Fermentology • Book

The Evolutionary History of Bread and Beer Yeast

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Editors note: This publication contains the video of the talk from the Fermentology webinar series, as well as a lightly edited transcript of the lecture. The transcript has been enriched with media, annotations, and links to other material by the digital publication team in order to amplify and extend the content for a reading experience.

Abstract

[Caiti Heil](#) is an assistant professor at NC State's [Department of Biological Sciences](#). She studies the evolution of yeasts (including their hybridization). Here she will tell the story of the evolution of the yeasts used in bread and wine and how those yeasts have changed as they've been domesticated. She'll also mention the ways in which the wild yeasts that colonize sourdough starters are likely to differ from commercial yeasts (and why). Caiti Heil will team up with her colleague Caiti LaHue for this talk. The Caitis will also consider the ways in which the evolution of yeast reminds us about and elucidates the workings of evolution and natural selection more generally.

Watch the talk

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The Evolutionary History of Bread and Beer Yeast | Fermentology mini-seminars

Introduction

In this talk we're going to inform you about our friend, *Saccharomyces cerevisiae*, and why it should be one of your best friends, as well.

Family Trees + Fungi

We make our family trees based on shared ancestry — and evolutionary biologists do this, too. By looking at shared traits and similarities and differences in our DNA, we can make evolutionary trees. Today we're actually going to talk about one specific branch: fungi.

Fungi include many types of organisms, like mushrooms and all yeasts. Additionally, many fungi you might find in your sourdough fit into the budding yeast group, so-called due to their method of clonal reproduction in which a cell makes a copy of itself

and buds off the existing cell. Which gives you something that looks like this:

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From University of California, accessed from their [Giphy](#) (@uofcalifornia).

The diversity of budding yeasts can be studied through a scale of number of changes to protein sequence, which is similar to the process of making an evolutionary tree to understand how closely or distantly-related species are to one another. Although all of these budding yeasts may look similar to the human eye, we can tell from their DNA that they actually have been diverging from one another for hundreds of millions of years.

"A budding model yeast cell. Ultrastructure details. 3D printed. *Saccharomyces cerevisiae*. Baker's or Brewer's yeast."

Image from Rosser1954 on [Wikimedia Commons](#).

Dr. McKenney and Lauren Nichols have explored the many different types of strains and species that may be present in your sourdough starter.^[1] And incredibly, the diversity of yeasts in your sourdough starter could actually span the evolutionary distance from human to roundworm.¹ Which is pretty fascinating.

Saccharomyces cerevisiae

Here we are going to focus on *Saccharomyces cerevisiae* in particular, which is one of the most commonly found yeasts in bread and beer. Which is also why it's known as the "bakers yeast" or "brewer's yeast."

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[Model Bakery and Brewery from the Tomb of Meketre](#), ca. 1981–1975 B.C. Image from The Metropolitan Museum of Art.

Saccharomyces cerevisiae is a [unicellular eukaryote](#). As mentioned above, yeast belong to the domain of life that includes plants and animals; however, they are much simpler than many plants and animals, being just a single cell. This trait, along with other traits, make them very useful for studying basic biological and chemical processes in the lab, which is why we often call them a model organism.

We use *Saccharomyces cerevisiae* to help us understand topics including evolution, genetics, biochemistry, and even human disease. And one of the reasons why we can do this is because humans and yeasts share many genes in common. Actually, around 2,300 yeast genes have a human "ortholog," meaning a gene that was evolved from a common ancestor of human and yeast. Many of these genes actually retain the same function. But unlike in humans, in yeast we can delete, edit, or replace genes to see what they do, making them a really powerful system for better understanding biology across the tree of life.

Top: An ancestral gene duplicates to produce two [paralogs](#) (Genes A and B). A speciation event produces [orthologs](#) in the two daughter species. **Bottom:** in a separate species, an unrelated gene has a similar function (Gene C) but has a separate evolutionary origin and so is an [analog](#).

[Image from Thomas Shafee](#) on Wikimedia Commons.

Recent evidence shows us that *Saccharomyces cerevisiae* likely originated in China and spread across the world from there, often associated with humans.^[2] The reason for this association with humans comes down to this metabolic pathway.

Saccharomyces cerevisiae need sugar to grow. They eat simple sugar, glucose. And in the presence of oxygen, this can produce a lot of cellular energy in the form of ATP. But without oxygen, this turns into ethanol and carbon dioxide.

In the wild, the rapid production of ethanol kills most other microbes. This is a very successful, competitive strategy for *Saccharomyces cerevisiae*. But, of course, the production of ethanol in CO₂ has made yeast instrumental in the evolution of human society.

Saccharomyces cerevisiae takes sugar found in grains and fruits and turns it into fermented beverages, including beer, wine, cider, palm wine, saki — as well as other products, including cheese and bread, olive oil, cocoa. And *cerevisiae* is even found in or on our bodies.

In fact, it was widely believed for a long time that there was no such thing as a wild *Saccharomyces cerevisiae*, and they were only associated with humans. However, more recent sampling also revealed that you can find yeast *Saccharomyces cerevisiae* on trees, fruits, flowers, cactus, and insects. All of these represent very different environments.

As an evolutionary biologist, I'm really interested in the question: How does *Saccharomyces cerevisiae* adapt to all of these different environments?

Now we are going to focus on two environments that *Saccharomyces cerevisiae* has adapted to: beer and bread.

***Saccharomyces cerevisiae* + Beer**

Much like the selection and breeding for traits like smushed face and short stature of a pug, humans have been selecting for certain traits of yeasts in human-made environments like beer. Some of the conditions that are selected for in beer include, the ability to break down complex sugar like maltotriose, that's found in malt, and the selection against off flavors like clove, and in certain cases selection on cold temperature.

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Saccharomyces cerevisiae has come to tolerate the cold temperatures found in the lager style of beer. Below we're seeing two main styles of beer depicted, the lager and the ale.² Lager is typically fermented at quite cold temperatures, a range of 9 to 14 degrees Celsius, much below the preferred temperature of *Saccharomyces cerevisiae* of 30 degrees Celsius. So how does this work?

Fermentation Temperature Charts. Image from [North Slope Chillers](http://www.northslopechillers.com).

In the case of lager beer, a hybridization event actually occurred, meaning two different species mated and produced hybrid offspring. This hybrid was originally called *Saccharomyces carlsbergensis* after the lager beer, Carlsberg, made in Denmark, but is now referred to as *Saccharomyces pastorianus*.³ The parent species of the lager hybrid are *Saccharomyces cerevisiae* and its relative, *Saccharomyces eubayanus*, which is a cold-tolerant species about 20 million years distantly related from *Saccharomyces cerevisiae*.

There are at least two independent hybridization events that occurred hundreds of years ago that gave rise to all modern lager-brewing strains. Turns out that the contributions to the hybrid from the cold tolerant parent, *eubayanus*, included a cellular organelle called the *mitochondria*, which is typically responsible for producing energy for the cell. But in this case, researchers determined that the contribution of the mitochondria, along with other components found in the *eubayanus* genome, actually helped confer the ability to grow at cold temperatures in this hybrid.

The *cerevisiae* parent actually helps donate part of its genome to the hybrid. This helps the hybrid break down the complex sugar maltotriose, which *eubayanus* cannot naturally do. So in this case, the hybrid brings beneficial traits together from both species.

Many other combinations of hybrids have been found in beer and wine. In our lab, we are working to understand how hybridization can help populations adapt to new environments.⁴ And in my own work, I've illustrated another mechanism through which yeast can adapt to different temperatures.^[3]

“Loss of heterozygosity directionality results from selection on different species’ alleles at different temperatures.” Image from [Temperature preference can bias parental genome retention during hybrid evolution](#) published in PLoS Genetics.

By propagating yeast in the lab, either hot or cold temperatures for hundreds of generations, a process called experimental evolution, over time we can see the replacement of one species genome by the other in the hybrid. Where in warm temperatures, the *cerevisiae* parent genome becomes overrepresented in the hybrid. Whereas at cold temperatures, in this case, the cold-tolerant parent *saccharomyces uvarum* becomes overrepresented in the hybrid genome.

Experimental evolution is a really useful and interesting way to study evolution in real time. We’ve just heard an example of adaptation through hybridization. And while we haven’t found any hybrids in bread, yet bread yeasts actually face a number of similar selection pressures as beer, including having to use complex sugars and the production of certain desirable flavors.

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Yeast: In the Wild and in the Industry

What are some of the differences between wild and domesticated yeasts? Most yeasts exist as diploids, which just means they have two sets of chromosomes — one from each parent, just like humans. However, unlike humans, yeasts can tolerate even more chromosomes in each cell, which would be lethal in a human. This can happen from a mistake during cell division, meaning the newly created cell can have both sets of chromosomes from one parent instead of just the intended one. Which leads to a triploid cell, or, if both parents make this mistake, you can end up with the tetraploid, which has four copies of each chromosome.

Commercial yeasts, having three or four copies of each chromosome, actually makes them better at handling the stresses of their environment. It can allow them to have multiple copies of useful genes, such as those that break down the sugar maltose, the main food source for yeast and bread. These genes are called MAL genes. Wild yeast have one or two copies of MAL genes, while industrial yeast can have as many as five — with each copy having subtle differences in use and ability.

In addition to gaining new genes, industrial yeasts can also lose or deactivate them according to human demand. Normally, yeasts eat or metabolize glucose first, as it is the easiest sugar for them to digest. To ensure they get as much of this cheap, easy, energy source as they can, they physically shut down systems that digest other sugars. Only when all of the glucose is gone do they start eating other sugars, such as the maltose. Maltose costs the cell extra energy to break it down into its two glucose components.

In the wild, eating glucose first is useful. In baking or brewing, however, this creates a lag time where the yeasts aren't producing as much CO₂ as they could be and increases the amount of time the yeasts need to ferment. Some industrial strains have lost the mechanism which prevents the cell from eating maltose while glucose is present. This drastically reduces the fermentation time of the yeast.

Beyond just efficient use of sugars, domesticated yeasts have also had to adapt to the rather harsh conditions of industrial fermentation. While sugar is the main food source of yeast, it can also be a huge stress factor for them. High amounts of sugar can cause water to flood out of the yeast cells, turning them to shriveled little yeast raisins.

Industrial yeast must also handle being frozen, as well as dried, for packaging. Here, the yeast's multiple copies of chromosomes become a hindrance. Strains with fewer copies tend to fare better. However, industrial yeasts have found three main molecules that help protect the cell from osmotic, freezing, and drying stress:

1. First is proline ($C_5H_9NO_2$), which is an amino acid. Proline acts as an antioxidant scavenger during osmotic stress.

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National Center for Biotechnology Information (2021). PubChem Compound Summary for CID 145742, Proline. <https://pubchem.ncbi.nlm.nih.gov/compound/Proline>.

2. The second is glycerol ($C_3H_8O_3$), a sweetening agent we also use antifreeze. Glycerol collects inside the cell to balance out the sugar outside the cell and lessen the movement of the water going out. During drying stress, glycerol creates an osmotic pull into the cell, thus keeping more water in the cell and helping keep it alive.

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National Center for Biotechnology Information (2021). PubChem Compound Summary for CID 753, Glycerol. <https://pubchem.ncbi.nlm.nih.gov/compound/Glycerol>.

3. Finally, there's trehalose ($C_{12}H_{22}O_{11}$), which, like maltose, is made up of two glucose molecules. The bond connecting them is slightly different. And it needs its own enzyme to break it, so it counts as a different sugar.

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National Center for Biotechnology Information (2021). PubChem Compound Summary for CID 7427, Trehalose. <https://pubchem.ncbi.nlm.nih.gov/compound/Trehalose>.

Together, these three molecules help protect the yeast cells. All three protect the cell, either acting as an antifreeze or an antioxidant.

Yeasts also produce many of the molecules that give bread its smell and taste. These aroma-producing molecules, or aromatics, come from yeast metabolism, just like

alcohol. Wild yeasts produce a wide variety of aromatics, but not all of them are pleasing to humans. These are dubbed “off-flavors”, such as body odor, onion, et cetera. Industrial yeasts have had their off flavors bred out of them over centuries of selecting only those that produce tastier and better smelling loaves. With the sequencing of the yeast genome, we can even look into the pathways that produce aromatics and engineer strains to stop producing off flavors, or increase production of pleasant scents like banana, and butter, and more.

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Need a beer buzz? Ask a bee.

“Only two species of yeast --- ale yeast and lager yeast -- have been used for traditional beer brewing for the last 600 years. A lab in North Carolina may have found a third in the strangest place: On bees and wasps.” Accessed from [PBS NewsHour](#).

How do we find these yeasts? Insect guts are some of the best places to find yeast, actually.^[5] When sugars are scarce in the winter, some yeasts will move into wasp guts to survive. Beetles have a wide variety of yeast and bacteria living in their guts to help them digest food, especially cellulose, a tough plant sugar used in plant cell walls. Ants also have yeast in their guts, which digest the abundant sugar sources the ants carry back to their nests. Both *Saccharomyces* yeasts and a wide variety of other related budding yeasts are found this way.⁵

Wild Sourdoughs

Besides looking at insects to identify new strains of yeast, we can look directly at wild sourdoughs.⁶ Locations we've collected are shown on the map.

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Sourdough Starter Results Map by Lauren Nichols and Neil McCoy.

Any yeast caught by a sourdough starter is from the environment, thus creating a minimap of yeasts in a tiny area, say a house or a property. Multiply that by thousands and you create a map of where certain species of yeasts hang out, where the greatest diversity is, and trace how yeasts move. Identifying more strains of yeasts from starters allows us to see more and more differences between domesticated and specialized yeast strains and how those traits do or do not exist in wild, non-domesticated species.

Image from [The diversity and function of sourdough starter microbiomes](#), published in *eLife* (2021).

In fact, Dr. McKenney and the team sequenced a genome region from all yeast species found in over 500 sourdough starters submitted by citizen scientists, some of whom

may be watching right now.[6] That single genome stretch alone revealed at least 50 different *Saccharomyces cerevisiae* strains, not including other non-saccharomyces yeast species. We are planning on sequencing the whole genome of many of these *Saccharomyces* yeasts in the near future to get a better understanding of their ecology. There are likely many strains of *Saccharomyces cerevisiae* living in starters.

Footnotes

1. To learn more about the differences between yeast and sourdough, please read “[What’s The Difference Between Sourdough Starter And Yeast?](#)” by Leslie Nemo (2020) from *Discover Magazine*. [↵](#)
2. For more information on these beers, and how they are different, please read “[What is the Difference Between Ale and Lager?](#)” by Dave Carpenter from Craft Beer & Brewing. [↵](#)
3. The original description of *S. carlsbergensis* was by Emil Christian Hansen in 1883. It was published as - Undersøgelser over Alkoholgjærsvampenes Fysiologi og Morfologi. II. Om Askosporedannelsen hos Slægten Saccharomyces. Meddelelser fra Carlsberg Laboratoriet 2: 29-102. [↵](#)
4. To learn more about Heil Lab, please visit their website: <https://www.heillab.com/>. [↵](#)
5. Dr. Anne Madden does much research focusing on yeasts and insects. To learn more, please visit “[Wasp Beer & Bumblebee Beer](#).” [↵](#)
6. To learn more about wild sourdough, visit the [Wild Sourdough Project](#) website. [↵](#)

Citations

1. McKenney, E., Nichols, L., & Dufresne, K. (2021). Wild Sourdough. *Fermentology*. Retrieved from <https://fermentology.pubpub.org/pub/2g0rujqz> [↵](#)
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4. Sicard, D., and Legras, J. (2011). Bread, beer, and wine: Yeast domestication in the *Saccharomyces sensu stricto* complex. *C. R. Biol.* 334, 229–236. doi: 10.1016/j.crvi.2010.12.016 [↵](#)
5. **Madden AA**, Epps MJ, Fukami T, Irwin RE, Sheppard J, Sorger DM, and RR Dunn (2018) The ecology of insect-yeast relationships and its relevance to human industry. *Proceedings of the Royal Society B.* 285(1875). pii: 20172733. doi: 10.1098/rspb.2017.2733 [↵](#)
6. McKenney, E., Nichols, L., & Dufresne, K. (2021). Chapter 1: Wild Sourdough. Fermentology. Retrieved from <https://fermentology.pubpub.org/pub/2g0rujqz> [↵](#)