



Diverse yeasts for diverse fermented beverages and foods

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Yeasts play vital roles in food biotechnology, especially in fermented products. Yeasts are monoculture bioprocessing agents, are members of complex microbial communities, and are even consumed directly. Advances in genetic technologies, such as whole genome and environmental DNA sequencing, have shed light on the diverse yeasts used in both traditional and industrialized processes. The yeast *Saccharomyces cerevisiae* plays an outsized role in fermented beverage and food production, but new research has revealed a cornucopia of yeast biodiversity that includes dozens of species. These often surprising studies have shown how yeasts are related, how they interact with other microbes, and how valuable traits are encoded in their genomes. This deeper understanding illuminates current practices in food biotechnology, while foreshadowing future innovation.

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Introduction

Yeasts are unicellular fungi that represent some of the oldest biotechnologies [1]. Instead of being consumed directly like crops and livestock, they are generally used as bioprocessing organisms. Yeast monocultures are frequently used to create fermented beverages and foods, and yeasts play important roles in the microbial communities that make cheeses, breads, and other products (Figure 1). Although the genetic model system *Saccharomyces cerevisiae* is so widely used that it is often casually referred to as “The Yeast,” many specialty products deploy other species of diverse budding yeasts (subphylum

Saccharomycotina) that have evolved over half-a-billion years [2,3].

This review will focus on recent developments in our understanding of the diversity of these food-associated and beverage-associated yeasts. We will investigate three major questions: firstly, What? (i.e. *what food products*), secondly, Who? (i.e. *which yeasts*) and thirdly, Why? (i.e. *the reasons a specific yeast is used for a specific product*). We have structured our subsections around the first question (What?), but the second question (Who?) has seen the greatest advances in recent years as genetic approaches have allowed researchers to determine which yeasts are used to make which foods and to infer who is related to whom (Figure 2). Challenges remain concerning taxonomy [4], interspecies hybrids [5], and cryptic species [5], but an increasingly crisp portrait is emerging for monocultures. Patterns can even be discerned for yeast products made with microbial communities, but more research will be required to dissect the genetic and taxonomic significance of variation by region, practice, and sub-product. The third question (Why?) is more challenging, but answers are starting to come into focus. In many cases, we now know which traits are needed for specific products, while in a handful of cases, we know how those traits are genetically encoded. This knowledge, coupled with new technologies, offers possibilities for the development of new products and improved processes that use new strains isolated from nature, designer microbial communities, or even genetic engineering.

Beverages fermented with monocultures

Most recent advances in our understanding of the role of yeast biodiversity in biotechnology have been concentrated in beverages that are now predominantly fermented with monocultures [6]. *S. cerevisiae* produces a wide variety of fermented beverages, including wine, sake, and ales. It is so widespread in food biotechnology that it was once proposed to be a completely domesticated species [7]. Under this falsified model, rare isolates from natural settings, such as soil and bark, were interpreted to be feral escapees from vineyards, breweries, and bakeries. An early population genetic investigation found that wild isolates were genetically distinct and demonstrated that independent lineages of *S. cerevisiae* had been domesticated at least twice, once for fermenting wine and once for fermenting sake [8]. Recent population genomic analyses have confirmed and extended these findings, clarified the close relationship of wine-making monocultures with a globally distributed lineage of vineyard yeasts involved in

Figure 1



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Diverse products made with diverse yeasts. A cornucopia of products made with diverse yeasts is shown. Many products are made with the yeast *Saccharomyces cerevisiae*, but about half shown involve other species. Photograph used with permission (©Amanda Beth Hulfachor).

traditional spontaneous fermentations, and implicated several genes in domestication [9–13]. Building on this theme, population genomic studies have shown that at least two lineages of *S. cerevisiae* were domesticated for ale brewing [14*,15*]. In a remarkable case of parallel evolution, ale strain domestication led to several distinct loss-of-function mutations in the *PADI* and *FDC1* genes. These genes enable the production of 4-vinylguaiacol from the phenolic acids, such as ferulic acid, present in the wort used to ferment beer [14*,15*,16]. Although this smoky, clove-like flavor is prized in some beer styles, their inactivation led to the cleaner flavors that most modern beer drinkers prefer.

Lager beer, the most commonly fermented beverage with more than a quarter-trillion dollars of annual sales, is conspicuously absent from the impressive list of products made with *S. cerevisiae*. Lager brewing began in Central Europe in the 15th century as brewers began to ferment and store beer at colder temperatures to reduce contamination and off-flavors. Thus, lagers had a crisper and more consistent taste than the traditional ales that had been brewed for thousands of years. Lager yeasts were first recognized as interspecies hybrids more than 30 years ago [17], but the recent discovery of *Saccharomyces eubayanus* enabled completely new lines of inquiry [18]. First, it clarified that lager yeasts are represented by two major lineages of *S. eubayanus* × *S. cerevisiae*, an allotetraploid

lineage and an allotriploid lineage (previously known as *Saccharomyces pastorianus* and *Saccharomyces carlsbergensis*, respectively) [5,19–22]. Second, although only limited genetic diversity made it through hybridization and domestication bottlenecks [23,24**], *S. eubayanus* is genetically diverse in nature with a wide geographic distribution, including South America [18,23,25], North America [23,24**], Asia [26], and New Zealand [27]. Interestingly, pure isolates have still not been reported from Europe. Domesticated lager yeasts seem to have drawn alleles from a closely related lineage found in North America, Asia, and possibly Europe [24**]. Finally, research with synthetic hybrids of *S. eubayanus* × *S. cerevisiae* has suggested that cold-tolerance is provided by the *S. eubayanus* genome, while the *S. cerevisiae* genome enables the aggressive fermentation of all of the sugars in wort [28*,29*,30,31]. Specifically, no strain of *S. eubayanus* has been reported to ferment maltotriose, the second most abundant sugar after maltose. *S. eubayanus* also produces phenolic off-flavors, although these can be lost genetically in hybrids during propagation [32**]. Despite the apparent limitations of brewing with pure strains of *S. eubayanus*, Heineken recently launched ‘H41 Wild Lager,’ which is the first commercial product that exploits pure strains of this species. Determining the genetic basis of cold-tolerance is likely to be a challenging problem, in part because it is conferred by the newly discovered species; in contrast, maltotriose fermentation may simply

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