Yeasts from temperate forests

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Take-aways:

- Temperate forests are a widespread global biome, and host diverse yeasts.
- Well-studied model yeasts from other fields are in temperate forests.
- Isolation strategies depend on target yeasts and researcher questions.
- Temperate forest yeasts are potentially exciting biotechnological resources.
- Advancing technology is revealing yeast growth and life cycle secrets.

Abstract

Yeasts are ubiquitous in temperate forests. While this broad habitat is well-defined, the yeasts inhabiting it and their life cycles, niches, and contributions to ecosystem functioning are less understood. Yeasts are present on nearly all sampled substrates in temperate forests worldwide. They associate with soils, macroorganisms, and other habitats, and no doubt contribute to broader ecosystem-wide processes. Researchers have gathered information leading to hypotheses about yeasts' niches and their life cycles based on physiological observations in the laboratory as well as genomic analyses, but the challenge remains to test these hypotheses in the forests themselves. Here we summarize the habitat and global patterns of yeast diversity, give some information on a handful of well-studied temperate forest yeast genera, discuss the various strategies to isolate forest yeasts, and explain temperate forest yeasts' contributions to biotechnology. We close with a summary of the many future directions and outstanding questions facing researchers in temperate forest yeast ecology. Yeasts present an exciting opportunity to better understand the hidden world of microbial ecology in this threatened and global habitat.

1. Introduction

Yeasts, defined here as predominantly unicellular fungi that often reproduce asexually by budding or fission (Kurtzman et al., 2011; Boekhout et al., 2021a), and dimorphic fungi that have filamentous and unicellular phases, are ubiquitous throughout Earth's biomes (Péter et al., 2017; Boekhout et al., 2021a); however, they are often overlooked in favor of sporocarp-forming fungi. This is especially true in temperate forests, where researchers have paid considerable attention to decomposer and mycorrhizal fungi, many of which produce large macroscopic fruiting bodies (Albarracín et al., 2013; Tedersoo et al., 2010; Boddy & Hiscox 2016). Nevertheless, yeasts have colonized a diverse variety of available forest substrates, including soils and the microbiomes of plants, animals, and other fungi (Péter et al., 2017; Yurkov, 2018; Stefanini, 2018; Starmer & Lachance, 2011; Yurkov et al., 2012; Boekhout et al., 2021a). In addition to being ubiquitous, yeasts are involved in multiple ecosystem processes, acting as free-living saprobes, mutualists, parasites, and other symbionts (Starmer & Lachance, 2011). They likely have profound impacts on ecosystem functioning in temperate forests. However, most of mycologists' and ecologists' current knowledge about yeasts in temperate forests comes from *ex-situ* studies of model organisms. In response, research on natural history and ecology throughout this fascinating fungal group in the temperate forest environment is currently expanding.

Because yeasts are so diverse, they have the potential to have diverse impacts on temperate forest ecosystems. Genomic surveys have associated yeasts with higher stress tolerance, simpler carbon utilisation, and higher nitrogen uptake compared to filamentous fungi

(Treseder & Lennon 2015; Romero-Olivares et al., 2021), although these genomic surveys are biased toward model organisms. In temperate forests, yeast communities respond to changes in forest properties including tree age, density, management, and wood deposition, and these changes may feed back on forest ecosystem function (Birkhofer et al., 2012; Yurkov et al., 2012; Yurkov et al., 2012b; Yurkov et al., 2016). While data on yeasts' impacts on temperate forest ecosystem functioning is still in its infancy, temperate forest yeasts may impart ecosystem resilience in the face of climate change. For example, researchers speculate that stress-tolerant yeasts will respond positively to stressful environmental changes relative to filamentous fungi, leading to decreased filamentous fungal decomposition and increased carbon storage in forest environments (Treseder & Lennon 2015).

In this review, we define temperate forests broadly as forests in the temperate zone, found between boreal and tropical forests. Overall, forests cover nearly a third of global land area, and 16% of forested area is occupied by temperate forests (10 million km^2) (FAO & UNEP 2020). Transitions between temperate and boreal, or temperate and tropical, are not sharp. Temperate forest vegetation is diverse, including coniferous, deciduous, and mixed forests in Köppen classification climate groups C and D (Beck et al., 2018). This vegetation ranges from nearly boreal (continental, with pronounced cold seasons) to subtropical with mild climates (only rarely with temperatures below 0 ºC) and can include climates with a pronounced dry season (Mediterranean climate). In several geographic areas, temperate forests border large grasslands, including the North American great plains and tallgrass prairie, Patagonian grasslands, Eurasian steppes, and Humid Pampas (Myster (ed.) 2012). The majority of temperate forests are located in the northern hemisphere (Beck et al., 2018).

Most forests in the temperate zone are included in two terrestrial biomes (Olson & Dinerstein 2002), the temperate broadleaf and mixed forests biome and the temperate coniferous forest biome. The former includes most broadleaf and mixed forests in both hemispheres, and the latter includes Alpine, coastal Scandinavian, Asian (Himalayan and Tian Shan), Mediterranean, and coastal North American Pacific forests. Dominant tree families include Fagaceae (*e.g*. *Betula, Fagus, Nothofagus, Quercus*), Pinaceae (*e.g. Abies, Picea, Pinus*), Cupressaceae (*e.g*. *Fitzroya, Juniperus, Sequoia*), and, exclusively in the southern hemisphere, Araucariaceae (*e.g. Agathis, Araucaria*), Podocarpaceae (*e.g. Dacrydium, Podocarpus, Saxeogathea*), and tree ferns (*Cyatheales*) (Reyna et al., 2018; Mao et al., 2012; Beard,, 1990; Brock et al., 2016). Temperate forests also include unique and interesting plant communities such as dry Mediterranean-type forests (*e.g.* Oak and Eucalyptus forests), humid temperate rainforests (*e.g.* Valdivian forest in South America) and relict laurel forests (*e.g.* Macaronesian Laurisilva) (Cowling et al., 1996; Claudino-Sales 2019; Noh et al., 2019).

Human activities have had a large impact on forests, mainly through continuous deforestation (e.g. for timber and energy) and forest conversion into agricultural lands (FAO &

UNEP 2020). Additionally, global warming and fires are devastating for forest ecosystems, with fire destroying 1% of temperate forest area in 2015 (FAO & UNEP 2020). Recently recognized biodiversity hotspots in temperate forests highlight the unique character of these ecosystems and need for forest conservation (Myers et al., 2000). We expect high numbers of endemic plants and animals to similarly harbor high numbers of endemic microorganisms, including yeasts.

In this review, we address the current knowledge of yeast diversity in temperate forests, their ecology, and their biotechnological applications. We discuss biases in the literature and how an unbiased picture of yeasts' roles and biodiversity will emerge from future studies.

2. Yeast biodiversity and abundance in temperate forests

2.1 Yeast distributions from environmental sequencing

Based on environmental sequencing data, yeasts are widespread globally in temperate forest soil and leaf litter (Figure 1), but their frequencies tend to be low. However, there are potential biases and errors in environmental sequencing due to incomplete databases, detection of dead or dormant cells, technical biases, and different detection limits between sequence- and culture-based studies; conclusions from environmental sequencing should therefore be made cautiously and confirmed using culture-based studies whenever possible (Lücking et al., 2020). A comprehensive screening of temperate forest soil and leaf litter internal transcribed spacer (ITS) barcode sequences deposited in the GlobalFungi database (Vetrovsky et al., 2020) and analysed for this review revealed 3,783,412 total yeast sequences belonging to 859 yeast species hypotheses (SHs); yeasts here were "yeast" or "facultative yeast" as in Polme et al. (2020), with some manual curation (Table S1); and only samples with more than 5000 fungal sequences were considered. Fungal ITS-targeting primers perform well with all important fungal lineages containing yeasts as well as individual yeasts in a mock community (Větrovský et al., 2016; 2019) and no significant PCR bias is observed when comparing the yeast share in metagenomic data (without PCR) and ITS amplicon data (Tláskal et al., 2021); nor does there seem to be important DNA extraction bias against selected yeast taxa (Větrovský et al., 2016). This screening showed that the median yeast abundance in soil was significantly higher than in litter (Wilcoxon Rank-Sum test, $W = 722187$, $p = 2.9 \times 10^{-15}$). Yeasts were generally not common: only 12% of soil samples and 3% of litter samples included more than 8% yeast ITS sequences (Figure S1). Richness ranged from 1-31 in soil and 1-35 in litter (Table S1). Because of geographical sampling biases (Figure 1) and the overall low frequencies of yeasts in most individual samples, we could not conduct analyses correlating yeast incidence with season, climate, or host plant. However, we

anecdotally noticed a weak amount of seasonality in yeast communities; this seasonality remains to be investigated with targeted studies.

The global temperate forest yeast community emerging from barcode sequencing includes some widespread and dominant taxa. Specifically, the most frequently detected classes containing yeasts were *Tremellomycetes* (87.7% of yeast sequences), *Dothiomycetes* (4.6%) and *Eurotiomycetes* (3.1%). The most prevalent yeast species, with prevalence meaning the percent of temperate forest and soil samples on which a species was found, were *Saitozyma podzolica*, *Solicoccozyma terricola*, *Apiotrichum xylopini/porosum*, *Tausonia pullulans*, and *Cutaneotrichosporon moniliforme* (Table S2). These five yeast species are widespread and cosmopolitan, and have broad climatic niches (Větrovský et al., 2019).

2.2 Yeasts in culture collections

While culture-independent methods to profile microbial species and their functions are gaining prominence, the vast majority of the current knowledge about the biodiversity and distributions of yeasts in temperate forests has been garnered through direct isolation and subsequent study of yeast cultures. Currently, thousands of yeast strains isolated from temperate forests are preserved in both public and private microbial culture collections. Researchers have used collections to demonstrate that yeast communities in natural unmanaged forests can be more species-rich than in managed ones (Yurkov et al., 2012; Yurkov et al., 2016); below-ground communities reflect properties of plant cover, such as canopy density and diversity; and seasonality impacts total quantity and species richness of yeasts (Yurkov et al. 2016). However, these conclusions rely on targeted sampling, which is currently limited by locality, season and substrates.

Many culture collections throughout the globe contain lots of yeast isolates from temperate forests. In many cases, researchers can search culture collection catalogs for keywords or substrate, such as “soil”, “forest”, or “bark” to help identify temperate forest yeasts. The Global Catalog of Microorganisms (https://gcm.wdcm.org), organized with the World Data Centre for Microorganisms (WDCM), has combined the catalogs of over 140 public microbe collections to streamline the process of locating a specific yeast species or yeasts isolated from a certain location or habitat (Wu et al., 2013). In addition, the list of Culture Collections Information Worldwide (CCINFO), created by the WDCM and the World Federation for Culture Collections (WFCC), provides an overview of more than 800 repositories worldwide. For more information about the history and ongoing use of culture collections, we recommend the review of Boundy-Mills and coauthors (2016). Not all culture collections index strain habitat information in a searchable way, and a reliable summary of yeast cultures from temperate forests is a current challenge.

3. Model yeast genera in temperate forests

Beginning with the genus *Saccharomyces* in the days of Louis Pasteur (Pasteur 1876), several groups of yeasts have been used as model organisms for biotechnology, cell biology, medicine, genetics, and genomics. While the impacts of these yeast groups extend well beyond yeast biology, many of them have also been isolated from temperate forest ecosystems. These include the genera *Saccharomyces, Komagataella*, and *Lachancea*, and yeasts that until recently were classified in the genus *Cryptococcus*, and comprise a polyphyletic group. These yeast groups have the potential to be valuable models for temperate forest ecology, and some—especially the genus *Saccharomyces*—are already well-developed ecological and evolutionary models.

3.1 The genus *Saccharomyces*

The genus *Saccharomyces* is the most frequently studied model yeast group in temperate forests. There are eight known species: *S. cerevisiae, S. paradoxus, S. mikatae, S. jurei, S. kudriavzevii, S. arboricola*, *S. eubayanus* and *S. uvaraum* (Batschinskaya, 1914; Libkind et al., 2011; Meyen, 1839; Naseeb et al., 2017; Naumov et al., 2000; Ono et al., 2020; Pulvirenti et al., 2000; Wang et al., 2012). *S. cerevisiae* is a famous industrial and laboratory model organism, and hybrids between *Saccharomyces* species are also industrially important (Gallone et al., 2019; Langdon et al., 2019; Peréz-Torrado et al., 2018). All *Saccharomyces* species, including *S. cerevisiae*, have been isolated from temperate forest substrates, including tree bark, leaf litter, soil, fruits, insects, and leaf surfaces (Phaff et al., 1956; Libkind et al., 2011; Sampaio & Gonçalves, 2008, 2017; Naseeb et al., 2017; Naumov et al, 2000; Wang & Bai 2008; Glushakova et al., 2007). The genus includes several rare naturally-occurring hybrids and incipient hybrid species (Barbosa et al., 2016; Leducq et al., 2016; Eberlein et al., 2019) in addition to the eight *Saccharomyces* species, although most hybrids are from domesticated environments (Liti et al., 2005; Gibson et al., 2017). Interspecies *Saccharomyces* hybrids are rare outside of domesticated environments, although genomic introgressions (e.g., *S. paradoxus* open reading frames in *S. cerevisiae* genomes) have been found in temperate forest yeasts, and are evidence of past hybridization (Almeida et al., 2014; Peter et al., 2018).

Of the eight known *Saccharomyces* species, *S. paradoxus* has been most frequently isolated from temperate forests, and it is the best-studied *Saccharomyces* species outside of domesticated environments. The species was first described in 1914 based on strains isolated from oak and elm exudates in Russia (Batschinskaya, 1914). Its native range includes much of the northern hemisphere with average summer temperatures below 31 ºC (Robinson et al., 2016). Its infrequent isolation in New Zealand is consistent with a recent migration of isolates with European ancestry (Zhang et al., 2010)**.** Most isolates have been obtained from bark, sap

exudates, leaf litter, and soil; host trees are often but not always oaks (Phaff et al., 1956; Kodama, 1974; Banno & Mikata, 1981; Naumov, 1996; Naumov et al., 1998; Kowallik & Greig, 2016; Kowallik et al., 2015; Glushakova et al., 2011; Sampaio & Goncalves, 2008, 2017; Sniegowski et al., 2002). *S. paradoxus* is generally infrequent in forest habitats, but its frequency can spike seasonally or after rain events to as many as 100% of isolated colonies (Glushakova et al., 2007; Anderson et al., 2018; Charron et al., 2014); these spikes are less evident when sampling is less frequent, with a pattern of approximately even frequency year-round in at least one study (Kowallik & Greig, 2016).

Similar surveys also identified other northern hemisphere *Saccharomyces* species (Sampaio & Goncalves 2008). For instance, recent studies suggest that eastern Asia harbors several *Saccharomyces* species characterized by high genetic diversity (Duan et al., 2018; Han et al., 2021; Lee et al., 2021; Wang et al., 2012; Bing et al., 2014; Bendixen et al., 2021; Peter et al., 2018), including temperate forest *S. cerevisiae* populations that are strongly diverged from domesticated populations (Duan et al., 2018; Wang et al., 2012). Some examples of successful sampling efforts that uncovered multiple species include a study in which *S. kudriavzevii*, *S. uvarum*, and *S. cerevisiae were* isolated from oak bark in Portugal (Sampaio & Gonçalves, 2008, 2017), and another in which *S. arboricola*, *S. kudriavzevii*, and *S. cerevisiae* were isolated from mushrooms, litter and leaves in Taiwan (Naumov et al., 2013). In contrast, *S. jurei*, *S. arboricola*, and *S. mikatae* geographic ranges appear more limited. For example, the strains of *S. arboricola* were only isolated from trees of the Fagacee family in China in 2008 (Wang et al., 2008), and *S. mikatae* has only been isolated so far in soil and decayed leaves from Japan and China (Naumov et al., 2000, Sampaio & Gonçalves 2017). Along the same line, *S. jurei* has been recently isolated twice in different locations in Europe (Naseeb et al., 2017, Hutzler et al., 2021) and a metagenomic study also detected *S. jurei* in temperate forests in the Italian Alps (Alsammar et al., 2019), but it is not yet known if different populations exist outside Europe. *S. jurei* and *S. mikatae* share some genomic rearrangements, suggesting a shared evolutionary history (Naseeb et al., 2018).

Northern hemisphere *Saccharomyces* species isolated from temperate forests show generally low genetic admixture. Forest *S. paradoxus* populations have high clonality and low heterozygosity, and they experience infrequent sex with even less frequent outcrossing (3×10^{-6} to 10^{-5} per cell division) (Tsai et al., 2008; Johnson et al., 2004; Liti et al., 2006; Liti et al., 2009; Bergström et al., 2014). Researchers sampling *S. paradoxus* in temperate forests frequently find the same clonal genotype, with the probability of uncovering the same clone decreasing with distance (Koufopanou et al., 2006). The same clone can also persist over consecutive years (Koufopanou et al., 2006) (Xia et al., 2017; Anderson et al., 2018). Similarly, *S. cerevisiae* outcrossing rates are also estimated to be low at 9×10^{-5} to 2×10^{-5} per cell division (Jensen et al., 2001; Ruderfer et al., 2006). However, outcrossing rates of *S.*

cerevisiae increased at least ten-fold when yeast spores were digested by an insect dispersal vector such as *Drosophila* (Reuter et al., 2007); insect digestive systems may promote outcrossing and hybridization by bringing ascospores together (Stefanini et al., 2016).

Surveys in the southern hemisphere have further expanded our understanding of *Saccharomyces* diversity. During the past decade, *S. uvarum* and *S. eubayanus* have emerged as the most frequently isolated *Saccharomyces* species in bark, fruits and soil in the southern hemisphere, particularly in Australasian and South American temperate forests (Figure 1) (Almeida et al., 2014; Eizaguirre et al., 2018; Langdon et al., 2020; Libkind et al., 2011; Nespolo et al., 2020; Rodriguez et al., 2014). Patagonia, in particular, harbors high *S. uvarum* and *S. eubayanus* diversity (Nespolo et al., 2020; Langdon et al., 2020; Peris et al., 2016). *S. eubayanus* is widely distributed in South Patagonia and associates with cold environments, and it has also been isolated in Asia (Bing et al., 2014; Peris et al., 2016), Oceania, (Gayevskiy & Goddard, 2016) and North America (Peris et al., 2014). Interestingly, *S. eubayanus*, a parent of the hybrid lager species *S. pastorianus*, has never been isolated in Europe, challenging our understanding of the origin of lager beer yeast hybrids. While *S. eubayanus* may indeed be rare in Europe, the lack of *S. eubayanus* in Europe could also be due to insufficient sampling or absence of the species due to deforestation. Recent evidence collected from a targeted metagenomics study of *Saccharomyces* diversity in the Italian Alps suggests that *S. eubayanus* may be present in Europe, although future culture-based work is needed to confirm this (Alsammar et al., 2019).

In addition to members of the genus *Saccharomyces* isolates from throughout the globe, genome sequencing of isolates from hybrid zones have revealed admixture among partially reproductively isolated *S. paradoxus* populations (Leducq et al., 2016; Xia et al., 2017; Eberlein et al., 2019). For instance, studies on genetically diverged and partially reproductively isolated North American *S. paradoxus* lineages revealed the presence of hybrid, phenotypically diverged, and reproductively isolated lineages, which were found at intersections of the parental geographic distributions. These incipient hybrid species evolved following post glacial admixture between parental lineages (Leducq et al., 2016; Xia et al., 2017; Eberlein et al., 2019).

The ecological determinants of different *Saccharomyces* lineages' ranges are still unclear. Temperature has been suggested as an important abiotic niche determinant because experimental work found different temperature optima among *Saccharomyces* lineages (Sweeney et al., 2004; Salvado et al., 2011). In the northern hemisphere, it has been hypothesized that *S. cerevisiae* is better adapted to warmer temperatures than *S. paradoxus* (Charron et al., 2014; Robinson et al., 2016). Climatic modeling of *S. eubayanus* has also recapitulated much of its known distribution (Langdon et al., 2020). In some locations, multiple *Saccharomyces* species with different temperature optima coexist at the same site. For

example, cold-tolerant *S. kudriavzevii* and *S. uvarum* are readily isolated from the same samples that yielded warm-tolerant *S. cerevisiae* or *S. paradoxus*, when these same samples were incubated at two different temperatures (Sampaio & Goncalves 2008; Sweeney et al., 2004). Diversity in genes related to glycerol accumulation and acetaldehyde production has been implicated in temperature tolerance diversity and may therefore be important for temperature niche partitioning (Paget et al., 2014).

While temperature may indeed determine the ranges of *S. paradoxus* and *S. cerevisiae* in the northern hemisphere, this does not directly translate to a correlation between latitude and sampling success. We surveyed the literature for studies that isolated either *S. paradoxus* or *S. cerevisiae* from temperate forests and clearly stated the number of positive and negative sampling attempts (Table S3). Across these studies, rates of success in isolating either species does not correlate with latitude (Figure 2). However, *Saccharomyces cerevisiae* has been less frequently isolated at higher latitudes than *S. paradoxus* when isolation frequency is compared within the same study (Figure S2); more data are needed to further evaluate this observation. While several studies have reported isolation of one, but not both species, others have indeed isolated both *S. paradoxus* and *S. cerevisiae* from the same location (Boynton et al., 2019; Dashko et al., 2016; Kowallik et al. 2016; Sniegowski et al., 2002). This result suggests that additional factors influence these species' ranges beyond temperature.

A similar pattern of partial coexistence of *Saccharomyces* species is mediated by host tree identity in the southern hemisphere. For instance, South American *S. uvarum* and *S. eubayanus* partly share their habitat, but while *S. uvarum* is mainly found on *Nothofagus dombeyi*, *S. eubayanus* is mainly found on *Nothofagus pumilio* (Eizaguirre et al., 2018; Langdon et al., 2020; Libkind et al., 2011; Mardones et al., 2020). In spite of this apparent specialization, both species can inhabit the same tree, and elsewhere in Tibet they coexist in similar niches (Bing et al., 2014). Because dominant forest trees and species distributions change with latitude, there is a correlation between species isolated and latitude in the southern hemisphere (Figure 2, Table S3). *S. uvarum* is more frequently found at lower latitudes with warmer climates than *S. eubayanus* (Figure S2). In contrast, *S. eubayanus* is frequently found at higher latitudes and altitudes, near the treeline in extremely cold environments (Figure 2). The data used for this analysis are derived from a single study in which all samples were collected and processed using the same methods, suggesting that variability among isolation protocols across labs could add a confounding effect when estimating species ranges.

3.2 The genus *Cryptococcus* and former *Cryptococcus*

Taxonomic challenges over the past decades have drastically changed our understanding of the prevalence and frequency of the genus *Cryptococcus* in temperate

forests. Historically, sexual and asexual fungal forms were given separate names and the genus epithet "*Cryptococcus*" described asexual (*i.e.,* mitotically reproducing) species of basidiomycetous yeasts (Vuillemin 1901; Liu et al., 2015). This system of dual nomenclature for fungi with asexual and sexual forms was abolished in 2012 (Lücking et al., 2021). At about the same time, modern DNA sequencing technology regrouped the previous polyphyletic genus *Cryptococcus* into a monophyletic genus in the former sexual *Filobasidiella* clade, plus several other basidiomycete genera. The genus *Cryptococcus* now comprises prominent human pathogens (the *C. neoformans* species complex) and a few closely related non-pathogenic yeasts with a possible link to mycoparasites (Liu et al., 2015; Passer et al., 2019). All other former *Cryptococcus* species were transferred to other genera, emended, resurrected, or newly erected (Liu et al., 2015) (Table S4). As a consequence, historic reports of *Cryptococcus* from natural substrates can be dubious because they may be reports of species no longer circumscribed in the genus *Cryptococcus* (Lücking et al., 2021).

Members of the currently delineated genus *Cryptococcus* inhabit temperate forests worldwide (Cogliati et al., 2016; Lin et al., 2021; Chowdhary et al., 2012; Kidd et al., 2007). Non-pathogenic *Cryptococcus* species are rare and only known from a very few isolates of plant-insect origin, including *C. amylolentus*, *C. wingfieldii*, and *C. floricola* (Passer et al., 2019). The limited number of reports of environmental *Cryptococcus* are restricted to selective cultivation surveys of pathogenic species and single-strain isolations of potential new species (Mittelbach et al., 2015; Yurkov et al., 2016; Passer et al., 2019). The species *Cryptococcus neoformans* and *Cryptococcus gattii* are best known as human pathogens, but they have also been isolated from soils, water, air and tree samples from temperate forests (Chowdhary et al., 2012; Kidd et al., 2007; MacDougall et al., 2007). The exchange between host niches in the forest and human hosts contributes to disease incidence (Kidd et al., 2004).

Since the taxonomic revision of the genus (Liu et al., 2015), *Cryptococcus* has not been present in the list of prevalent genera found in forests. In contrast, many yeast genera previously assigned to the genus *Cryptococcus* have been found in temperate forests, and these genera are composed of several species. They mostly inhabit soil and plant (including moss) habitats (Table S4), and many have been detected using environmental barcode sequencing, with the genera *Vishniacozyma*, *Filobasidium*, *Piskurozyma*, *Saitozyma* and *Solicoccozyma* among those with the most abundant DNA sequences recovered in environmental samples (Kemler et al., 2017). In fact, several of the species identified as most common in our global analysis of yeast sequence diversity belong to this group (Table S2). We do not know what makes these taxa so common, but speculate that some of them may be generalists, inhabiting many different global environments, or have an as-yet unexplored, but very common, ecological niche in temperate forests. For example, many members of the genera *Filobasidium*, *Papiliotrema*, and *Vishniacozyma* inhabit aboveground substrates

(Yurkov et al., 2015; Kemler et al., 2017). Moreover, *Cryptococcus* and former *Cryptococcus* species (Table S4) use a variety of nutrient acquisition and stress tolerance strategies in temperate forest environments. Many of these yeasts from temperate regions are opportunistic saprobionts, consuming the products of decomposing plant material released by other microorganisms, such as filamentous fungi (Babjeva and Golovleva, 1963; Yurkov, 2017; Mašínová et al., 2018). However, others can use complex compounds directly. For example, forest soil strains of *Solicoccozyma terricola* and *Holtermanniella wattica* (formerly *Cryptococcus terricola* and *C. watticus*) exhibit a wide assimilation spectrum of carbon sources and extracellular enzymes, including growth on oligosaccharides (Mašínová et al., 2018). Similarly, *S. terrea* and some *Apiotrichum* species can grow on phenolic compounds (Botha 2006; Yurkov et al., 2017). Many former *Cryptococcus* have physiological features that can increase their chances of survival under stress as other temperate forest yeasts, including drought, nutrient limitation, and radiation in soil and phylloplane environments (Kemler et al., 2017; Yurkov, 2017). For example, members of the genera *Naganishia* and *Solicoccozyma* produce extracellular polysaccharide capsules that promote growth in low nutrient and low water activity environments (Vishniac et al., 1995, 2006; Botha et al., 2011), and some *Naganishia* species produce mycosporines as radiation protection in extreme environments (Nizovoy et al., 2021**)**. This variety of nutrient acquisition and stress tolerance strategies illustrates the diversity and explains the heterogeneity of the former polyphyletic genus *Cryptococcus*.

3.3 The genus *Komagataella*

The seven species in the methanol-assimilating model genus *Komagataella* are all present in temperate forest ecosystems (Naumova et al., 2020). They have been isolated from tree exudates, bark, associated insects, and rotten wood of temperate forest trees including *Quercus* spp., *Populus* spp., *Ulmus* spp., *Castanea* spp. and *Betula* spp. in the northern hemisphere (Lachance et al., 1982; Naumova et al., 2020). Species in this genus have substrate preferences. For example, while most *Komagataella* species have been isolated from broad-leaved trees, *K. kurtzmanii* has been isolated only from fir flux. Additionally, *K. pseudopastoris* has higher sensitivity to the tannic acids in *Quercus* species than *K. pastoris* (Dlauchy et al., 2003; Péter et al., 2019).

Geography contributes to the taxonomic structure of the genus *Komagataella*. The genus itself includes three groups of closely related species: *K. pastoris/K. ulmi, K. kurtzmanii/K. phaffii*, and *K. mondaviourum/K. pseudopastoris/K. populi* (Figure S3) (Dlauchy et al., 2003; Kurtzman 2005, 2012; Naumov et al., 2013, 2018). As with *Saccharomyces*, *Komagataella* species readily hybridize in the laboratory, but hybrids are post-zygotically reproductively isolated and generate mostly unviable ascospores (0-7%) (Naumov 2015;

Naumov et al., 2016); they may also be pre-zygotically isolated by substrate or geography. We are not aware of naturally-occurring *Komagataella* hybrids in temperate forests, although the shared mating system among *Komagataella* species makes hybrids likely. *K. kurtzmanii, K. mondaviorum, K. phaffii, K. populi,* and *K. ulmi* have frequently been isolated from North America, while *K. pastoris* and *K. pseudopastoris* are spread across Europe (Dlauchy et al., 2003; Kurtzman, 2011a, 2012; Miller et al., 1962, Naumov 2013; 2018; Phaff et al., 1972). Large-scale screening of methanol-assimilating ascomycetous yeasts failed to isolate *Komagataella* strains in Thailand and Brazil (Limtong et al., 2013; Santos et al., 2015), suggesting that the genus might be absent from these areas. However, rare *Komagataella* isolates have been documented in Japan (Phaff et al., 1972; Kodama 1974) and Argentina (Spencer et al., 1995, 1996). Future sampling may uncover more species in this genus, which would likely expand our understanding of their ranges and ecology.

3.4 The genus *Lachancea*

The genus *Lachancea* comprises eleven species from a wide variety of ecological niches (Figure S4). Members of this genus are among the most commonly isolated yeasts worldwide and their relationship with temperate forest environments is understudied. *Lachancea* species share common physiological properties: they ferment glucose, can grow on raffinose, maltose, ethanol, and mannitol, and have similar temperature preferences and fermentation characteristics (Bandara et al., 2009; Naumova et al., 2007; S. Benito, 2018). They have been isolated from a wide variety of ecological niches, including plants (Esteve-Zarzoso et al., 2001; Gonzalez et al., 2007; Romano & Suzzi, 1993a, 1993b), tree bark (Nespolo et al., 2020), tree exudates (Varela et al., 2020), insects (Phaff et al., 1956), soil (Lee et al., 2009; Mesquita et al., 2013; Sylvester et al., 2015), water (Kenkichi. & Tadashi., 1974), and food and beverages (Magalhães et al., 2011; Marsh et al., 2014; Nova et al., 2009; Pereira et al., 2011; Tzanetakis et al., 1998; Wojtatowicz et al., 2001). While the most common species in the genus, *L. thermotolerans* and *L. fermentati*, are often associated with domesticated food and beverage environments (Aponte & Blaiotta, 2016bnt; Bagheri et al., 2016; Baleiras Couto et al.,, 2005; Clavijo et al., 2010; Cordero-Bueso et al., 2013; Fernández et al., 1999; Hsieh et al., 2012; Senses-Ergul et al., 2006), they are also frequently isolated from natural substrates (Sylvester et al., 2015; Spurley et al., 2021). *L. cidri*, a close relative of *L. fermentati*, has also been recently reported on *Nothofagus* bark in temperate southern Chile (Villarreal et al., 2021). Despite the large number of ecosystems where *Lachancea* is present, ranging from fermented beverages to temperate forests, there is a lack of information on why the different species inhabit such a wide variety of ecological niches (Porter et al., 2019b) and which roles they play in those ecosystems.

4. Practical suggestions for collecting yeasts from forests

Sampling and isolation steps both play a crucial role in yeast discovery and estimation of species richness (Lachance & Starmer 1998; Yurkov & Pozo 2017). When making a sampling and isolation plan, researchers should determine whether they wish to characterize the entire diversity of the environment or focus on a particular group of yeasts. Researchers' goals will ultimately inform their sampling and isolation strategies.

4.1 Collecting substrate samples from temperate forests for yeast isolation

Wild yeasts can be isolated from diverse habitats and ecological niches in temperate forests around the world, including soil, leaf litter, tree bark, rotten fruits, insect bodies, mushrooms, and other plant, animal, and fungal material. Generally, one to a few grams of material are sampled at a time (Boynton et al., 2019; Kowallik et al., 2015; Spurley et al., 2021). It is important to use proper aseptic technique to avoid contamination by wearing gloves and sterilizing tools with a solution of 70% ethanol. Substrate heterogeneity should be accounted for, either by mixing (in the case of soils), or deep and repeated sampling (in the case of difficult to mix substrates, such as phylloplane, nectar, and fluxes) (Boundy-Mills, 2006; Yurkov 2017, 2018; Yurkov & Pozo, 2017).

Because of substrate diversity and heterogeneity, researchers designing field surveys to isolate yeasts should also consider the ecological factors that might affect sampling results. These ecological factors include the geographic region of the forest, sampling substrates, and seasonal conditions. For example, *Saccharomyces* isolation success can be dependent on season, temperature, and surrounding flora; (Robinson et al., 2016; Charron et al. 2014; Leducq et al., 2014; Sylvester et al., 2015; Eizaguirre et al., 2018; Langdon et al., 2020). Additionally, genetic diversity, including levels of heterozygosity and admixture, can vary among sampled substrates: for example, wild *Saccharomyces* strains from forests have lower admixture and heterozygosity than strains isolated from fruits, flowers, insects, or human-associated substrates (Magwene et al., 2011, Hyma and Fay 2013; Tilakaratna and Bensasson 2017; Günther et al., 2019). Finally, because the number of observed species depends on the sampling intensity, species-rich substrates require more samples than species-poor ones to determine species richness (Yurkov & Pozo 2017).

Researchers should record sampling conditions carefully when conducting sampling schemes to effectively answer their research questions. Across studies, it is essential to record standard data about every yeast isolation sample, including the GPS coordinates of sampling sites; collection dates; descriptions of isolation substrates such as tree species and substrate material; descriptions of field sites; and climate data such as temperature or humidity. This metadata can be used for resampling across time and makes field collections repeatable. Metadata is also important for putting patterns of habitat preference and genetic diversity into

environmental context. Collected samples with appropriate metadata recorded can now be processed for strain isolation.

4.2 Strain isolation for diversity estimation and new species discovery

Direct streaking and dilution plating on universal media is preferable over enrichment techniques and selective media to have a broad overview of yeast biodiversity (Lachance & Starmer 1998; Boundy-Mills 2006; Yurkov et al., 2011). Yeast yield can be increased by filtration and sample concentration steps (Lachance & Starmer 1998; Boundy-Mills 2006). Media used for yeast isolation and enumeration are generally complex and nutritionally rich. Additives that suppress bacteria and filamentous fungi and special cultivation conditions increase the chances of isolating yeasts (Boundy-Mills 2006).

Inoculated tubes and plates are grown and visually inspected every two to three days for a minimum of two weeks or until growth is visualized. Isolation of slow-growing yeasts may require a prolonged incubation for more than four weeks. Purified cultures can be stored in 15-20% glycerol stocks at -80 ºC, but some yeasts should be safely cryopreserved at ultra-low (-196 or -140 ºC) temperatures to avoid their loss. Isolates are often identified using barcode sequencing of genomic loci, including ribosomal RNA (Robinson, Pinharanda, and Bensasson 2016; White et al., 1990; Spurley et al. 2021), using physiological tests, or other techniques such as MALDI-TOF (Boekhout et al., 2021a; Lücking et al., 2020).

4.3 Strain isolation targeting individual taxa

Strategies for isolating targeted taxa rely on phenotypic differences between target and other taxa. Selective isolation involves any unique physiological condition (e.g. fermentation ability) or tolerance to inhibitors (e.g. ethanol tolerance). These strategies include plating onto a selective medium, which has additives or environmental conditions that prevent growth of non-target taxa. Similarly, researchers can establish enrichment cultures, which have conditions that allow target taxa to grow more quickly than non-target taxa. Both strategies require some knowledge of target yeast physiology to design selective culturing conditions.

When plating, selective media can be taxon-specific (Boynton et al., 2019; Mašínová et al., 2018). When targeting yeasts, acidification and broad spectrum antibiotics reduce bacterial growth; and incubation at low temperatures, benomyl, calcium propionate and Rose Bengal may help to reduce mold growth (Boundy-Mills, 2006). Although this cultivation method can also reveal rare and minor species, selective isolation must be accompanied by an additional replicate with a complete medium when assaying diversity to ensure the complete assessment of the community (Yurkov & Pozo, 2017), and a negative control for contamination errors. Yeasts that produce forcefully ejected ballistospores can be isolated from substances such as leaves using the (ballisto)spore-fall method, (Boundy-Mills, 2006). A sample is placed

above an agar plate, and ballistospores fall and germinate onto the surface of the plate (Boundy-Mills, 2006).

Enrichment culturing, which can be especially efficient for isolation of target taxa, has been used for over a century to isolate microorganisms from mixed communities (Beijerinck 1961). It involves taking a small amount of sampled substrate, mixing the substrate with a liquid selective growth medium in which the target microbe can outcompete other non-desired microbes, and then plating enriched samples onto solid growth medium to isolate individual colonies to be tested. Enrichment media vary depending on the targeted species and multiple compositions have been developed.

Researchers have isolated a broad diversity of yeasts in the subphylum Saccharomycotina and phylum Basidiomycota using glucose-based enrichment media, and they have developed targeted enrichment strategies for more narrow yeast groups. Examples of enrichment media that target a taxonomically broad collection of yeasts include a synthetic complete (SC) based medium with a mixture of amino acids (Sylvester et al., 2015), and media containing glucose concentrations ranging from 0.8 to 8% (Spurley et al., 2021). As with selective solid media discussed above, researchers often adjust pH, add broad spectrum antibiotics, or add ethanol to reduce non-yeast microbial growth and enrich for fermentative yeast (Sylvester et al., 2015; Sampaio & Gonçalves, 2008; Fingerman et al., 2002). To increase recovered yeast diversity, enrichment cultures are incubated at different temperatures. For instance, growth at lower temperatures (< 12 °C) may favor cryotolerant yeast species (Sampaio & Gonçalves, 2008). To target specific yeast groups, such as nitrate or nitrite-utilizing fungi (Kurtzman et al., 2011a; Opulente et al., 2018; Shen et al., 2018), researchers can alter the carbon or nitrogen sources in enrichment media or adjust pH (Table S5). For example, sucrose is often used in media to enrich *Saccharomyces* and related taxa (Sniegowski et al., 2002, Robinson et al., 2016; Charron et al., 2014; Boynton et al., 2021, 2019). Negative and positive controls, to help detect contamination or media errors, can include tubes with enrichment medium only or tubes inoculated with a known culture, respectively.

Once samples are introduced into liquid enrichment media, they are usually grown for a minimum of two weeks or until growth is visualized. The presence of yeast may be visible in the form of a white sediment, bubbles, or a cloudy medium. Upon visualization of growth, a second round of enrichment is sometimes done in the same or a different liquid medium until growth is visible. Cultures are diluted and plated to solid agar plates with a medium amenable to target yeasts. Growth on plates is checked daily and separated colonies are picked for species identification. Colony preservation and identification is conducted as described above.

5. Forest yeast exploitation

Brewers, winemakers, and industrial biologists are using a variety of yeasts from temperate forests to improve their biotechnological processes. Some of the most recent and innovative attempts at wild yeast exploitation relate to the use of wild *Saccharomyces* species in the brewing industry (Cubillos et al., 2019), but diverse research and development have been carried out with a broad range of temperate forest yeasts for decades (Wegner 1983; Kurtzman 2009, 2011a). Use of wild yeasts may be a viable strategy to reintroduce diversity that was lost during modernization of the brewing process (Aquilani et al., 2015), which coincided with the use of pure brewing yeast cultures. This development greatly improved fermentation consistency and efficiency but may also have resulted in a severe drop in genotypic and phenotypic diversity among brewing yeasts. Many traditional strains have been discarded in favor of a small number of high-performing pure strains (Gallone et al., 2018). However, recently isolated wild strains have phenotypic traits useful for brewing. For instance, 353 strains of *Saccharomyces* species recently isolated from oak niches in Slovenian Sub-Mediterranean forests and nearby vineyards had useful phenotypes, including resistance to high concentrations of copper, sulfite, and ethanol (Dashko et al., 2016). Notably, *S. eubayanus* has been used in commercial beer production (Gibson et al., 2017). *Saccharomyces paradoxus* has likewise shown potential for brewing and has been used commercially (Nikulin et al., 2020b). Recent studies have also demonstrated the potential of the newly discovered *Saccharomyces jurei* for beer brewing (Giannakou et al., 2021; Hutzler et al., 2021). Though not adapted to the brewing environment, these temperate forest strains possess several traits beneficial for brewing, such as the ability to utilize the main wort sugar maltose (and in *S. jurei*'s case also maltotriose), tolerance to low temperatures, and production of desirable flavor volatiles (Gallone et al., 2016; Naseeb et al., 2017; Giannakou et al., 2021; Hutzler et al., 2021). Studies involving other fermentation systems such as winemaking and baking have likewise shown the application potential of wild yeasts (Magalhães et al., 2017a, 2017b, 2021).

A number of wild *Saccharomyces* phenotypic traits are amenable to modification by evolutionary engineering (Gibson et al., 2020). While this approach had previously been employed to enhance the potential of existing production strains, there are several recent examples of the approach being applied to the wild yeast *S. eubayanus* to improve its applicability in brewing, such as removing phenolic off-flavor, adaptation to ethanol, and utilization of the wort sugar maltotriose (Diderich et al., 2018; Mardones et al., 2021; Baker and Hittinger 2019; Brouwers et al., 2019). Increased diversity of brewing strains may be achieved through hybridization of wild and domesticated yeast strains. Several studies have shown how a lager yeast phenotype can be recapitulated by combining beneficial traits of the wild yeast *S. eubayanus* (cold tolerance) with domesticated *S. cerevisiae* strains (efficient sugar utilization) (Gibson et al., 2013; Hebly et al., 2015; Krogerus et al., 2015; Mertens et al.,

2015). Moreover, several novel approaches have been proposed to generate genetic diversity of extant or de-novo hybrids that can be exploited in industrial applications (Nikulin et al., 2018; Peris et al., 2020; Naseeb et al., 2021; Mozzachiodi et al., 2021).

Non-*Saccharomyces* yeasts from temperate forests have also been exploited in industrial applications. For example, *Lachancea* species have been used for sour beer fermentation because of their lactic acid production (Domizio et al., 2016), and for mead fermentation (Villarreal et al., 2021). Additionally, *L. thermotolerans* and *L. fermentati* produce large amounts of extracellular enzymes, which have important protease, polygalacturonase, and β-glucosidase activity for wine fermentation and aroma production (Belda et al., 2016; Porter et al., 2019a; Strauss et al, 2001). *Lachancea* spp. also could be used as biological control agents (BCAs) (Medina et al., 2017) because some members of the genus can inhibit growth or sporulation of other fungi using killer toxins or volatile organic compounds (Fiori et al., 2014; Kono & Himeno, 1997; Aponte & Blaiotta, 2016b; González-Arenzana et al., 2017). Outside of the genus *Lachancea*, *Komagataella* species isolated from broad-leaved trees have been used since the early 1970s for the production of single-cell protein from methanol, and more recently other yeasts belonging the genus *Ogataea* have been used with the same aim (Wegner 1983; Kurtzman 2009, 2011b). Subsequently, researchers developed a protein expression system in *Komagataella*, and the genus is currently used to produce biopharmaceutical proteins, recombinant enzymes, and chemicals (Cregg et al., 1985; Tschopp et al., 1987; Gasser et al., 2013; Karbalaei et al., 2020; Duman-Özdamar et al., 2021; Gao et al., 2021).

6. Future perspectives

In this review, we have presented an up-to-date overview of yeast biodiversity and abundance in temperate forests. Most of this progress is a result of technological changes that enabled more reliable yeast identification using molecular genetic information instead of phenotypic tests. Yeast researchers' next steps include investigating how temperate forest yeast diversity has been shaped by dispersal and adaptation to changing environments across a long evolutionary time frame. Temperate forest yeasts are only a subset of yeast strains available in culture collections: most of the available yeast isolates have instead been derived from fungal infections (O'Brien et al., 2021) or substrates that are related to human activities (Almeida et al., 2015; Gallone et al., 2016). Moreover, none of the yeast species described in this review has been found among the most frequent species in environmental DNA from temperate forests, as reported in the GlobalFungi database. Our understanding of their roles in ecosystem functioning, if any, is still incomplete. Recent advances in sequencing and large population genomic surveys of various yeast species revealed their possible origins, population structure, and historical admixtures between lineages (Duan et al., 2018; Peter et

al., 2018; Ropars et al., 2018). Additional applications of whole-genome resequencing include interrogating genetic diversity to reveal how species adapt in nature and using genome-wide association studies (GWASes) to pinpoint genetic variants regulating yeasts' life cycles in temperate forests (Alonso-Blanco et al. 2016; De Chiara et al., 2020). Such studies have been conducted in some model species, such as *S. cerevisiae*, and can be expanded across many other yeast species to provide a holistic view of microbial ecology.

6.1 Microbial life cycle inferred through population genomics

Population genomics will be especially useful in inferring yeast life cycle parameters. Interpreting yeasts' natural history requires the inference of various fundamental parameters in molecular evolution, such as generation time, population size, mutation rate, and frequency of sex and outcrossing (Tsai et al. 2008). From population genomic data, historical events such as hybridization (Eberlein et al., 2019) or domestication (Jeffares et al., 2015; Gallone et al., 2016) have been estimated by calculating generation numbers. However, the generation times can depend on how much time cells spend in a non-dividing state (Gray et al., 2004) or in the spore state (Freese et al., 1982) in nature. For example, generation times can vary dramatically in *Saccharomyces* between about 90 minutes per generation in laboratory culture (Herskowitz 1988) and 150 generations per year in brewing environments (Gallone et al., 2016); these clocks need to be calibrated for temperate forest conditions to be useful to understand yeast growth and evolution in natural settings. In particular, we note that laboratory calibrations disagree widely with molecular clocks calibrated against the fossil record (Shen et al., 2018). The interplay of genetic variation, mutation rate, and generation time are further complicated by other aspects of yeast biology. One example is many yeasts' predominant asexual reproduction alternates with sporulation under harsh conditions and sexual contexts. Large variations exist in the frequency of sex in yeast (for a review see Nieuwenhuis and James 2016). Population genomic methods can be used to estimate the relative frequency of asexual and sexual reproduction by comparing differences in mutation and recombination rates (Tsai et al., 2008; Lee et al., 2021; Friedrich et al., 2015) and have shown population-level differences (Tsai et al., 2008; Liti et al., 2009; Drott et al., 2020; Koufopanou et al., 2020).

6.2 Genotype-phenotype through a reverse ecology approach

With our understanding of yeasts still biased towards research conducted in laboratory settings, we need to continue sampling naturally-occurring yeasts and recording abiotic and biotic factors, which will be helpful to conduct a reverse ecology approach (Li et al., 2008) to learn how yeasts live in nature. It is especially important to identify the factors that contribute to species' fitnesses in nature and try to replicate those as closely as possible in laboratory experiments (Liti, 2015). After establishing a collection of strains, we can start addressing how

genetic diversity is shaped by the adaptation to different environments, population drift, or bursts of population expansion associated with specific substrates. Such clonal lineages are especially suitable for GWAS-based approaches. Extensive collections are already available for the yeasts *Schizosaccharomyces pombe* (Jeffares et al., 2015) and *Saccharomyces cerevisiae* (Peter et al., 2018) and have allowed development of genetic tools, such as deletion strains (Giaever and Nislow 2014; Rai et al., 2018). However, sampling biases are still present, even in these established collections, with a low number of wild isolates from sparse geographic locations. The renewed interest in yeast biodiversity from natural habitats, including from temperate forests, will close this gap to provide a holistic view of the different species biology, their interaction among them and with the environment.

Box: Outstanding questions

1. How do we resolve differences in conclusions from culture-dependent and culture-independent studies of yeast diversity?

   Sequencing and culture-based studies often uncover different diversity patterns and rare species are difficult to detect with either strategy. Both culture-dependent and culture-independent assays of yeast diversity have biases, including PCR and sequencing biases, unreliable barcode and genome databases, difficult-to-culture (i.e., fastidious) taxa, and taxa that can only survive within complex microbial communities. Additionally, sequence-based methods usually only report taxon frequencies, not abundances, although abundances can be inferred by scaling frequencies to another measure of cell abundances, such as qPCR or colony counts. Future studies will explore how to combine information from both strategies to get an accurate view of yeast diversity in temperate forests.

2. What role do broader sampling biases play in influencing conclusions about yeast ecology?

   Enrichment culturing introduces sampling biases. Media and other enrichment conditions influence the yeast strains recovered, as do interactions among microorganisms in enrichment cultures. How can we quantify such biases to understand the effect of sampling strategies on our understanding of culturable yeast diversity? One possible strategy might be to release yeast cells into the environment and test different recovery strategies. Year-round sampling without enrichment could also help reduce the impact of sampling biases for some targeted yeasts.

3. How do we quantify life history parameters in temperate forest yeasts?

Our current understanding of life history parameters in temperate forest yeasts relies on estimates from genome sequencing and assumptions based on laboratory experiments. Direct observations or experimental conditions that closely mimic forest environments are needed to inform genomic models. The discrepancy with molecular clocks calibrated against the fossil record also needs to be addressed and extended to non-model yeast groups.

4. What are the contributions of temperate forest yeasts to ecosystem functioning?
   While we know that yeasts are common and diverse, and we often have information about their genetics and physiology, few studies have directly investigated their impacts on other members of forest communities. However, research examining microbial communities from a guild-centered point of view shows promise in helping us to understand yeasts' contributions to ecosystem functioning (Martinović et al., 2021).

5. What are the wild niches of well-studied laboratory yeasts?
   Saccharomyces, *Cryptococcus*, *Komagataella*, *Lachancea*, and others are studied in the laboratory and exist in temperate forests. Understanding their natural ecologies would help laboratory researchers to put the genetics, genomics, and biotechnology of their systems into a more holistic context. These organisms have the potential to be interesting ecological models in addition to their roles in laboratory research.

6. How do we reliably identify temperate forest yeasts species and determine boundaries among yeast taxonomic units?
   Mycologists often use DNA barcodes, such as ribosomal sequences, to identify yeast taxa, but barcodes do not always reliably delimit species (Schoch et al., 2012). Recent studies combined barcode sequences and physiological characteristics to describe new temperate forest yeast taxa from Bulgaria (Gouliamova et al., 2016; Gouliamova and Dimitrov, 2020). Such studies, especially when combined with genome sequencing and genetic crosses, can help determine how phenotypic characteristics shift across the boundaries of taxonomic units.

7. How will our understanding of yeast ecology in temperate forests change as we focus away from well-studied systems and towards full temperate forest yeast communities?
   Yeast research in general has a bias towards a few well-studied genera, such as the genus *Saccharomyces,* which are not representative of yeast diversity. Instead, temperate forest yeast ecology needs to integrate entire yeast communities.

Author contributions:

All authors participated in manuscript planning and review of the final draft. PBo, SM, and GL conceptualized the project, organized the team, and edited the final draft for submission. PBo and SM edited and synthesized all contributed material. PBo and AY wrote the introduction; PBa, and TM contributed the section on global yeast diversity, including providing new analyses for this review; KBM, PBu, BT, NC, and AY contributed the section on yeasts in culture collections; FB, GB, PBo, FC, DGr, VK, CRL, SM, ESN, and IJT contributed the section on the *Saccharomyces* genus; VK compiled data from the literature for Table S3 and Figures on *Saccharomyces cerevisiae/paradoxus* isolating success; FC provided the data on *uvarum/eubayanus*; PBu, BT, and AY contributed the section on *Cryptococcus* and former *Cryptococcus*; LH, MJ, and ESN contributed the section on *Komagataella*; FC and PV contributed the section on *Lachancea*; GB, FC, KJF, DGr, CTH, DO, JP, and AY contributed the section on yeast isolation; NC, SD, BRG, and UP contributed the section on yeast exploitation; PBo, RD, DGo, DGr, GL, SM, IJT, and AY contributed the sections on future perspectives and the contents of the outstanding questions box.

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Figure legends:

Figure 1: Geographic distribution of yeast sequences within temperate forest samples in the database GlobalFungi. Points on this map were used for analyses mentioned in the text. Relative abundances represent the share of ITS yeast sequences of each species in the global fungal ITS sequence pool. Each point represents a sequenced environmental sample and blue regions represent the distribution of temperate forest biomes. Points with a relative abundance of zero represent samples with a single yeast sequence, and these were rounded down to zero for the map. Points outside blue regions are from forest environments contiguous with temperate forests; we included these in the map and analyses to avoid breaking up information from individual forests. The world map with temperate forest biomes was obtained from https://earthobservatory.nasa.gov/biome/maptemperate.php

Figure 2: Success rates in isolating different Saccharomyces species across different geographical regions. The only significant correlation regards the success rate of S. uvarum isolation in South America, which decreases with latitude (Spearman coefficient, rs = -0.94286, two-tailed p-value = 0.0048). Data from table S3.