cell*, *176*(6), 1356–1366.e10. https://doi.org/10.1016/j.cell.2019.01.034

Koricha, A. D., Han, D. Y., Bacha, K., & Bai, F. Y. (2019). Occurrence and molecular identification of wild yeasts from Jimma Zone, South West Ethiopia. *Microorganisms*, *7*(12), 633. https://doi.org/10.3390/microorganisms7120633

Kurtzman, C. P., Robnett, C. J., Basehoar, E., & Ward, T. J. (2018). Four new species of *Metschnikowia* and the transfer of seven *Candida* species to *Metschnikowia* and *Clavispora* as new combinations. *Antonie Van Leeuwenhoek*, *111*(11), 2017–2035. https://doi.org/10.1007/s10482-018-1095-8

Kurtzman, C. P., Robnett, C. J., & Blackwell, M. (2016). Description of *Teunomyces* gen. nov. for the *Candida kruisii* clade, *Suhomyces* gen. nov. for the *Candida tanzawaensis* clade and *Suhomyces kilbournensis* sp. nov. *FEMS Yeast Research*, *16*(5), fow041. https://doi.org/10.1093/femsyr/fow041

Lachance, M. A. (2011a). *Clavispora* Rodrigues de Miranda (1979). In C. P. Kurtzman, J. W. Fell, & T. Boekhout (Eds.), *The yeasts: A taxonomic study* (5th ed., pp. 349–353). Elsevier.

Lachance, M. A. (2011b). *Metschnikowia* Kamienski (1899). In C. P. Kurtzman, J. W. Fell, & T. Boekhout (Eds.), *The yeasts: A taxonomic study* (5th ed., pp. 575–620). Elsevier.

Lachance, M. A. (2011c). *Sporopachydermia* Rodrigues de Miranda (1978). In C. P. Kurtzman, J. W. Fell, & T. Boekhout (Eds.), *The yeasts: A taxonomic study* (5th ed., pp. 799–803). Elsevier.

Lachance, M. A., Boekhout, T., Scorzetti, G., Fell, J. W., & Kurtzman, C. P. (2011). *Candida* Berkhout. In C. P. Kurtzman, J. W. Fell, & T. Boekhout (Eds.), *The yeasts: A taxonomic study* (5th ed., pp. 987–1277). Elsevier.

Lachance, M. A., Bowles, J. M., Mueller, C., & Starmer, W. T. (2000). On the biogeography of yeasts in the *Wickerhamiella* clade and description of *Wickerhamiella lipophila* sp. nov., the teleomorph of *Candida lipophila*. *Canadian Journal of Microbiology*, *46*, 1145–1148.

Lachance, M. A., Dobson, J., Wijayanayaka, D. N., & Smith, A. M. E. (2010). The use of parsimony network analysis for the formal delineation of phylogenetic species of yeasts: *Candida apicola*, *Candida azyma*, and *Candida parazyma* sp. nov., cosmopolitan yeasts associated with floricolous insects. *Antonie Van Leeuwenhoek*, *97*, 155–170.

Lachance, M. A., Ewing, C. P., Bowles, J. M., & Starmer, W. T. (2005). *Metschnikowia hamakuensis* sp. nov., *Metschnikowia kamakouana* sp. nov., and *Metschnikowia mauinuiana* sp. nov., three endemic yeasts from Hawaiian nitidulid beetles. *International Journal of Systematic and Evolutionary Microbiology*, *55*, 1369–1377.

Lachance, M. A., Klemens, J. A., Bowles, J. M., & Janzen, D. H. (2001). The yeast community of sap fluxes of costa rican *Maclura* (*Chlorophora*) *tinctoria* and description of two new yeast species, *Candida galis* and *Candida ortonii*. *FEMS Yeast Research*, *1*(2), 87–92.

Lachance, M. A., & Kurtzman, C. P. (2013). The yeast genus *Tortispora* gen. nov., description of *Tortispora ganteri* sp. nov., *Tortispora mauiana* fa, sp. nov., *Tortispora agaves* fa, sp. nov., *Tortispora sangerardonensis* fa, sp. nov., *Tortispora cuajiniquilana* fa, sp. nov., *Tortispora starmeri* fa, sp. nov. and *Tortispora phaffii* fa, sp. nov., reassignment of *Candida caseinolytica* to *Tortispora caseinolytica* fa, comb. nov., emendation of *Botryozyma*, and assignment of *Botryozyma*, *Tortispora* gen. nov. and *Trigonopsis* to the family Trigonopsidaceae fam. nov. *International Journal of Systematic and Evolutionary Microbiology*, *63*(8), 3104–3114.

Lachance, M. A., Lawrie, D., Dobson, J., & Piggott, J. (2008). Biogeography and population structure of the neotropical endemic yeast species *Metschnikowia lochheadii*. *Antonie Van Leeuwenhoek*, *94*, 403–414.

Lachance, M. A., Lee, D. K., & Hsiang, T. (2020). Delineating yeast species with genome average nucleotide identity: A calibration of ANI with haplontic, heterothallic *Metschnikowia* species. *Antonie Van Leeuwenhoek*, *113*, 2097–2106.

Lachance M. A., Rosa C. A., Carvajal E. J., Freitas L. F. D., & Bowles J. M. (2012). *Saccharomycopsis fodiens* sp. nov., a rare preadacious yeast from three distant localities. *International Journal of Systematic and Evolutionary Microbiology*, *62*(11), 2793–2798. https://doi.org/10.1099/ijs.0.043109-0

Lachance, M. A., Rosa, C. A., Starmer, W. T., Schlag Edler, B., Barker, J. S., & Bowles, J. M. (1998). *Wickerhamiella australiensis*, *Wickerhamiella cacticola*, *Wickerhamiella occidentalis*, *Candida drosophilae*, and *Candida lipophila*, five new related yeast species from flowers and associated insects. *International Journal of Systematic Bacteriology*, *48 Pt 4*, 1431–1443.

Lachance, M. A., Starmer, W. T., & Phaff, H. J. (1990). Metschnikowia hawaiiensis sp. nov., a heterothallic haploid yeast from Hawaiian morning glory and associated drosophilids. *International Journal of Systematic Bacteriology*, *40*, 415–420.

Lachance, M. A., Starmer, W. T., Rosa, C. A., Bowles, J. M., Barker, J. S. F., & Janzen, D. H. (2001). Biogeography of the yeasts of ephemeral flowers and their insects. *FEMS Yeast Research*, *1*, 1–8.

Lachance, M. A., Vale, H. M. M., Sperandio, E. M., Carvalho, A. O. S., Santos, A. R. O., Grondin, C., Jacques, N., Casaregola, S., & Rosa, C. A. (2018). *Wickerhamiella dianesei* fa, sp. nov. and *Wickerhamiella kurtzmanii* fa, sp. nov., two yeast species isolated from plants and insects. *International Journal of Systematic and Evolutionary Microbiology*, *68*(10), 3351–3355.

Lee, D. K., Hsiang, T., & Lachance, M. A. (2018). *Metschnikowia* mating genomics. *Antonie Van Leeuwenhoek*, *111*(10), 1935–1953.

Lee, T. J., Liu, Y. C., Liu, W. A., Lin, Y. F., Lee, H. H., Ke, H. M., Huang, J. P., Lu, M. Y. J., Hsieh, C. L., Chung, K. F., Liti, G., & Tsai, I. J. (2022). Extensive sampling of *Saccharomyces cerevisiae* in Taiwan reveals ecology and evolution of predomesticated lineages. *Genome Research*, *32*, 864–877. https://doi.org/10.1101/GR.276286.121

Lee, D. K., Santos, A. R. O., Hsiang, T., Rosa, C. A., & Lachance, M. A. (2020). Catching speciation in the act—act 2: *Metschnikowia lacustris* sp. nov., a sister species to *Metschnikowia dekortorum*. *Antonie Van Leeuwenhoek*, *113*, 753–762.

Li, S., Youwei, C., Liyuan, Y., Aiqi, F., Lingqi, Z., Huiqiong, Y., & Wang, X. (2002). A study on yeasts of yunnan. I. Yeasts of tropical rain forest, Xishuangbanna. *Journal of Yunnan University (Natural Sciences)*, *24*(5), 378–380.

Li, A. H., Yuan, F. X., Groenewald, M., Bensch, K., Yurkov, A. M., Li, K., Han, P. J., Guo, L. D., Aime, M. C., Sampaio, J. P., Jindamorakot, S., Turchetti, B., Inacio, J., Fungsin, B., Wang, Q. M., & Bai, F. Y. (2020). Diversity and phylogeny of basidiomycetous yeasts from plant leaves and soil: Proposal of two new orders, three new families, eight new genera and one hundred and seven new species. *Studies in Mycology*, *96*, 17–140. https://doi.org/10.1016/j.simyco.2020.01.002

Limtong, S., Am-In, S., Kaewwichian, R., Kaewkrajay, C., & Jindamorakot, S. (2020). Exploration of yeast communities in fresh coconut, palmyra, and nipa palm saps and ethanol-fermenting ability of isolated yeasts.

Antonie Van Leeuwenhoek, *113*, 2077–2095. https://doi.org/10.1007/S10482-020-01479-2/TABLES/5

Limtong, S., Imanishi, Y., Jindamorakot, S., Ninomiya, S., Yongmanitchai, W., & Nakase, T. (2008). *Torulaspora maleeae* sp. nov., a novel ascomycetous yeast species from Japan and Thailand. *FEMS Yeast Research*, *8*, 337–343. https://doi.org/10.1111/j.1567-1364.2007.00324.x

Limtong, S., & Yongmanitchai, W. (2010). *Candida chanthaburiensis* sp. nov., *Candida kungkrabaensis* sp. nov. and *Candida suratensis* sp. nov., three novel yeast species from decaying plant materials submerged in water of mangrove forest. *Antonie Van Leeuwenhoek*, *98*(3), 379–388. https://doi.org/10.1007/s10482-010-9451-3

Limtong, S., Yongmanitchai, W., Kawasaki, H., & Fujiyama, K. (2009). *Wickerhamomyces edaphicus* sp. nov. and *Pichia jaroonii* sp. nov., two ascomycetous yeast species isolated from forest soil in Thailand. *FEMS Yeast Research*, *9*(3), 504–510. https://doi.org/10.1111/j.1567-1364.2009.00488.x

Limtong, S., Yongmanitchai, W., Tun, M. M., Kawasaki, H., & Seki, T. (2007). *Kazachstania siamensis* sp. nov., an ascomycetous yeast species from forest soil in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *57*(2), 419–422. https://doi.org/10.1099/ijs.0.64539-0

Liti G. (2015). The fascinating and secret wild life of the budding yeast *S. cerevisiae*. *Elife*, *4*, e05835. https://doi.org/10.7554/eLife.05835.001

Liu, W. Q., Han, P. J., Qiu, J. Z., & Wang, Q. M. (2012). *Naumovozyma baii* sp. nov., an ascomycetous yeast species isolated from rotten wood in a tropical forest. *International Journal of Systematic and Evolutionary Microbiology*, *62*, 3095–3098. https://doi.org/10.1099/ijs.0.044909-0

Lopes, M. R., Ferreira, M. C., Carvalho, T. F. C., Pagnocca, F. C., Chagas, R. A., Morais, P. B., Rosa, L. H., Lachance, M. A., & Rosa, C. A. (2015). *Yamadazyma riverae* sp. nov., a yeast species isolated from plant materials. *International Journal of Systematic and Evolutionary Microbiology*, *65*(12), 4469–4473.

Lopes, M. R., Lara, C. A., Moura, M. E. F., Uetanabaro, A. P. T., Morais, P. B., Vital, M. J. S., & Rosa, C. A. (2018). Characterisation of the diversity and physiology of cellobiose-fermenting yeasts isolated from rotting wood in Brazilian ecosystems. *Fungal Biology*, *122*(7), 668–676. https://doi.org/10.1016/j.funbio.2018.03.008

Luong, D. T., Takashima, M., Ty, P. V., Dung, N. L., & Nakase, T. (2000). Four new species of *Kockovaella* isolated from plant leaves collected in Vietnam. *The Journal of General and Applied Microbiology*, *46*(6), 297–310. https://doi.org/10.2323/jgam.46.297

Luong, D. T., Takashima, M., Ty, P. V., Dung, N. L., & Nakase, T. (2005). *Bullera hoabinhensis* sp. nov., a new ballistoconidiogenous yeast isolated from a plant leaf collected in Vietnam. *The Journal of General and Applied Microbiology*, *51*(6), 335–342. https://doi.org/10.2323/jgam.51.335

Lüttge, U. (2008). *Physiological ecology of tropical plants*. Springer. https://doi.org/10.1007/978-3-540-71793-5

Lv, S. L., Chai, C. Y., Wang, Y., Yan, Z. L., & Hui, F. L. (2020). Five new additions to the genus *Spathaspora* (Saccharomycetales, Debaryomycetaceae) from southwest China. *MycoKeys*, *75*, 31–49. https://doi.org/10.3897/mycokeys.75.57192

Marques, A. R., Resende, A. A., Gomes, F. C. O., Santos, A. R. O., Rosa, C. A., Duarte, A. A., de Lemos-Filho, J. P., & dos Santos, V. L. (2021). Plant growth-promoting traits of yeasts isolated from the tank bromeliad *Vriesea minarum* L.B. Smith and the effectiveness of *Carlosrosaea vrieseae* for promoting bromeliad growth. *Brazilian Journal of Microbiology*, *52*(3), 1417–1429. https://doi.org/10.1007/s42770-021-00496-1

Matos, Í. T. S. R., de Souza, V. A., D'Angelo, G. R., Astolfi Filho, S., do Carmo, E. J., & Vital, M. J. S. (2021). Yeasts with fermentative potential associated with fruits of Camu-Camu (*Myrciaria dubia*, Kunth) from North of Brazilian Amazon. *The Scientific World Journal*, *2021*, 1–6. https://doi.org/10.1155/2021/9929059

Maugeri, F., & Hernalsteens, S. (2007). Screening of yeast strains for transfructosylating activity. *Journal of Molecular Catalysis B: Enzymatic*, *49*, 43–49. https://doi.org/10.1016/j.molcatb.2007.08.001

Melo, W. G. P., de Oliveira, T. B., Arcuri, S. L., de Morais, P. B., & Pagnocca, F. C. (2021). Yeasts in the nests of the leaf-cutter ant *Acromyrmex balzani* in a Savanna biome: exploitation of community and metabolic diversity. *Antonie Van Leeuwenhoek*, *114*(6), 751–764. https://doi.org/10.1007/s10482-021-01555-1

Mok, W. Y., Luizão, R. C., do Socorro Barreto da Silva, M., Teixeira, M. F., & Muniz, E. G. (1984). Ecology of pathogenic yeasts in Amazonian soil. *Applied and Environmental Microbiology*, *47*(2), 390–394.

Monteiro Moreira, G. A., & Martins do Vale, H. M. (2020). Soil yeast communities in revegetated post-mining and adjacent native areas in central Brazil. *Microorganisms*, *8*(8), 1116. https://doi.org/10.3390/microorganisms8081116

Morais, C. G., Batista, T. M., Kominek, J., Borelli, B. M., Furtado, C., Moreira, R. G., Franco, G. R., Rosa, L. H., Fonseca, C., Hittinger, C. T., Lachance, M. A., & Rosa, C. A. (2017). *Spathaspora boniae* sp. nov., a D-xylose-fermenting species in the *Candida albicans/Lodderomyces* clade. *International Journal of Systematic and Evolutionary Microbiology*, *67*(10), 3798–3805. https://doi.org/10.1099/ijsem.0.002186

Morais, C. G., Cadete, R. M., Uetanabaro, A. P. T., Rosa, L. H., Lachance, M. A., & Rosa, C. A. (2013). D-xylose-fermenting and xylanase-producing yeast species from rotting wood of two Atlantic Rainforest habitats in Brazil. *Fungal Genetics and Biology*, *60*, 19–28. https://doi.org/10.1016/j.fgb.2013.07.003

Morais, P. B., Hagler, A. N., Rosa, C. A., Mendonca-Hagler, L. C., & Klaczko, L. B. (1992). Yeasts associated with *Drosophila* in tropical forests of Rio de Janeiro, Brazil. *Canadian Journal of Microbiology*, *38*(11), 1150–1155. https://doi.org/10.1139/m92-188

Morais, P. B., Martins, M. B., Klaczko, L. B., Mendonça-Hagler, L. C., & Hagler, A. N. (1995). Yeast succession in the Amazon fruit *Parahancornia amapa* as resource partitioning among *Drosophila* spp. *Applied and Environmental Microbiology*, *61*(12), 4251–4257. https://doi.org/10.1128/aem.61.12.4251-4257.1995

Morais, P. B., Pagnocca, F. C., & Rosa, C. A. (2006). Yeast communities in tropical rain forests in Brazil and other South American ecosystems. In C. A. Rosa & P. Gabor (Eds.), *Biodiversity and ecophysiology of yeasts* (pp. 461–484). Springer. https://doi.org/10.1007/3-540-30985-3_18

Morais, P. B., Rosa, C. A., & Hagler, A. N. (1995). Yeast communities as descriptors of habitat use by the *Drosophila fasciola* subgroup (*repleta* group) in Atlantic rain forests. *Oecologia*, *104*(1), 45–51. https://doi.org/10.1007/BF00365561

Morais, C. G., Sena, L. M. F., Lopes, M. R., Santos, A. R. O., Barros, K. O., Alves, C. R., Uetanabaro, A. P. T., Lachance, M. A., & Rosa, C. A. (2020). Production of ethanol and xylanolytic enzymes by yeasts inhabiting rotting wood isolated in sugarcane bagasse hydrolysate. *Fungal Biology*, *124*(7), 639–647. https://doi.org/10.1016/j.funbio.2020.03.005

Morais, P. B., Teixeira, L.C., Bowles, J. M., Lachance, M. A., & Rosa, C. A. (2005). *Ogataea falcaomoraisii* sp. nov., a sporogenous methylotrophic yeast from tree exudates. *FEMS Yeast Research*, *5*(1). 81–85. https://doi.org/10.1016/j.femsyr.2004.05.006

Morais, P. B., de Sousa, F. M. P., & Rosa, C. A. (2020). Yeast in plant phytotelmata: Is there a "core" community in different localities of rupestrian savannas of Brazil? *Brazilian Journal of Microbiology*, *51*(3), 1209–1218. https://doi.org/10.1007/s42770-020-00286-1

Morais, P., Teixeira, L., Bowles, J., Lachance, M., & Rosa, C. (2004). sp. nov., a sporogenous methylotrophic yeast from tree exudates. *FEMS*

Yeast Research, *5*(1), 81–85. https://doi.org/10.1016/j.femsyr.2004.05.006

Moreira, G. A. M., Pires, E. C. C., Barreto, C. C., & Vale, H. M. M. (2020). Total fungi and yeast distribution in soils over native and modified vegetation in central Brazil. *Revista Brasileira de Ciência do Solo*, *44*, 1–19. https://doi.org/10.36783/18069657rbcs20200097

Morellato, L. P. C., & Haddad, C. F. B. (2000). Introduction: The Brazilian Atlantic Forest. *Biotropica*, *32*, 786–792.

Mozzachiodi, S., Bai, F. Y., Baldrian, P., Bell, G., Boundy-Mills, K., Buzzini, P., Čadež, N., Cubillos, F. A., Dashko, S., Dimitrov, R., Fisher, K. J., Gibson, B., Gouliamova, D., Greig, D., Heistinger, L., Hittinger, C. T., Jecmenica, M., Koufopanou, V., Landry, C. R., … Boynton, P. (2022). Yeasts from temperate forests. *Yeast*, *39*(1–2), 4–24. https://doi.org/10.1002/yea.3699

Murray, A. (1864). Monograph of the family Nitidulariae. *Transactions of the Linneun Society*, *24*, 211–414.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nagahama, T. (2006). Yeast biodiversity in freshwater, marine and deep-sea environment. In C. A. Rosa & G. Peter (Eds.), *The yeast handbook, biodiversity and ecophysiology of yeasts* (pp. 241–262). Springer-Verlag.

Nakase, T., Jindamorakot, S., Am-In, S., Potacharoen, W., & Tanticharoen, M. (2006). Yeast biodiversity in tropical forests of Asia. In C. A. Rosa & P. Gabor (Eds.), *Biodiversity and ecophysiology of yeasts* (pp. 441–460). Springer. https://doi.org/10.1007/3-540-30985-3_17

Nakase, T., Jindamorakot, S., Ninomiya, S., Imanishi, Y., & Kawasaki, H. (2009). *Candida wancherniae* sp. nov. and *Candida morakotiae* sp. nov., two novel ascomycetous anamorphic yeast species found in Thailand. *The Journal of General and Applied Microbiology*, *55*(2), 93–100.

Nasanit, R., Imklin, N., & Limtong, S. (2020). Assessment of yeasts in tropical peat swamp forests in Thailand. *Mycological Progress*, *19*, 1559–1573. https://doi.org/10.1007/s11557-020-01646-9

Naumov, G. I., James, S. A., Naumova, E. S., Louis, E. J., & Roberts, I. N. (2000). Three new species in the *Saccharomyces* sensu stricto complex: *Saccharomyces cariocanus*, *Saccharomyces kudriavzevii* and *Saccharomyces mikatae*. *International Journal of Systematic and Evolutionary Microbiology*, *50*, 1931–1942. https://doi.org/10.1099/00207713-50-5-1931/CITE/REFWORKS

Naumov, G. I., Lee, C.-F., & Naumova, E. S. (2013). Molecular genetic diversity of the *Saccharomyces* yeasts in Taiwan: *Saccharomyces arboricola*, *Saccharomyces cerevisiae* and *Saccharomyces kudriavzevii*. *Antonie Van Leeuwenhoek*, *103*, 217–228. https://doi.org/10.1007/s10482-012-9803-2

Naumov, G. I., Naumova, E. S., Hagler, A. N., Mendonça-Hagler, L. C., & Louis, E. J. (1995). A new genetically isolated population of the *Saccharomyces* sensu stricto complex from Brazil. *Antonie Van Leeuwenhoek*, *67*, 351–355. https://doi.org/10.1007/BF00872934/METRICS

Navarro, H. M. C., Félix, C. R., Tavares, V. D. F. S., de Sousa, F. M. P., Santos, A. R. O., Morais, P. B., Rosa, C. A., Valente, P., & Landell, M. F. (2022). *Tremella ananatis* sp. nov. and *Tremella lamprococci* sp. nov., two yeast species associated with bromeliads. *International Journal of Systematic and Evolutionary Microbiology*, *72*(2), 005261. https://doi.org/10.1099/ijsem.0.005261

Neves, K. C. S., Porto, A. L. F., & Teixeira, M. F. S. (2006). Seleção de leveduras da Região Amazônica para produção de protease extracelular. *Acta Amazonica*, *36*(3), 299–306. https://doi.org/10.1590/S0044-59672006000300002

Nitiyon, S., Khunnamwong, P., Lertwattanasakul, N., & Limtong, S. (2018). *Candida kantuleensis* sp. nov., a D-xylose-fermenting yeast species isolated from peat in a tropical peat swamp forest. *International Journal of Systematic and Evolutionary Microbiology*, *68*, 2313–2318. https://doi.org/10.1099/ijsem.0.002835

Nwaefuna, A. E., Boekhout,T., Garcia-Aloy, M., Vrhovsek, U., & Zhou, N. (2023). Diversity of dung beetle-associated yeasts from pristine environments of Botswana. *Yeast*, *40*(5–6), 182–196. https://doi.org/10.1002/yea.3852

Palilu, P. T., Kasiamdari, R. S., & Ilmi, M. (2019). Potential yeast from Indonesian wild forest honey showing ability to produce lipase for lipid transesterification. *Microbiology and Biotechnology Letters*, *47*, 555–564. https://doi.org/10.4014/mbl.1907.07008

Paludo, C. R., Menezes, C., Silva-Junior, E. A., Vollet-Neto, A., Andrade-Dominguez, A., Pishchany, G., Khadempour, L., do Nascimento, F. S., Currie, C. R., Kolter, R., Clardy, J., & Pupo, M. T. (2018). Stingless bee larvae require fungal steroid to pupate. *Scientific Reports*, *8*(1), 1122. https://doi.org/10.1038/s41598-018-19583-9

Paludo, C. R., Pishchany, G., Andrade-Dominguez, A., Silva-Junior, E. A., Menezes, C., Nascimento, F. S., Currie, C. R., Kolter, R., Clardy, J., & Pupo, M. T. (2019). Microbial community modulates growth of symbiotic fungus required for stingless bee metamorphosis. *PLoS One*, *14*(7), e0219696. https://doi.org/10.1371/journal.pone.0219696

de Paula, G. T., Menezes, C., Pupo, M. T., & Rosa, C. A. (2021). Stingless bees and microbial interactions. *Current Opinion in Insect Science*, *44*, 41–47. https://doi.org/10.1016/j.cois.2020.11.006

Pignal, L. C., & Lachaise, D. (1979). Les levures des drosophilidesde savanne d'Afrique intertropicale (Savannes de Lamto, C8te d'Ivoire). *Mycopathologia*, *68*,155–165.

Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Pliego, P., Hansen, A. J., Watson, J. E., & Venter, O. (2022). Tropical forests are home to over half of the world's vertebrate species. *Frontiers in Ecology and the Environment*, *20*(1), 10–15. https://doi.org/10.1002/fee.2420

Pimenta, R. S., Alves, P. D. D., Almeida, G. M. F., Silva, J. F. M., Morais, P. B., Corrêa Jr., A., & Rosa, C. A. (2009). Yeast communities in two Atlantic Rain Forest fragments in Southeast Brazil. *Brazilian Journal of Microbiology*, *40*(1), 90–95. https://doi.org/10.1590/S1517-83822009000100015

Polburee, P., Lertwattanasakul, N., Limtong, P., Groenewald, M., & Limtong, S. (2017). Nakazawaea todaengensis f.a., sp. nov., a yeast isolated from a peat swamp forest in Thailand. *International Journal of Systematic and Evolutionary Microbiology*, *67*, 2377–2382. https://doi.org/10.1099/ijsem.0.001961

Pozo, M. I., van Kemenade, G., van Oystaeyen, A., Aledón-Catalá, T., Benavente, A., Van den Ende, W., Wäckers, F., & Jacquemyn, H. (2020). The impact of yeast presence in nectar on bumble bee behavior and fitness. *Ecological Monographs*, *90*(1), e01393. https://doi.org/10.1002/ecm.1393

Rahbar Saadat, Y., Yari Khosroushahi, A., & Pourghassem Gargari, B. (2021). Yeast exopolysaccharides and their physiological functions. *Folia Microbiologica*, *66*, 171–182. https://doi.org/10.1007/s12223-021-00856-2

dos Reis, J. B. A., do Vale, H. M. M., & Lorenzi, A. S. (2022). Insights into taxonomic diversity and bioprospecting potential of Cerrado endophytic fungi: A review exploring an unique Brazilian biome and methodological limitations. *World Journal of Microbiology and Biotechnology*, *38*, 202.

Ren, Y., Chen, L., Niu, Q., & Hui, F. (2014). Description of *Scheffersomyces henanensis* sp. nov., a new D-xylose-fermenting yeast species isolated from rotten wood. *PLoS One*, *9*(9), e92315.

Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C. A., Metzger, J. P., Strassburg, B. B. N., Tabarelli, M., Fonseca, G. A., & Mittermeier, R. A. (2018). From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, *16*(4), 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Robinson, H. A., Pinharanda, A., & Bensasson, D. (2016). Summer temperature can predict the distribution of wild yeast populations. *Ecology and Evolution*, *6*, 1236–1250. https://doi.org/10.1002/ece3.1919

Rosa, C., Lachance, M., Silva, J., Teixeira, A., Marini, M., Antonini, Y., & Martins, R. (2003). Yeast communities associated with stingless bees. *FEMS Yeast Research*, *4*(3), 271–275.

Rosa, C. A., Pagnocca, F. C., Lachance, M. A., Ruivo, C. C. C., Medeiros, A. O., Pimentel, M. R. C., Fontenelle, J. C. R., & Martins, R. P. (2007). *Candida flosculorum* sp. nov. and *Candida floris* sp. nov., two yeast species associated with tropical flowers. *International Journal of Systematic and Evolutionary Microbiology*, *57*(12), 2970–2974.

Rosa, C. A., Viana, E. M., Martins, R. P., Antonini, Y., & Lachance, M. A. (1999). *Candida batistae*, a new yeast species associated with solitary digger nesting bees in Brazil. *Mycologia*, *91*(3), 428–433.

Sachs, E. J., Abbas, H. K., Mengistu, A. (2006). First report of endophytic *Candida ipomoeae* isolated from ovules of upland cotton in Mississippi. *Plant Disease*, *90* (10), 1362. https://doi.org/10.1094/PD-90-1362B

Sampaio, P., & Gonçalves, P. (2008). Natural populations of *Saccharomyces kudriavzevii* in Portugal are associated with oak bark and are sympatric with *S. cerevisiae* and *S. paradoxus*. *Applied and Environmental Microbiology*, *74*, 2144–2152. https://doi.org/10.1128/AEM.02396-07

Sampaio, J. P., & Gonçalves, P. (2017). Biogeography and ecology of the genus *Saccharomyces*. In P. Buzzini, M. A. Lachance, & A. Yurkov (Eds.), *Yeasts in natural ecosystems: Ecology*. Springer. https://doi.org/10.1007/978-3-319-61575-2_5

Santos, A. R. O., Aires, A., Pontes, A., Silva, M., Brito, P. H., Groenewald, M., Melo, C. G. S., Lachance, M. A., Sampaio, J. P., & Rosa, C. A. (2021). *Phaffia brasiliana* sp. nov., a yeast species isolated from soil in a Cerrado-Atlantic Rain Forest ecotone site in Brazil. *International Journal of Systematic and Evolutionary Microbiology*, *71*(11), 005080. https://doi.org/10.1099/ijsem.0.005080

Santos, A. R. O., Lee, D. K., Ferreira, A. G., do Carmo, M. C., Rondelli, V. M., Barros, K. O., Hsiang, T., Rosa, C. A., & Lachance, M. A. (2020). The yeast community of *Conotelus* sp. (Coleoptera: Nitidulidae) in Brazilian passionfruit flowers (*Passiflora edulis*) and description of *Metschnikowia amazonensis* sp. nov., a large-spored clade yeast. *Yeast*, *37*, 253–260.

Santos, A. R., Leon, M. P., Barros, K. O., Freitas, L. F. D., Hughes, A. F., Morais, P. B., Lachance, M. A., & Rosa, C. A. (2018). *Starmerella camargoi* fa, sp. nov., *Starmerella ilheusensis* fa, sp. nov., *Starmerella litoralis* fa, sp. nov., *Starmerella opuntiae* fa, sp. nov., *Starmerella roubikii* fa, sp. nov. and *Starmerella vitae* fa, sp. nov., isolated from flowers and bees, and transfer of related *Candida* species to the genus *Starmerella* as new combinations. *International Journal of Systematic and Evolutionary Microbiology*, *68*(4), 1333–1343.

Santos, A. R. O., Perri, A. M., Andrietta, M. G. S., Rosa, C. A., & Lachance, M. A. (2015). The expanding large-spored *Metschnikowia* clade: *Metschnikowia matae* sp. nov., a yeast species with two varieties from the Brazilian Atlantic Forest. *Antonie Van Leeuwenhoek*, *108*, 753–763.

Santos, A. R. O., Souza, G. F. L., Barros, K. O., Alvarenga, F. B. M., Lopes, M. R., Souza, L. M. D., Rosa, L. H., Góes-Neto, A., Morais, P. B., Lachance, M. A., & Rosa, C. A. (2023). *Spathaspora brunopereirae* sp. nov. and *Spathaspora domphillipsii* sp. nov., two D-xylose-fermenting ascosporogenous yeasts from Amazonian Forest biomes. *International Journal of Systematic and Evolutionary Microbiology*, *73*(3), 005752. https://doi.org/10.1099/ijsem.0.005752

Sapsirisuk, S., Polburee, P., Lorliam, W., & Limtong, S. (2022). Discovery of oleaginous yeast from mountain forest soil in Thailand. *Journal of Fungi*, *8*, 1100. https://doi.org/10.3390/jof8101100

Satianpakiranakorn, P., Khunnamwong, P., & Limtong, S. (2020). Yeast communities of secondary peat swamp forests in Thailand and their antagonistic activities against fungal pathogens cause of plant and postharvest fruit diseases. *PLoS One*, *15*(3), e0230269. https://doi.org/10.1371/journal.pone.0230269

Sayer, J. A., Harcout, C. S., & Collins, N. M. (1992). *The conservation Atlas of Tropical Forests: Africa*. Macmillian Publishers Ltd.

Seike, T., Takekata, H., Uchida, Y., Sakata, N., Furusawa, C., & Matsuda, F. (2023). *Wickerhamiella bidentis* sp. nov., a novel yeast species isolated from flowers and insects in Japan. *International Journal of Systematic and Evolutionary Microbiology*, *73*(3), 005739. https://doi.org/10.1099/ijsem.0.005739

Sena, L. M. F., Morais, C. G., Lopes, M. R., Santos, R. O., Uetanabaro, A. P. T., Morais, P. B., Vital, M. J. S., de Morais Jr., M. A., Lachance, M. A., & Rosa, C. A. (2017). D-xylose fermentation, xylitol production and xylanase activities by seven new species of *Sugiyamaella*. *Antonie Van Leeuwenhoek*, *110*(1), 53–67. https://doi.org/10.1007/s10482-016-0775-5

Silva, J. M. C., Barbosa, L. C. F., Leal, I. R., & Tabarelli, M. (2017). The Caatinga: Understanding the challenges. In J. M. C. Silva, I. R. Leal, & M. Tabarelli (Eds.), *Caatinga: The largest tropical dry forest region in South America* (pp. 3–19). Springer.

Silva, J. L. S., Cruz-Neto, O., Peres, C. A., Tabarelli, M., & Lopes, A. V. (2019). Climate change will reduce suitable Caatinga dry forest habitat for endemic plants with disproportionate impacts on specialized reproductive strategies. *PLoS One*, *14*(5), e0217028. https://doi.org/10.1371/journal.pone.0217028

Sipiczki, M. (2022). Taxonomic revision of the pulcherrima clade of *Metschnikowia* (fungi): Merger of species. *Taxonomy*, *2*(1), 107–123.

Sipiczki, M., Pfliegler, W. P., Safar, S. V. B., Morais, P. B., & Rosa, C. A. (2016). *Metahyphopichia laotica* gen. nov., sp. nov., a polymorphic yeast related to *Hyphopichia*. *International Journal of Systematic and Evolutionary Microbiology*, *66*(7), 2550–2557. https://doi.org/10.1099/ijsem.0.001091

van der Sluis, C., Tramper, J., & Wijffels, R. H. (2001). Enhancing and accelerating flavour formation by salt-tolerant yeasts in Japanese soy-sauce processes. *Trends in Food Science & Technology*, *12*(9), 322–327. https://doi.org/10.1016/S0924-2244(01)00094-2

Smith, M. T., & Groenewald, M. (2012). The treasure trove of yeast genera and species described by Johannes van der Walt (1925-2011). *IMA Fungus*, *3*(2), 179–187. https://doi.org/10.5598/imafungus.2012.03.02.10

Sniegowski, P., Dombrowski, P., & Fingerman, E. (2002). and coexist in a natural woodland site in North America and display different levels of reproductive isolation from European conspecifics. *FEMS Yeast Research*, *1*, 299–306. https://doi.org/10.1016/S1567-1356(01)00043-5

Souza, G. F. L., Barros, K. O., Alvarenga, F. B. M., Santos, A. R. O., Fonseca, C. R. V., Abegg, M. A., Lachance, M. A., & Rosa, C. A. (2023). *Sugiyamaella bielyi* f. a., sp. nov. and *Sugiyamaella amazoniana* f. a., sp. nov., two yeast species isolated from passalid beetles and rotting wood in Amazonia. *International Journal of Systematic and Evolutionary Microbiology*, *73*(4), 005839. https://doi.org/10.1099/ijsem.0.005839

Souza, G. F. L., Valentim, L. T. C. N., Nogueira, S. R., & Abegg, M. (2017). Efficient production of second generation etanoland xylitol by yeasts from Amazonian beetles (Coleopter) and their galleries. *African Journal of Microbiology Research*, *11*(20), 814–824. https://doi.org/10.5897/AJMR2017.8522

Souza Jr., C. M., Z. Shimbo, J., Rosa, M. R., Parente, L. L., A. Alencar, A., Rudorff, B., Hasenack, H., Matsumoto, M., G. Ferreira, L., Souza-Filho, P., de Oliveira, S. W., Rocha, W. F., Fonseca, A. V., Marques, C. B., Diniz, C. G., Costa, D., Monteiro, D., Rosa, E. R., Vélez-Martin, E., … Azevedo, T. (2020). Reconstructing three decades of land use and land cover changes in Brazilian biomes with landsat archive and earth engine. *Remote Sensing*, *12*(17), 2735. https://doi.org/10.3390/rs12172735

Sperandio, E. M., Martins do Vale, H. M., & Moreira, G. A. M. (2015). Yeasts from native Brazilian Cerrado plants: Occurrence, diversity and use in the biocontrol of citrus green mould. *Fungal Biology*, *119*(11), 984–993. https://doi.org/10.1016/j.funbio.2015.06.011

Stevens, G. (1983). *Bursera simaruba* (Indio desnudo, jiñocuave, gumbo limbo). In D. H. Janzen (Ed.), *Costa Rican natural history* (pp. 2201–2202). University of Chicago Press.

Sudbery, P. E. (2011). Growth of *Candida albicans* hyphae. *Nature Reviews Microbiology*, *9*(10), 737–748.

Suh, S. O., Nguyen, N. H., & Blackwell, M. (2005). Nine new *Candida* species near *C. membranifaciens* isolated from insects. *Mycological Research*, *109*(9), 1045–1056.

Surussawadee, J., Jindamorakot, S., Nakase, T., Lee, C. F., & Limtong, S. (2015). *Hannaellaphyllophila* sp. nov., a basidiomycetous yeast species associated with plants in Thailand. *International Journalof Systematic and Evolutionary Microbiology*, *65*(7), 2135–2140. https://doi.org/10.1099/ijs.0.000231

Sweeney, J., Kuehne, H., & Sniegowski, P. (2004). Sympatric natural and populations have different thermal growth profiles. *FEMS Yeast Research*, *4*, 521–525. https://doi.org/10.1016/S1567-1356(03)00171-5

Teixeira, A. C. P., Marini, M. M., Nicoli, J. R., Antonini, Y., Martins, R. P., Lachance, M. A., & Rosa, C. A. (2003). *Starmerella meliponinorum* sp. nov., a novel ascomycetous yeast species associated with stingless bees. *International Journal of Systematic and Evolutionary Microbiology*, *53*(1), 339–343.

Teixeira, M. G., Venticinque, E. M., Lion, M. B., & Pinto, M. P. (2021). The Brazilian Caatinga protected areas: An extremely unbalanced conservation system. *Environmental Conservation*, *48*(4), 287–294. https://doi.org/10.1017/S0376892921000308

Thanh, V. N. (2006). *Lipomyces orientalis* sp. nov., a yeast species isolated from soil in Vietnam. *International Journal of Systematic and Evolutionary Microbiology*, *56*, 2009–2013. https://doi.org/10.1099/ijs.0.64241-0

Thongekkaew, J., Khumsap, A., & Chatsa-nga, P. (2012). Yeasts in mixed deciduous forest areas of Phujong Nayoy National Park and their ability to produce xylanase and carboxymethyl cellulase. *Songklanakarin Journal of Science and Technology*, *34*(2), 157–163.

Tiago, M. R. M., Cortez, A. C. A., Souza, J. V. B., Brito, D. V., & Carvalho-Zilse, G. A. (2022). Fungi associated with hives and castes of the Amazonian stingless bees *Melipona interrupta* and *Melipona seminigra*. *Research Square*. https://doi.org/10.21203/rs.3.rs-2355604/v1

Trochine, A., Turchetti, B., Vaz, A. B. M., Brandao, L., Rosa, L. H., Buzzini, P., Rosa, C., & Libkind, D. (2017). Description of *Dioszegia patagonica* sp. nov., a novel carotenogenic yeast isolated from cold environments. *International Journal of Systematic and Evolutionary Microbiology*, *67*(11), 4332–4339. https://doi.org/10.1099/ijsem.0.002211

Urbina, H., Schuster, J., & Blackwell, M. (2013). The gut of Guatemalan passalid beetles: A habitat colonized by cellobiose and xylose-fermenting yeasts. *Fungal Ecology*, *6*(5), 339–355. https://doi.org/10.1016/j.funeco.2013.06.005

Vale, S. C. S., Guimarães, A. P. M., & Morais, P. B. (2015). Occurrence andbiotechnological potential of yeasts associated with almond fruits of Attalea speciosa Mart ex Spreng. *Journalof Bioenergy and Food Science*, *2* (4),1–5. https://doi.org/10.18067/jbfs.v2i4

de Vega, C., Albaladejo, R. G., Guzmán, B., Steenhuisen, S. L., Johnson, S. D., Herrera, C. M., & Lachance, M. A. (2017). Flowers as a reservoir of yeast diversity: Description of *Wickerhamiella nectarea* f.a. sp. nov., and *Wickerhamiella natalensis* f.a. sp. nov. from South African flowers and pollinators, and transfer of related *Candida* species to the genus *Wickerhamiella* as new combinations. *FEMS Yeast Research*, *17*(5), fox054. https://doi.org/10.1093/femsyr/fox054

de Vega, C., Guzmán, B., Lachance, M. A., Steenhuisen, S. L., Johnson, S. D., & Herrera, C. M. (2012). *Metschnikowia proteae* sp. nov., a nectarivorous insect–associated yeast species from Africa. *International Journal of Systematic and Evolutionary Microbiology*, *62*, 2538–2545.

de Vega, C., Guzmán, B., Steenhuisen, S. L., Johnson, S. D., Herrera, C. M., & Lachance, M. A. (2014). *Metschnikowia drakensbergensis* sp. nov. and *Metschnikowia caudata* sp. nov., endemic yeasts associated with *Protea* flowers in South Africa. *International Journal of Systematic and Evolutionary Microbiology*, *64*, 3724–3732.

Vital, M. J. S., Abranches, J., Hagler, A. N., & Mendonça-Hagler, L. C. (2001). Mycocinogenic yeasts isolated from Amazon soils of the Maracá Ecological Station, Roraima-Brazil. *Brazilian Journal of Microbiology*, *33*, 217–223.

Wang, S. A., Jia, J. H., & Bai, F. Y. (2008). *Candida alocasiicola* sp. nov., *Candida hainanensis* sp. nov., *Candida heveicola* sp. nov. and *Candida musiphila* sp. nov., novel anamorphic, ascomycetous yeast species isolated from plants. *Antonie Van Leeuwenhoek*, *94*, 257–265. https://doi.org/10.1007/s10482-008-9238-y

Wang, Q.-M., Liu, W.-Q., Liti, G., Wang, S.-A., & Bai, F.-Y. (2012). Surprisingly diverged populations of *Saccharomyces cerevisiae* in natural environments remote from human activity. *Molecular Ecology*, *21*, 5404–5417. https://doi.org/10.1111/j.1365-294X.2012.05732.x

Wang, J., Zhao, M., Xie, N., Huang, M., & Feng, Y. (2022). Community structure of yeast in fermented soy sauce and screening of functional yeast with potential to enhance the soy sauce flavor. *International Journal of Food Microbiology*, *370*, 109652. https://doi.org/10.1016/j.ijfoodmicro.2022.109652

Wardlaw, A. M., Berkers, T. E., Man, K. C., & Lachance, M. A. (2009). Population structure of two beetle-associated yeasts: Comparison of a New World asexual and an endemic Nearctic sexual species in the *Metschnikowia* clade. *Antonie Van Leeuwenhoek*, *96*, 1–15.

Wiens, F., Zitzmann, A., Lachance, M.-A., Yegles, M., Pragst, F., Wurst, F. M., von Holst, D., Guan, S. L., & Spanagel, R. (2008). Chronic intake of fermented floral nectar by wild treeshrews. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 10426–10431. https://doi.org/10.1073/pnas.0801628105

Zhai, Y. C., Huang, L. N., Xi, Z. W., Chai, C. Y., & Hui, F. L. (2019). *Candida yunnanensis* sp. nov. and *Candida parablackwelliae* sp. nov., two yeast species in the *Candida albicans/Lodderomyces* clade. *International Journal of Systematic and Evolutionary Microbiology*, *69*(9), 2775–2780. https://doi.org/10.1099/ijsem.0.003552

Zheng, J., Liu, K.-F., Liu, Z-J, Zhang, L., & Hui, F.-L. (2017). *Deakozyma yunnanensis* sp. nov., a novel yeast species isolated from rotten wood. *International Journal of Systematic and Evolutionary Microbiology*, *67*(7), 2436–2439. https://doi.org/10.1099/ijsem.0.001978

Zong, L. (2020). The path to effective national park conservation and management: Hainan Tropical Rainforest National Park System Pilot Area. *International Journal of Geoheritage and Parks*, *8*(4), 225–229. https://doi.org/10.1016/j.ijgeop.2020.11.009

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Rosa, C. A., Lachance, M.-A., Limtong, S., Santos, A. R. O., Landell, M. F., Gombert, A. K., Morais, P. B., Sampaio, J. P., Gonçalves, C., Gonçalves, P., Góes-Neto, A., Santa-Brígida, R., Martins, M. B., Janzen, D. H., & Hallwachs, W. (2023). Yeasts from tropical forests: Biodiversity, ecological interactions, and as sources of bioinnovation. *Yeast*, *40*, 511–539. https://doi.org/10.1002/yea.3903