

# History and Evolution of Farmhouse Yeast

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## Abstract

This document is a supplementary note to [1]. Current Biology does not allow the publication of supplementary notes in the journal, so this note has been published as a separate preprint in order to make additional context and results available to readers of that paper. This note has not been reviewed or endorsed by Current Biology.

This supplementary note provides more historical and ethnographic background on farmhouse brewing in general, and the farmhouse yeast cultures under evaluation in [1]. We also further speculate on how the obtained genomic data (phylogeny and inter-culture strain overlap) links to the historical records of the different cultures. Additionally, we discuss the cultures in which allochthonous yeast, i.e. yeast found in farmhouse yeast cultures that are genetically closely related to commercially available (ale) yeasts, was detected.

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## 1. The origin of farmhouse brewing

Historically, farmers relied on grain cultivation for their livelihoods and used the surplus grain not required for sustenance to brew beer. This brewing followed strictly traditional methods, with each generation passing down their knowledge to the next. As a result, brewing practices varied significantly across geographic regions. These methods are substantially different from today's modern brewing techniques and are now collectively referred to as 'farmhouse brewing'.

Farmhouse brewing occurred over most of the world, until in some regions brewing was replaced by wine-making (Southern Europe), brewing was prevented by religious bans (e.g. by Islam), or legislation suppressed brewing for the purposes of taxation (common in Germany and Eastern Europe). There is no direct evidence documenting the origins of farmhouse brewing. However, the oldest archaeological evidence of beer from the Middle East, near the cradle of agriculture, predates the invention of farming, suggesting that early farmers were likely brewers from the very beginning [2]. In Europe, the oldest archaeological finds of beer, e.g. those dating to the 5th millennium BCE in Germany [3], and the 3rd millennium BCE in Denmark [4], all point to practices associated with farmhouse brewing. Most farmhouse brewers produced beer solely for their own households, with commercial farmhouse brewing being a rare practice, both historically and today [5].

Following the industrial revolution in the 19th century, the population in European rural districts dropped, and farmers switched from subsistence agriculture to cash crops [6], [7]. As transportation improved, farmers began buying their beer rather than making it themselves, or

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switched to drinks like coffee and milk, and the role of farmhouse ale in social customs began to decline. Consequently, farmhouse brewing was reduced drastically, or even disappeared altogether, in most regions. Farmhouse brewing still survives in some regions, often isolated or remote, in countries such as Norway, Sweden (the island of Gotland), Denmark, Finland, Estonia (the islands in the Baltic), Latvia, Lithuania (the region of Aukštaitija), Belarus, Russia, and the UK [5].

## 2. Farmhouse brewing: current practices

Farmhouse brewing practices have varied enormously both geographically and over time, so here can only be provided a brief outline of European farmhouse brewing practices over the last two centuries. For more detail, see [5], [8], [9], [10], [11].

In many regions, such as Denmark and Sweden, the farmhouse ale was the main daily drink of the household, often available in a tankard permanently placed on a table in the living room. In these regions brewing typically took place whenever the barrel was empty, which might be once every second or fourth week. In other regions, such as Norway and Germany, beer was mainly used for special occasions, such as celebrations or bouts of heavy work. In these regions beer was typically brewed 1-3 times a year. In general, the beer brewed was the same regardless of season or occasion, although for some purposes it might be weaker (for example for work) or stronger (such as for weddings or Christmas).

The farmers were brewing from their own grain, so for malting they were restricted to what grain types they could grow themselves. Barley was by far the most common, but rye was common further east, and oats were common in coastal climates. Wheat was rarely used, and only in more southerly regions [12]. Since the farmers brewed from their own grains, they usually malted it themselves, although in Denmark some farmers handed in grain to a local maltster who malted it in return for keeping some of the grain. Over the last few decades most farmhouse brewers have shifted to buying commercial malts.

Hops are by far the most common spice in farmhouse ale as in commercial beer, but juniper branches have also been extremely common in areas where these were easy to obtain (the UK, Denmark, and Lithuania being the main exceptions). The branches have been used to filter the wort from the mash, or to steep a juniper infusion that was then used as the brewing liquor. Alder branches were also used to some extent, and herbs like wormwood, *Myrica gale*, and *Rhododendron tomentosum* have also been used, as well as many more. In the second half of the 20th century there was in many regions a fashion for using sugar to make the beer stronger, but where brewers have stopped making their own malts this practice has largely ended.

Brewing processes in farmhouse brewing have differed dramatically from those in commercial brewing, and the subject is too large to survey adequately here, but surveys can be found in [5], [11]. A very large variety of methods have been used for mashing, including mashing by heating directly in the kettle, infusion mashing, decoction mashing, heating the mash in an oven, and heating the mash with hot stones [13]. In the Baltic countries some brewers baked the mash in the oven after mashing [14], [15]. A very common trait in large parts of Europe has been to not boil the wort after mashing, but instead relying on the heat during mashing to pasteurize the mash.

The strengths of the worts produced have been highly variable, depending on region, the wealth of the farmer, and the intended use of the beer. Most original gravities seem to have fallen in the range 1.018-1.100, relatively evenly distributed by frequency within that range (estimate from unpublished data). Making general statements about the sugar composition of the worts is difficult,



Figure 1. A: Terje Raftvold harvesting culture #5 from the fermenting beer, Innvik, Norway, July 2015. B: Dainis Rakstiņš pitching culture #45 into the wort, Bērzpils, Latvia, May, 2025. C: Jarand Eitrheim pitching culture #14 into the wort, Bleie, Norway, December 2016. D: Marina Fyodorovna making a yeast starter with culture #39, Kshaushi, Chuvash Autonomous Republic, Russia.

but mashes of many hours have been very common, and so the proportion of more complex sugars like maltotriose has likely been lower than in modern commercial worts.

A striking trait in farmhouse fermentations was the tendency to pitch the beer at very high temperatures, typically around body temperature, which was common all over Europe [16]. Fermentation times before racking were astonishingly short compared to industrial brewing, often only 1-2 days [17]. There is very little evidence for the actual fermentation temperatures, but, at least in Norway, it was very common to insulate the fermentor and/or place it in a warm location. Simulations of fermentation indicate that this, together with relatively high gravities and very short fermentations, tended to lead to very hot fermentations, in the range 25-42°C, with most above 35°C [11].

The practice of fermenting in the mash was by the 20th century very rare, but existed in isolated pockets in most European countries surveyed, very likely indicating that this method was more common in the past. Quite likely, this brewing process originates with the ancient practice of not filtering the beer at all, but fermenting in the mash and then drinking directly out of the fermented mash [18], [19].

### 3. Yeast maintenance in commercial and farmhouse brewing

Historically, all brewers, whether commercial or farmhouse, maintained their own yeast cultures by harvesting yeast from one batch and using it to inoculate subsequent batches, a practice known as backslopping. In 1883 Emil Chr. Hansen laid the foundation of modern yeast handling in the

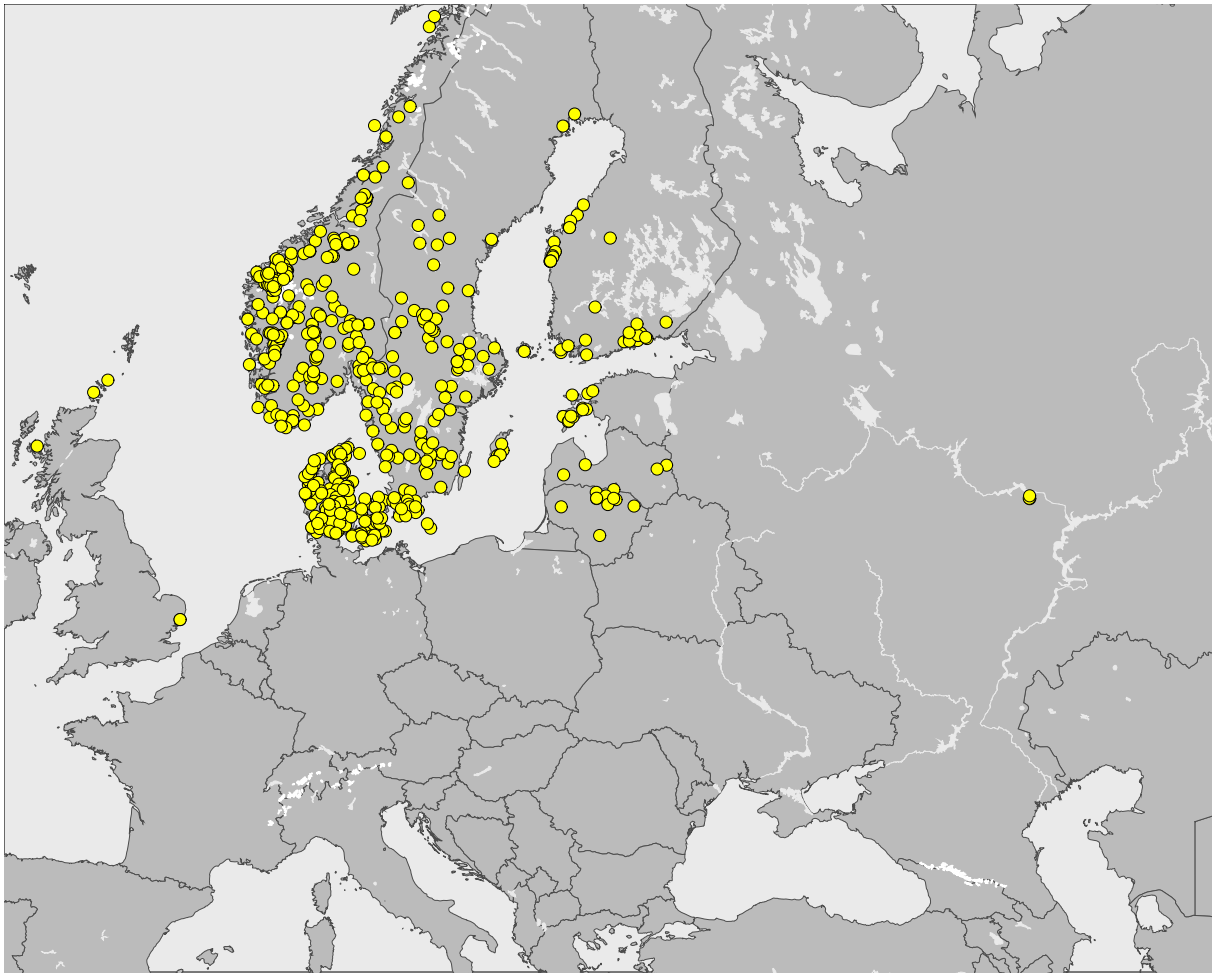


Figure 2. Map of regions where it can be documented that farmers historically maintained their own beer yeast cultures [5], [11]

Carlsberg brewery [5], [20], [21]. This technology is based on isolation of single-strain yeast cultures, and the use of these pure yeasts as a seeding culture for fermenting new batches. This process, known as “Hansen’s method”, greatly increased reproducibility of the fermentation and therefore largely replaced backslopping in modern beer brewing. However, adoption of Hansen’s method amongst brewers also caused a massive decline in beer yeast diversity for two main reasons. First, the complex, mixed cultures traditionally used for backslopping were replaced with a single yeast strain. Secondly, commercial brewers increasingly started to share their isolated yeast strains, particularly those that fermented the fastest, causing other local yeast variants to go extinct.

While Hansen’s method became near-universal in commercial brewing, it was often not adopted in farmhouse brewing, where brewers preferred to adhere to their traditional backslopping practices, thereby preserving the local beer yeast biodiversity. In practice, once the farmers harvested their yeast, they preserved it by storing it wet in a jar (common in Denmark and Sweden), or by drying, e.g. on specially made wooden equipment (such as yeast rings and yeast logs), on rings of straw or juniper branches, or simply on cloth (Figure S1 in [1]). Swedish brewers often harvested the yeast from the bottom of the empty beer barrel right before starting a new brew, instead of from the fermentor. A recent study [11] surveys the full range of methods used in Norway. Typically (with some exceptions), farmhouse brewers who brewed rarely (1-3 times per year) dried their yeast, while those who brewed often (12-30 times per year) were divided roughly equally between those who dried and those that did not.

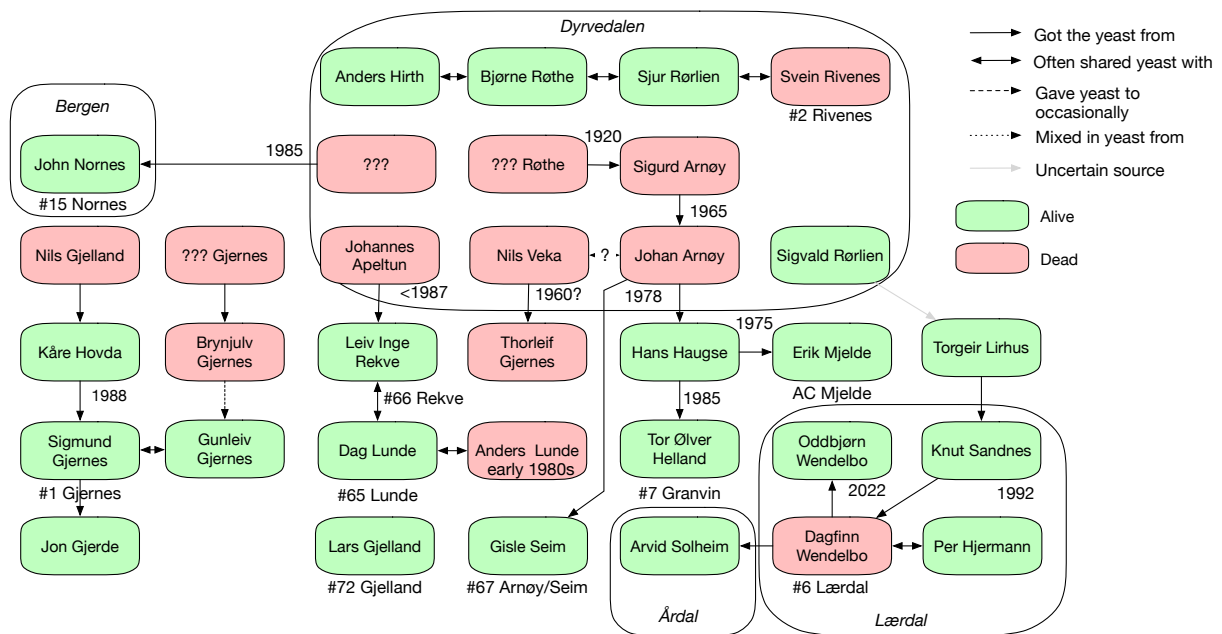


Figure 3. Graph of known exchanges of yeast in and around the Voss region in SW Norway.

Storing and reusing yeast with such primitive methods was of course not without risk, as the yeast might die or become contaminated. In some regions, it was therefore common for neighbours to exchange yeast when necessary [5], [11], while in other regions this was considered shameful and avoided as much as possible. Many brewers in the North-West Norwegian region would also occasionally mix different cultures, as they believed this made the cultures healthier [11]. It is clear, however, that nearby farmhouse brewers exchanged yeast cultures, and that they continue to do so to this day [11], which is also evidenced by the data presented in [1] (see Figure 2).

#### 4. Farmhouse ale yeast cultures included in this study

As farmhouse brewing began to decline, many farmhouse yeast cultures were not maintained anymore and died out, and even in many regions where the farmhouse brewing continued, the yeast itself did not survive. Examples are Denmark, Finland, Sweden, Estonia, Belarus, and the United Kingdom, where the yeast was often replaced by baking yeast, very likely because this was easily available in shops, and had similar brewing properties. Finnish sahti [5], [8], [22], Swedish gotlandsdricke [5], [10] and Estonian koduõlu [5], [23] are today all largely brewed with commercial baking yeast. However, in some regions the brewers chose to continue to use their own yeast, and so far about 70 surviving cultures of farmhouse yeast have been identified in Europe [24]. It is likely that more cultures exist, and work is ongoing to find and preserve these (see website<sup>1</sup>). A very large number of cultures also exist outside of Europe, in South America [25], Africa [26], and South-east Asia [27], but unfortunately little is known about these, and they are not included in this study.

Given that farmhouse brewing practices (e.g. fast fermentation at high temperature) and yeast maintenance methods (particularly drying) are so fundamentally different from commercial ale brewing practices, it is unlikely that commercial ale beer yeast would be suitable in a farmhouse context. Therefore, [1] aims to systematically investigate farmhouse ale yeast cultures genetically as well as phenotypically. [1] includes yeasts from all the known European regions where farmhouse yeast still survives.

<sup>1</sup> <https://www.garshol.priv.no/download/farmhouse/kveik.html>

Below, we will provide more information on the farmhouse ale yeast cultures that were sourced for [1] (see also Figure 1A and Supplementary Table 1). The cultures derive from the following regions:

- **North-west Norway**, corresponding to the traditional districts of Nordfjord and Sunnmøre, known for brewing a farmhouse ale style called kornøl, characterized by use of juniper branches, unboiled wort, and farmhouse yeast belonging to the “kveik” family. Cultures belonging to this group are #5, #8, #9, etc.
- **South-west Norway**, corresponding to the traditional districts of Hardanger, Voss, and Sogn. The beer brewed here is known as heimabrygg, and differs from kornøl mainly by being boiled. Cultures belonging to this group are #1, #2, #6, etc.
- **Central-east Norway**, specifically the valley of Hallingdal, where the brewers also use juniper branches, but heat the mash in the kettle, boil the wort, and use yeast from a family tentatively named “gong”. Cultures belonging to this group are #27 and #28 in this study.
- **South-east Norway**, specifically the region of upper Telemark, where the brewers originally brewed traditional beers with methods similar to those of the Central-east, but the brewers who have their own yeast now use malt extract. This yeast family has been tentatively named “berm”. Cultures belonging to this group are #54 and #57.
- **Latvia**, specifically the eastern Latgale region, where some brewers make home-made smoked malt and brew beers from unboiled wort using farmhouse yeast. Cultures belonging to this group are #42 and #45.
- **Lithuania**, specifically the northern Aukštaitija region, where some brewers make a style called kaimiškas, similar to the Latvian beers, except they generally use unsmoked commercial malts. Some Lithuanian brewers brew a style called keptinis, where the mash is baked in an oven [5], [14], [15]. Cultures belonging to this group are #16, #46, and #68.
- **Russia**, specifically the Republic of Chuvashia, populated mainly by the Chuvash, a Turkic people, who brew farmhouse ale using a variety of methods, and some of whom still maintain their own yeast. Some Chuvashians brew using the oven, while others do not. Cultures belonging to this group are #39, #40, and #59.

## 5. Historical and cultural interpretation of the observed yeast phylogeny

Given that farmhouse yeasts have been used separately from commercial yeasts for so long, and exposed to different fermentation practices throughout that time, it was expected that they must be genetically distinct, as earlier found by [28], [29], [30]. The phylogeny in this study contains 78 strains isolated from farmhouse cultures, out of which 57 (73%) appear to be true farmhouse yeasts.

In this phylogeny 46 strains form a monophyletic clade of farmhouse yeasts, spanning Eastern and Western Norway, Latvia, and Lithuania (see Figure S6 in [1]). Preiss and coworkers [29] found similar results. An additional 9 strains form a paraphyletic group together with the abovementioned 46 strains. Within the monophyletic clade there are further monophyletic subclades corresponding to Western Norway, Latvia, and Eastern Norway.

The additional group of 9 strains are all from the Baltics, specifically Latvia and Lithuania. The Baltic strains thus appear in two different groups in this phylogeny, unlike in [28]. All of the Baltic

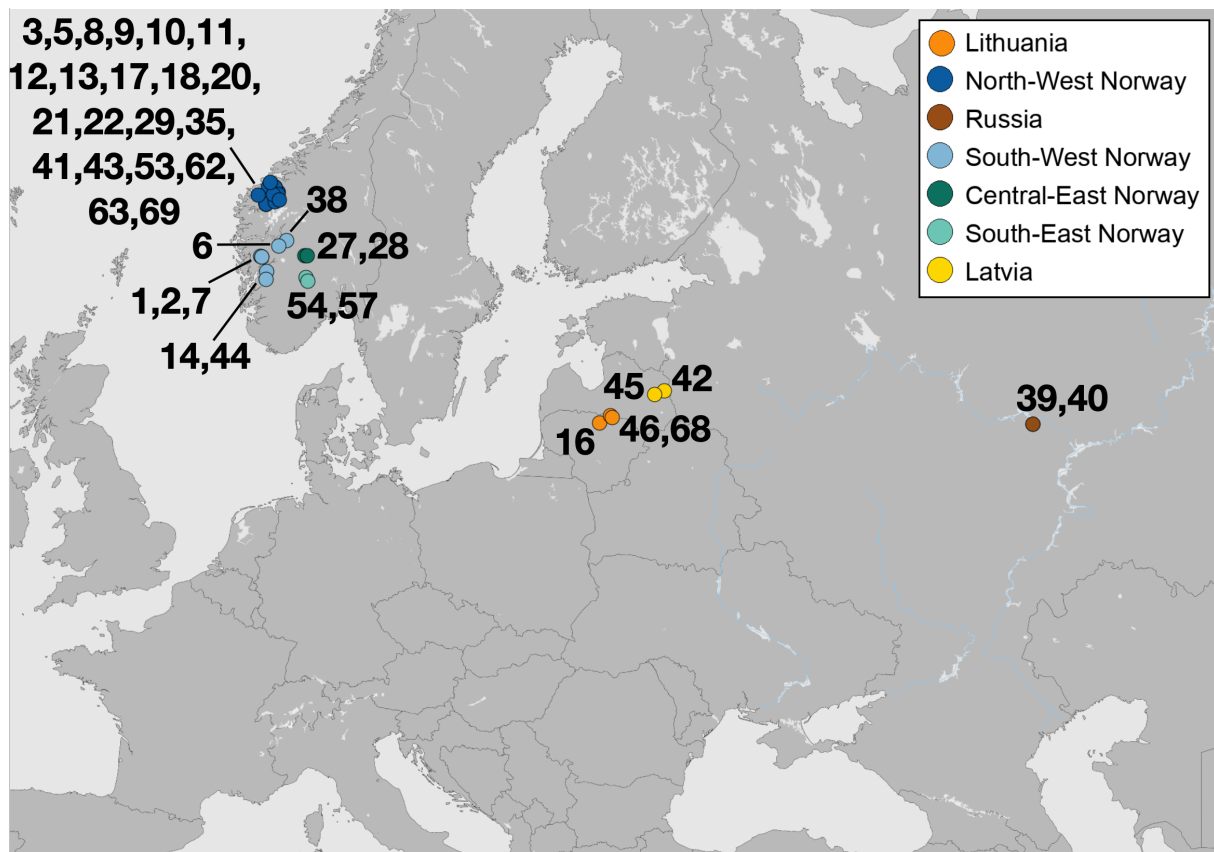


Figure 4. Origin locations of the cultures investigated in this study

strains in the monophyletic clade are from the same culture, #45. Sequencing more strains would be desirable, in order to determine whether there truly are two Baltic clades.

Figure 3 in [1] shows the phylogeny without the more recently sequenced strains from [28] and NCYC, and here the farmhouse clade is monophyletic, and all the Baltic strains appear in a single sub-clade. This result is consistent with that of [28]. Why the phylogeny is more complex when more strains are added is not clear, but adding even more strains should resolve question.

All the Russian strains fell outside the farmhouse clade, but this does not necessarily mean that all are allochthonous. Below, the observed phylogeny of farmhouse yeast is discussed, with attempts to link it to historical and geographical information on the cultures.

### 5.1. Norwegian farmhouse yeasts show geographical separation

Strikingly, the Norwegian strains form two cleanly separated monophyletic sub-clades, one for Western Norway and another for Central-Eastern Norway. Unfortunately, only a single strain from South-East Norway has ever been sequenced (from [28]). In this phylogeny that single strain appears on the edge of the Eastern Norwegian clade, thus making it tantalizingly unclear whether there is a genetic distinction within Eastern Norway between the south and the centre.

Norwegian beer culture in general shows very clear separation between Western and Eastern Norway, visible in terminology, mashing methods, the gender responsible for brewing, the design of yeast logs, and more [11]. The cause of these divergences is clear: the tall and wide chain of mountains running from southern to central Norway, separating the two regions from each other. The main division in Norwegian dialects follows the same divide [31].

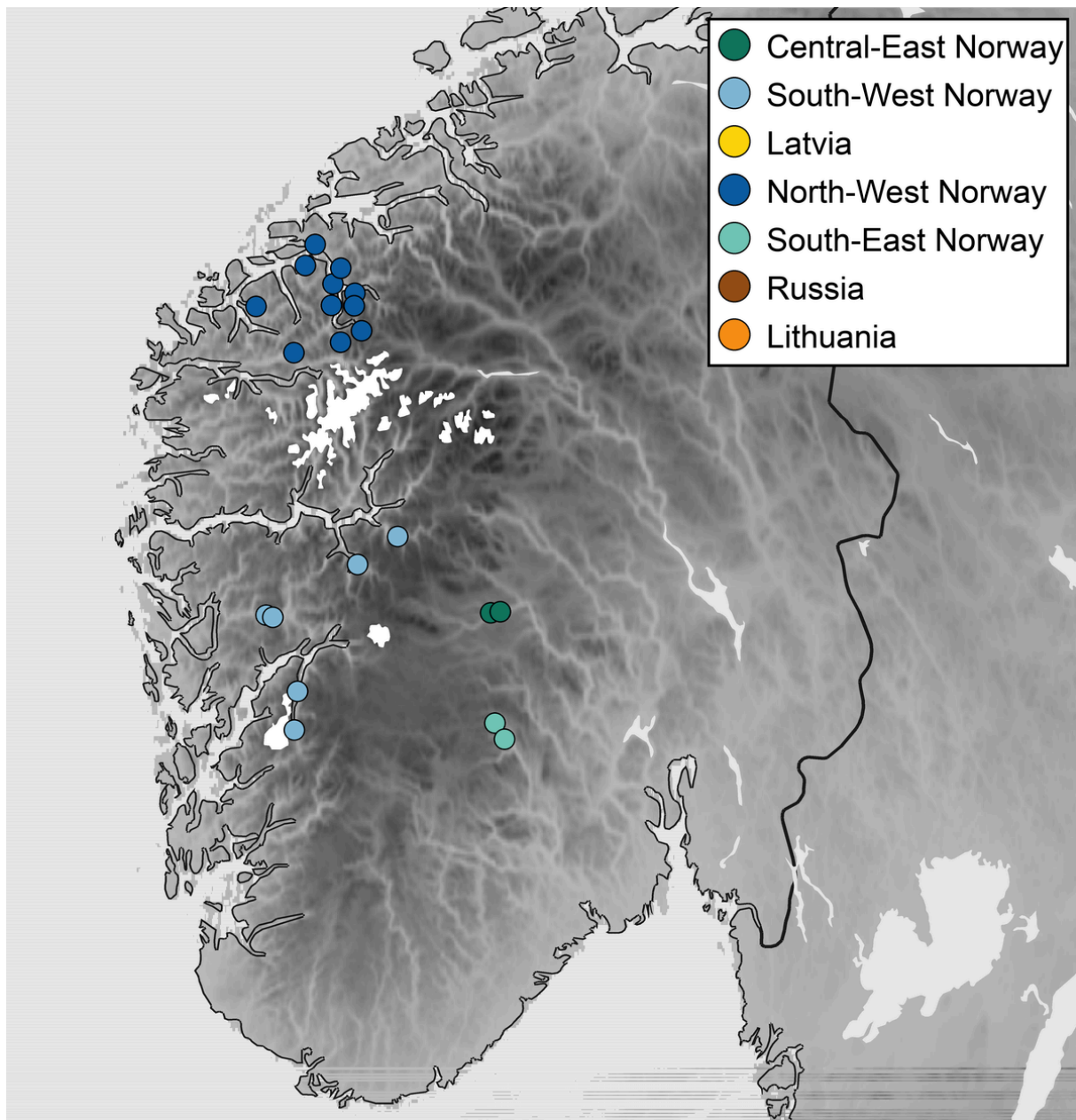


Figure 5. The origin locations of the Norwegian cultures investigated in this study.

In contrast, such clear division in yeast phylogeny is not observed in the north vs. south of West-Norway, although there is some degree of division. The two regions are separated by the mountain chain capped by the Jostedal Glacier and show clear differences in dialects and beer culture [11], [31]. A difference would therefore not be unexpected, and in the PCA clustering in Figure 3 of [1] the northern strains tend to be near the top and southern strains toward the bottom. The northern and southern strains also cluster clearly differently in the k-means clustering in Figure 3F. So, while the two regions do not divide into clearly separated subclades there are still indications of geographic differences.

## 5.2. The Asian link of European farmhouse yeasts

Two farmhouse strains group together, close to (yet separate from) the Asian fermentation strains: 39R20 and 16R23. Culture #39 was collected from Chuvashia (Russia), while #16 was collected from Lithuania. The Latvian Pundurs-2 strain (from culture #42) was likewise found previously to cluster

close to Asian fermentation strains [29], but in this phylogeny it appears in the external Baltic clade. How to interpret these two strains is as yet unclear, but they might be indications of a second, Eastern European, clade of farmhouse yeasts.

It is not clear how yeasts from Lithuania and Chuvashia, roughly 1400km apart, came to be related, but there have been historical connections between the two regions, so it is tempting to speculate on how yeast could have been transferred. During the Viking Era, there was considerable traffic from the Baltic into the Eastern European river systems, to the lower Volga and beyond [32], [33]. Chuvashia lies on the right bank of the middle Volga, and so will have been affected by this traffic. Indeed, in 922 CE, an Arab traveller famously met a Viking party near Itil on the middle Volga [34], and Arab sources describe Viking attacks in present-day Azerbaijan [32]. Chuvashia became part of the Russian Empire in the mid-16th century, while Aukštaitija in Lithuania was incorporated during the Third Partition of Poland in 1795. Exchange of yeast may have taken place during any of these two periods. An alternative explanation is that closely related farmhouse yeasts may have been in use in the regions in between, until it died out in the 20th century.

The phylogenetic placement of these two strains in the Asian lineage is interesting, as Russia has seen influence from Chinese and Central Asian culture, which is visible in Russian language and cuisine. A particularly strong influence was the Mongol invasion in the 13th century, after which Russia remained under Mongol domination for two centuries.

However, it remains possible that these strains are of commercial origin, for example as baking yeasts, so it is too early to draw any conclusions. Or, with more Baltic strains sequenced, they might turn out to belong to the Baltic clade after all, like Pundurs-2.

### **5.3. The mixed origin of the Russian farmhouse yeasts**

Two strains from culture #40 from Russia, 40R1 and 40R20, cluster together in the Mixed clade [35], close to a commercial beer and bread yeast. This could be caused by accidental contamination of the farmhouse culture by commercial yeast, or intentional use of the commercial strain to start a new fermentation culture, for example after the traditional yeast culture was deemed inviable (see also Section 6 of this note). Interestingly, 40R14, another isolate from culture #40, clusters closely with a wild yeast near the “Beer2” clade. However, based on the PCR fingerprinting of all #40 isolates, the variants close to the Mixed clade are by far the most predominant (87.5% of total culture isolates). #40 was collected during field work in Chuvashia, but the collector was never able to speak directly with the owner (Rima Il'inischna Petrova), so the origin story of the culture has therefore never been established.

Chuvashia appears to be a region with a large number of farmhouse yeast cultures in active use, but so far only three have been collected by researchers outside Russia (#39, #40, and #59), and only isolates of two of these were sequenced in the present study. Culture #39 was collected on the same day, in the same village, but from another brewer, and shows every indication of being an original farmhouse yeast culture (i.e. no link to current commercial strains). Further investigation of these cultures is required to yield additional insights.

## **6. Presence of commercial yeast in farmhouse cultures**

Given the omnipresence of modern commercial yeast in the fermentation industry, and the non-sterile way in which farmhouse yeast cultures are treated and stored, [1] investigated to what extent commercial strains have penetrated farmhouse yeast cultures. To our surprise, whole genome sequencing detected modern commercial strains in only three cultures (#7, #38, #40; see Figure 1B in

[1]). Based on this information, we analysed the genetic fingerprinting data obtained for all isolates, and found evidence of similar commercial strains in one additional culture (#57).

These commercial strains may have either been introduced in the farmhouse cultures by accidental cross-contamination, or deliberately added as a starter culture by the brewer, for example after loss of the original farmhouse culture. The brewer who took the modern yeast into use will have been aware of doing so, but later brewers may have gotten the culture from this person without being aware of the origin of the yeasts. But, regardless of whether these commercial strains were introduced accidentally or deliberately, they are collectively referred to as “allochthonous yeast” in this study, as they do not originate from the farmhouse brewing tradition itself. Throughout [1], they have been excluded from some analyses and are often highlighted separately in figures to avoid mixing noise into the analysis data from the traditional farmhouse yeast.

Of the 78 strains isolated from farmhouse cultures included in the phylogeny, 9 appear in the Mixed clade, 4 in Beer 2, and 3 in a nameless group adjacent to Beer 2 and Wine. Strikingly, not a single one appears in the Beer 1 clade, despite this being the largest and most commonly used in top-fermenting beer. The reason is very likely that Beer 1 yeasts are phenotypically highly unsuited to farmhouse yeast practices, and thus would likely not have survived in competition under farmhouse brewing conditions even were they to appear in a fermentation.

Below, we highlight some background information on the cultures in which allochthonous strains were detected, to gain further insights on how these may have been introduced.

### **6.1. #7 Granvin**

The sequenced isolate 7R25, which represents the dominant group (85%) within culture #7, clusters in the Beer2 clade, and is therefore considered an allochthonous yeast. The other 15% of isolates (represented by the sequenced isolate 7R7), clusters within the Norwegian farmhouse yeast clade.

Culture #7 has a checkered history. It was procured by a curator at Norsk Folkemuseum (Museum of Norwegian Ethnography), who had received it from a modern home brewer, who in turn received it from the current owner, a brewer on Nesodden near Oslo (Tor Ølver Helland). Helland learned farmhouse brewing from his father-in-law in Granvin (Hardanger, Western Norway), where he also received the yeast culture, which he has used in traditional farmhouse ale since the mid-1980s (see Figure 3). His father-in-law, in turn, got the yeast from Dyrvedalen in nearby Voss. Both the museum curator and the modern home brewer brew modern styles of beer using modern commercial yeast, and they also brewed with culture #7 before providing it for this study. It thus seems likely that culture #7 was accidentally contaminated with hefeweizen yeast while in their care. New yeast was collected from Helland, but arrived too late for inclusion in this study.

Interestingly, 7R25 clusters very closely to #4 Muri, which is a Norwegian farmhouse yeast culture (not included in this study), which has been previously described to contain commercial hefeweizen yeast, accidentally introduced by cross-contamination when reviving the original farmhouse yeast culture [36], [37].

### **6.2. #57 Tinn X**

The fingerprinting analysis showed that of the four different genotypes in this culture, two (which represent 95% of all isolates) cluster with commercial yeast. A different study also found allochthonous yeast in this culture, more specifically strains closely related to diastatic Belgian ale strains [29].

The analyzed sample was collected from a modern home brewer who had inherited the culture after the death of his uncle, a farmhouse brewer in the Telemark region of south-eastern Norway. He had brewed with it numerous times after inheriting it, and so it likely was accidentally contaminated with yeast from a previous home brew with commercial yeast. His aunt, who is still alive, had a glass of the original yeast culture still in her freezer, and this was collected, but arrived too late for inclusion in the study.

### **6.3. #38 Aurland**

One strain, 38R16, was fully sequenced and clustered in “Beer 2”, and is therefore likely a modern commercial yeast. This strain, however, did not cluster with any other isolate of #38 in the genetic fingerprint, where all the other strains clustered with kveik strains. Therefore, the proportion of allochthonous yeast in this culture is estimated to be very low (<5%).

#38 was collected from a former farmhouse brewer who had brewed only modern home brews with commercial yeasts for several decades. He found the dried #38 yeast culture in an outbuilding on his farm, and attempted to revive it, despite believing that it was last used in 1978. The revival attempt resulted in growth, and he has been using the yeast to brew with since.

### **6.4. #40 Rima**

This culture was collected from fermenting beer in the village of Kshaushi in the Chuvash Republic in Russia. The original owner, Rima Il'inischna Petrova, was not present on that day, and so permission to collect her yeast was obtained by phone via Chuvash-speaking intermediaries. She was not asked whether any other yeast had ever been mixed into it, nor where the yeast came from. The yeast was preserved between brews by mixing it with rye flour and storing it in the refrigerator. It was also used in baking, and apparently the owners baked almost every day.

40R1 and 40R20 were sequenced, and the genetic fingerprinting placed these two into the same group, containing nearly all isolates from the culture. This strain appears to match a known beer refermentation yeast in the ‘Mixed’ clade. Refermentation yeasts are often baker’s yeasts originally, and this may be how the strain made it into the culture. Only three strains were not in this group (40R14, 40R27, and 40R30) and the fingerprinting indicates they are all the same yeast. 40R14 was sequenced and clustered within the Wine yeast cluster. Most likely this is another allochthonous strain, possibly from a kit for homemade wine.

No traditional farmhouse yeasts were found in this culture, and in the fingerprinting all strains cluster with the three sequenced strains.

### **6.5. Conclusion**

This data is insufficient to draw firm conclusions, but it appears that farmhouse cultures are vulnerable to contamination by outside yeast in two main scenarios.

One is when the culture is revived after a long period of no use, when the original yeast has low viability. Presumably it is then vulnerable to other strains cross-contaminating the culture.

The other is when the culture is used by a modern home brewer who also brews (or bakes) with modern commercial yeast. Intriguingly, the same risk does not seem to be present when farmhouse brewers who have owned the cultures for decades brew modern styles with modern commercial yeast. The explanation may be that modern home brewers used the farmhouse yeast at temperatures around 20°C, making them more vulnerable to competition from modern yeast, while the farmhouse

Table 1. Number of unique strains at different cutoffs.

Cutoff	Unique strains	Percentage
2	1117	56%
3	859	43%
4	684	34%
<b>4.2</b>	<b>649</b>	<b>33%</b>
5	545	27%
7	378	19%

Table 2. Graph properties at different cutoffs.

Property	Explanation	2	3	4	4.2	5	7
Order	Nodes	44	44	44	44	44	44
Size	Edges	19	46	79	90	111	178
Components	Connected subgraphs	29	21	17	16	14	10
Circuit rank	Sum of the three above	92	111	140	150	169	232
Clique number	Nodes in largest component	13	22	28	28	30	34
Diameter	Largest distance between nodes	6	5	6	6	5	4

brewers today typically use their yeast at 30-40°C [24], making it difficult for modern commercial yeast to compete.

## 7. Shared strains between cultures

To investigate to what extent the same strains could be found in different cultures, all isolates were genetically fingerprinted and scored for similarity (see Materials and Methods in [1]). A custom-made Python script analyzed the output, grouping together all strains found by traversing up the tree from a strain node to the last internal node until a cutoff distance was reached, then including all strains reachable below that internal node at a distance less than the cutoff. This way, strains that are the same (or very similar) across different cultures can be identified. Table 1 shows the number of groups, effectively an estimate of the number of unique strains, found with different cutoff values. The percentage is the number of unique strains relative to the total number of isolates.

Using GraphViz we visualized the cultures as a graph, with lines connecting the cultures which share at least one strain. The thickness of the lines is proportional to the number of shared strains. Below, we will highlight some of the most prominent inter-culture connections at different cutoff values, and (where possible) provide historical information on the involved cultures.

We selected the cutoff by first doing a manual review of the fingerprinting results for all cultures and identifying groups of presumed identical strains within each culture. A Python script was then run to identify the cutoff that best reproduced the manual results, measured by precision and recall. The optimal cutoff was found to be 4.2.

Table 2 shows the graph properties at different cutoffs. All edge lengths are 1 in that analysis.

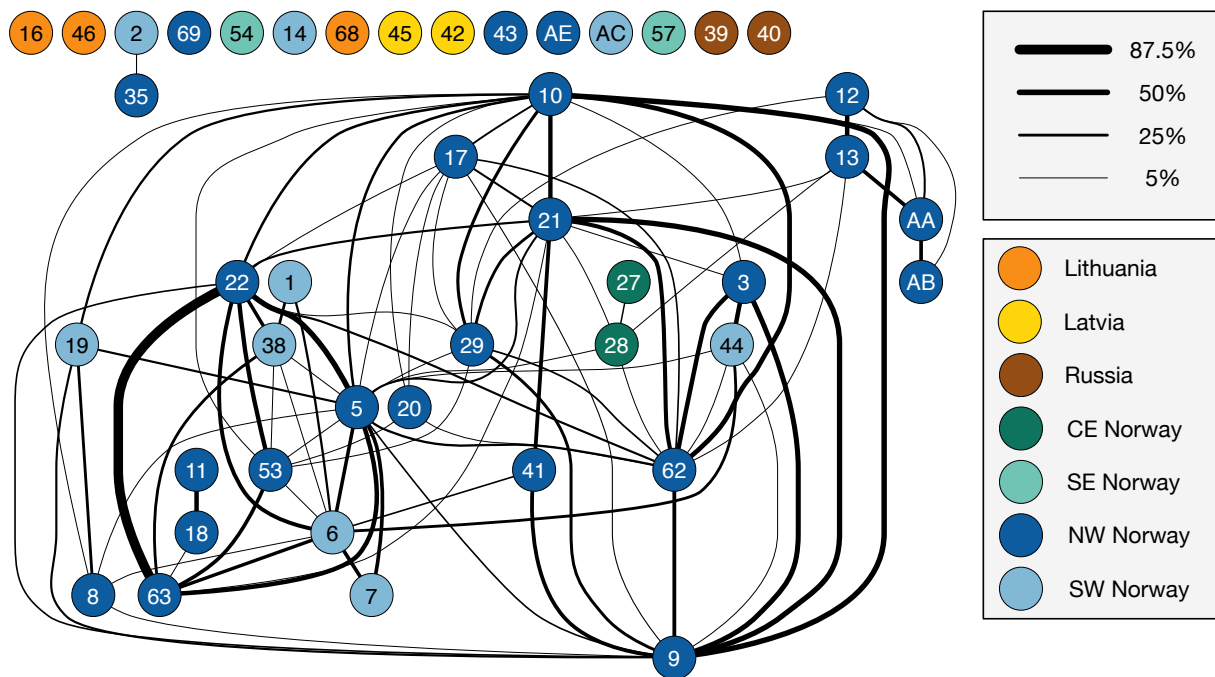


Figure 6. Graph over the culture overlap graph at cutoff 4.2, where thicker lines indicate more shared strains.

### 7.1. Interpretation of graph with cutoff ‘4.2’

None of the Baltic or Russian cultures have any overlap, nor do the two cultures from South-east Norway (“berm”). No overlap was to be expected, so to some extent this validates the method used.

What overlap exists is all within the kveik cultures and the two cultures from Central-east Norway (“gong”). That the “gong” cultures should show overlap with the “kveik” cultures is surprising, but persists even at cutoff 3, so it may point to east-west connections. The “gong” cultures are from Upper Hallingdal, which is close to mountain crossings into Western Norway, and there are clear signs of overlap in beer culture at exactly this point [11].

Table 3 shows the pairs of cultures that have the greatest overlaps. As can be seen, out of the 11 pairs in the table, in 6 cases both cultures are from the same place. In the remaining cases the pairs of cultures all originate close to each other: Hornindal-Stordal 50km, Stordal-Geiranger 35km.

The owner of culture #3 Stranda collected farmhouse yeasts from many places in Western Norway and no longer remembers where this particular one came from, so no conclusions can be drawn about that culture. Because one strain almost completely dominates that culture, any culture that contains that strain will show strong overlap in this analysis. The dominant strain in #3 is found in cultures from both Stordal and Geiranger, suggesting an origin in that area, although it is also found in #44 from Jordal in Hardanger, 230km away, several regions to the south. This is puzzling and not easily explained.

When #3 was collected it had not been used in a very long time, and the initial attempt at reviving it at NCYC failed. The complete sample had to be sent to NCYC, and even then revival initially failed, until some dry material in a corner of the flask was scraped out and revival retried. The initial NCYC analysis only found a single strain in the culture, and it was assumed that most of the original strains had died. This is likely the explanation for the very low number of strains in this culture.

The strongest overlap is 87.5%, between cultures #22 and #63, and closer analysis shows that the overlap consists of four different strains. Effectively this analysis finds the cultures to be almost the

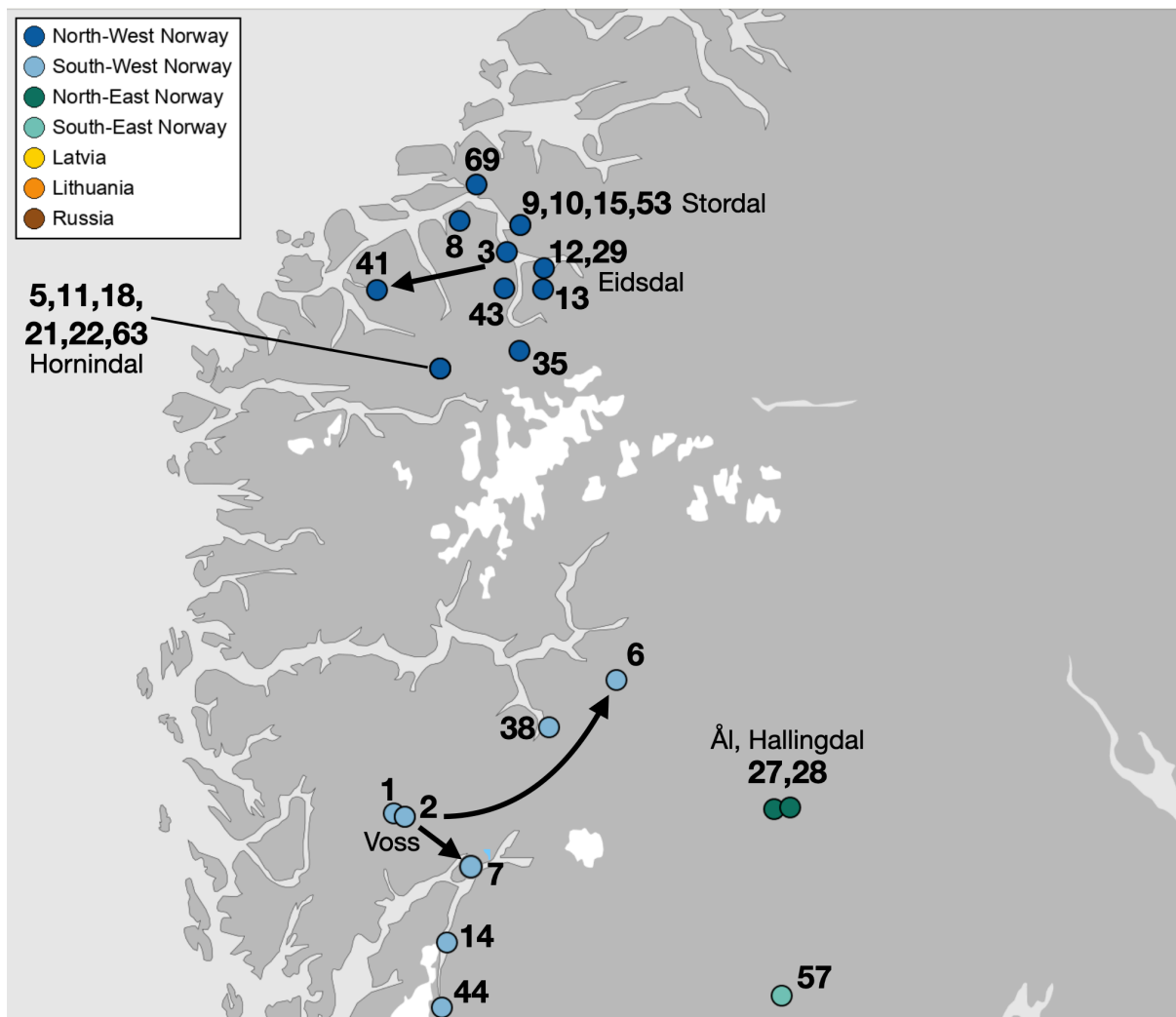


Figure 7. Map of the origins of the Norwegian cultures.

same. The owner of #63 says he created his culture in 1995 by mixing three or four other cultures – it appears that the contribution from #22 ended up dominating the culture. The culture also has 41.3% overlap with #5, which is only possible if #5 and #22 also overlap, and indeed the analysis finds 50% overlap between the two. (All three cultures are from Hornindal.)

The second strongest overlap, 50% between #9 and #10, is interesting, because not only are these two cultures both from Stordal, but they originate roughly 50 meters apart. Anecdotal experience in the farmhouse community is that these two cultures produce clearly different aromas, but genetically the similarity between them is considerable.

To analyze the graph further, the Louvain community detection algorithm [38] was run on the graph, using networkx version 3.6 [39] with the default parameters. This algorithm was used because it can take the size of the overlaps into account. The result is seven clusters containing more than one node.

C1 #11, #18: These two cultures (Figure 6 lower left) have one of the biggest overlaps (41.3%), and only a single, slight connection to another culture (#63), so treating them as a separate cluster makes perfect sense. Both are from Hornindal, but no connection between them was known previously, suggesting they are far closer than was previously known. #63 is also from Hornindal.

C2 #27, #28: Overlap between these two is 13.8%, and only #28 has connections to other cultures, all slight (upper middle). These two cultures are the only “gong” (CE Norway) cultures in

the analysis, and it's known that the owners often exchange yeast, so this is very much an expected cluster.

C3 **#2, #35**: These two cultures have 10% overlap and no other connections (upper left), but to find any connection between them at all is very surprising, as one is SW Norway and the other from quite far north in NW Norway.

C4 **#8, #19**: These two have 26.3% overlap (lower left), and #8 has little overlap with other cultures, while #19 has some overlap with other cultures, but they all belong to different clusters. #19 was collected from SE Norway (not a defined region in this study), but it does not originate in that area, and the owner does not know where it came from traditionally. The most likely theory is that it came from Granvin in SW Norway, but its strongest connections are all with cultures from NW Norway, suggesting that perhaps its origin is different from what was assumed.

C5 **#12, #13, AA, AB**: These four (upper right) are connected by strong overlaps, but only have weak overlaps with other cultures. AA and AB are the same culture, AA was cryopreserved from the 1960s while AB dates from 2021, from Skodje. #12 and #13 have one of the strongest overlaps, at 41.3%, and are both from Eidsdal. Eidsdal and Stavset in Skodje are only 27km apart, suggesting a recent exchange.

C6 **#3, #9, #10, #17, #20, #21, #29, #41, #44, #62**: This large cluster appears mostly in the middle left and may have been skewed by the inclusion of the "wildcard" culture #3 which has the highly dominant single strain that's also shared with other cultures, leading to large overlaps. However, if we ignore #3 (of unknown origin) and #44 from SW Norway (included because of the large overlap with #3), the remainder all originate relatively close to each other, in Stordal (#9, #10, #17), Hornindal (#20, #21) and Eidsdal/Geiranger (#29, #62).

C7 **#1, #5, #6, #7, #22, #38, #53, #63**: This large cluster (lower right) is easily justifiable on grounds of graph structure, having many very strong internal overlaps. It has an SW Norway component: #1, #6, #7, and #38, all of which originate in Voss, or may do so. The remainder, #5, #22, #53, and #63, all originate in Hornindal (3) and Stordal (1). There are strong overlaps between the SW and NW groups, however, #22-#38, #63-#38, #5-#7, #6-#22, #5-#6, which strongly suggests yeast exchange between the SW and NW regions in the not too distant past.

A surprise in this analysis is that #18 shows no overlap with #5, as #5 started out as an offshoot of #18 that has been maintained separately since the 1990s.

Five kveik cultures show no overlaps at all:

- #14, which is quite distant from the nearest cultures, and is known to have been isolated at least since the 1950s, and perhaps longer.
- #43, which also has a slightly isolated geographic origin, and derives from an old farmer. It, too, is likely to not have been involved in yeast exchange for a long time.
- #69, the northernmost culture, which is from a region that has been oriented more toward the coast, and somewhat isolated from the nearby regions to the south. AA and AB are from the same county, however.
- AC, which comes from the same brewer in Granvin as #7. It is thus surprising that the analysis finds no overlap. However, the culture has been maintained separately since 1975, and this may be the reason.
- AE, which was collected from the same person who owns #3, Stein Langlo. In the 1990s Langlo collected yeast from many farmhouse brewers in different areas, and he does not remember where this culture derives from.

Table 3. The largest culture overlaps at cutoff 4.2. The sample counts is the number of samples from each culture overlapping with the other culture. The overlap is the percentage the sum of these two figures make up out of 80 samples.

Culture 1	Culture 2	C1 samples	C2 samples	Overlap	Area
#22	#63	35	35	87.5%	Hornindal
#10	#9	21	19	50.0%	Stordal
#22	#5	34	6	50.0%	Hornindal
#21	#9	23	16	48.8%	Hornindal-Stordal
#3	#9	33	4	46.3%	?-Stordal
#10	#62	19	16	43.8%	Stordal-Geiranger
#11	#18	19	14	41.3%	Hornindal
#12	#13	12	21	41.3%	Eidsdal
#3	#62	32	1	41.3%	?-Geiranger
#3	#44	32	1	41.3%	?-Jordal
#5	#63	5	28	41.3%	Hornindal

Table 4. The most common strains that were found in more than one culture, and what cultures they were found in. The last column lists what isolates, if any, were sequenced.

Sample count	Cultures	Sequenced
51	#5, #9, #10, #17, #21, #22, #29, #62	
51	#5, #6, #22, #38, #53, #63	
36	#12, #13, AA	
36	#3, #9, #44, #62	3R11
29	#9, #21, #41	41R10
28	#5, #6, #7	7R7
25	AA, AB	
21	#1, #6, #38	
20	#5, #8, #9, #10, #19	

## 7.2. Interpretation of graph when cutoff is >4.2

At cutoff 5 #27 and #28 become more closely connected with the kveiks, but the overall picture does not change materially. A northern cluster focused on Hornindal and Eidsdal seems to become more prominent.

At cutoff 7 the kveik and gong groups form one subgraph so connected that GraphViz struggles to draw all the connections, only leaving out a single culture: #14. Outside kveik and gong the other cultures remain unconnected, with one exception: a Baltic connection between #46 and #68. That is not surprising, as the two originate about 10km apart, on opposite sides of the town Biržai in flat farmland. No strains were sequenced from #68, so the WGS results throw no further light on the connection.

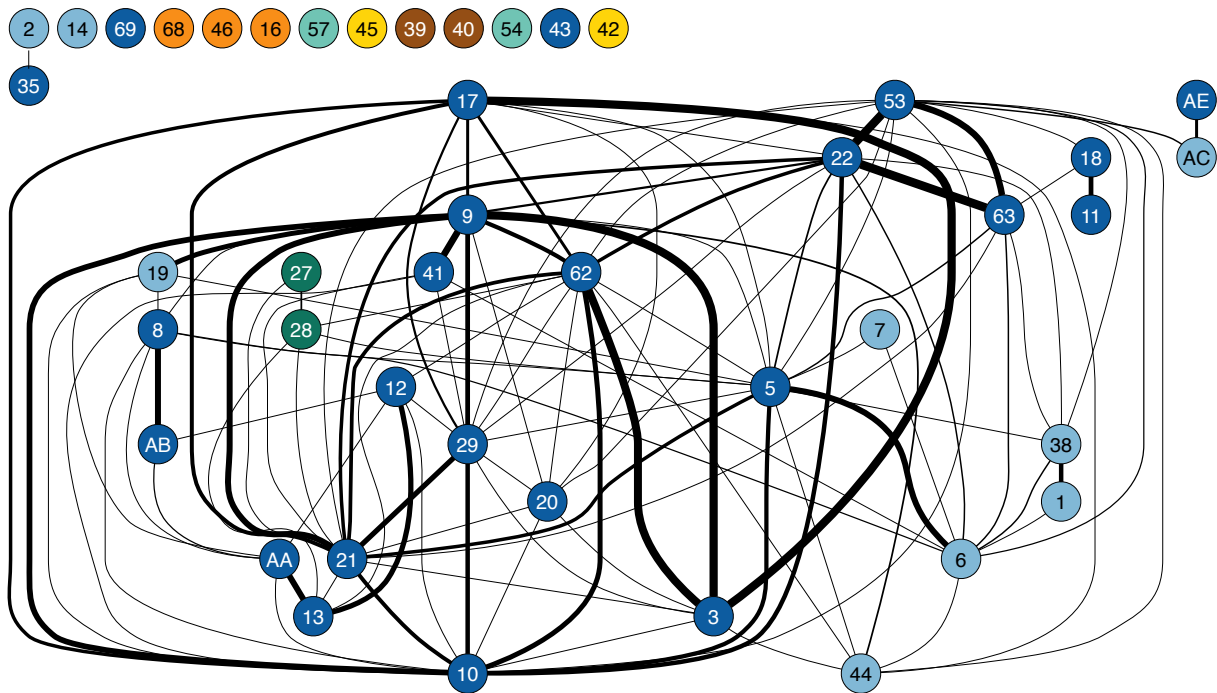


Figure 8. Culture overlap graph with cutoff 5.

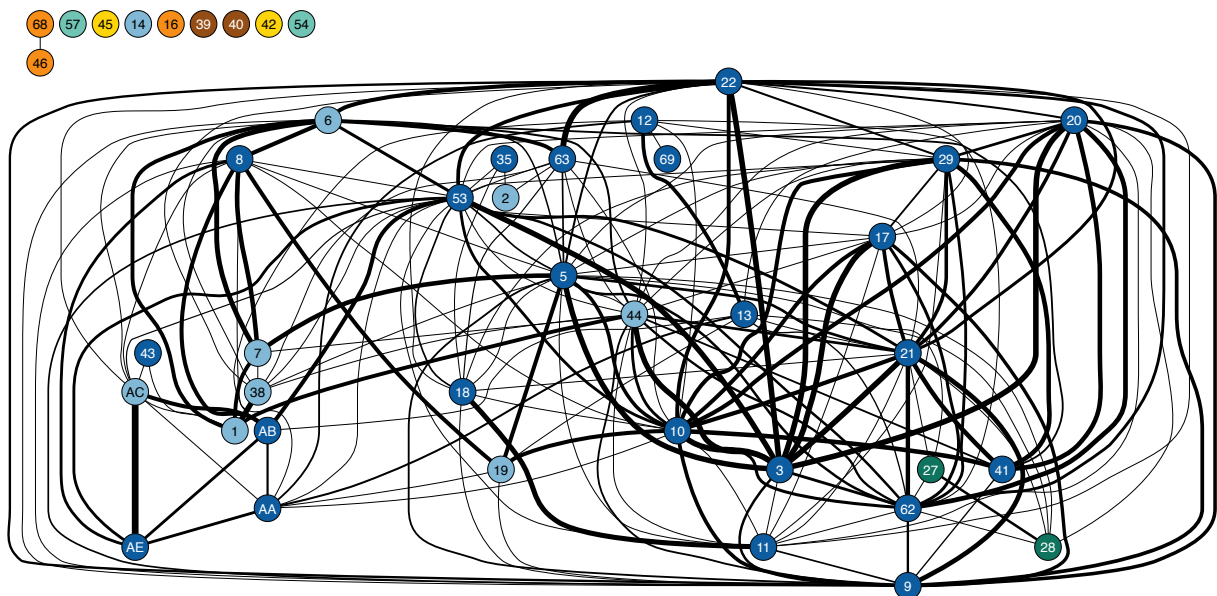


Figure 9. Culture overlap graph with cutoff 7.

## 8. Further work

Cultures such as these are often referred to as “mixed”, but the farmhouse cultures are fundamentally different from cultures formed by deliberately mixing a small number of strains. Essentially, these are communities of organisms that have developed organically together over very long timespans. For this reason Preiss suggested calling them “landraces” [29], by analogy with landrace varieties of grain and hops.

The population structure of landrace yeast cultures has been explored [28], [30], [29], [1], but remains little known. The stability of these cultures is even less understood. This lack of firm knowledge about population structure and stability injected considerable uncertainty into the analyses above, and suggests that much further work is needed.

## 8.1. Detailed population structure

The cell density of yeast dried by farmhouse brewers may be on average about 14 billion cells per gram of dry weight [40], while a brewer may harvest perhaps 100g of dried yeast from each brew, making for a total population of 1.4 trillion cells. The analysis in this note rests on a sample of 40 cells from this total, that is, 0.000000003%.

In this scenario, when the analysis finds 35 different strains out of 40 samples taken ([1] Figure 1B, culture #5), it seems virtually certain that the culture must contain more strains which by accident were not sampled. Assuming perfect mixing and randomness, a strain that makes up 99% or 50% of the culture is virtually guaranteed to be included in one of 40 samples, while a strain making up 10% has about 1.5% chance of being missed. For 1% of the culture the odds of being omitted are 67%, and for 0.1% of the culture 96%. At 0.01% a strain would still make up 140 million cells, but the odds of being missed rise to 99.6%.

While the method used would thus appear to have very good odds of capturing at least the rough structure of each culture, it seems virtually guaranteed that the cultures contain strains which are not included in the analysis. The strain proportions must inevitably be relatively rough estimates.

As can be seen in Figure 10 most strains were only found in a very small number of samples. In fact, out of 660 strains<sup>2</sup> 422, or 64%, were found only in a single sample. Only 62 strains, 9%, are found in more than five samples. Given this it seems very likely that a large number of the rare strains in each culture were not captured by the analysis. The true number of different strains in the 44 farmhouse yeast cultures investigated thus remains essentially unknown.

A very interesting experiment would be to perform plating and isolation on the same culture two or more times, then fingerprint the isolates, and compare the sets of samples from the same culture. How similar would they be? This experiment would greatly improve the understanding of how accurate the method is, and give a better basis for estimating the size of the unsampled population.

If 400 samples were taken from each culture instead of 40, what would the shape of the histogram be? Would it remain the same? Essentially, until the peak moves to a number considerably above 1, the actual number of strains will remain unknown.

## 8.2. Population stability

Essentially no empirical data exists on the stability of the strain proportions in landrace cultures over time, although [41] (unpublished) studied the evolution of single-strain cultures during serial repitching. Could a strain that is below detection thresholds at generation  $n$  be the dominant strain by generation  $n + 10$ ? Brewers even in the same area do not brew exactly the same way, so if the culture moves from one brewer to another, will changed competitive circumstances change the strain proportions?

Cultures AA and AB are the same culture from the same brewer, with one sample from the 1960s and one from 2021. In this analysis they had 33.8% overlap, suggesting substantial stability, at least as long as the culture remains with the same brewer, but that figure derives from 2 samples in AA overlapping with 25 in AB.

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<sup>2</sup> When the same strain found in different cultures is counted as a single strain the total is 649 strains, but here we are counting for each culture separately. When duplicates are collapsed 406 strains, 63%, occur only once. In [1] the total number of strains is given as 557, but this excludes the 'xxPxx' strains (which were hand-picked based on morphology), and only uses the 40 randomly picked strains per culture.

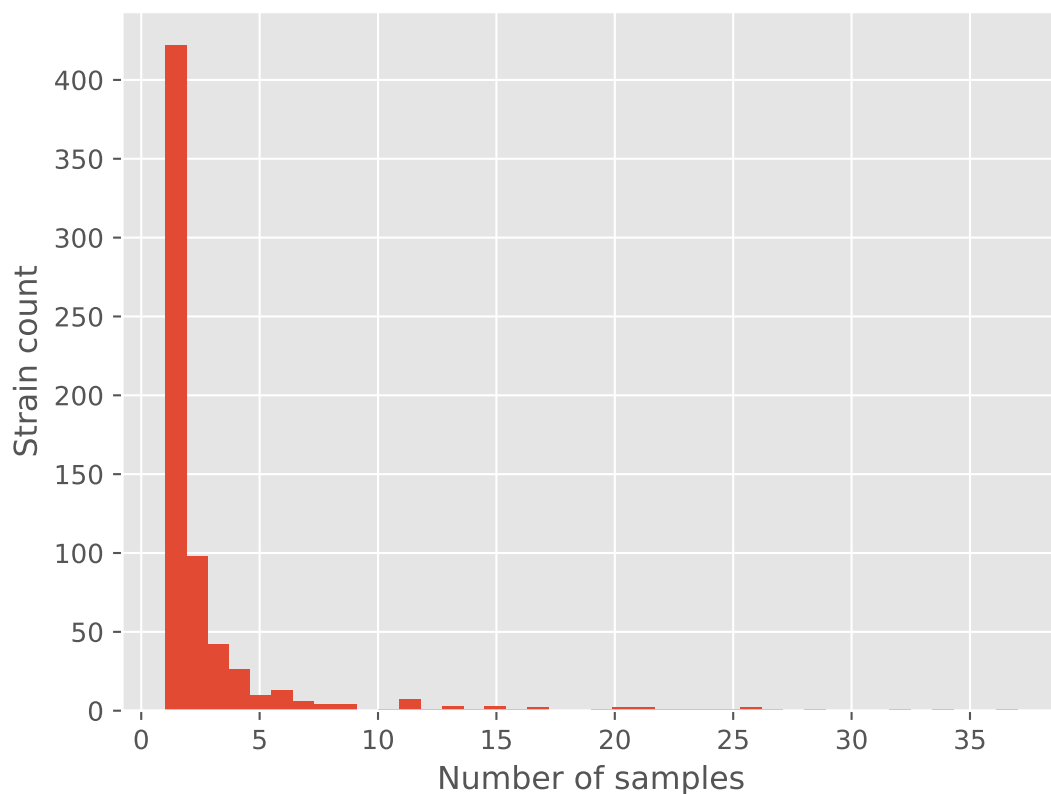


Figure 10. A histogram of how many samples were found of each strain in the analysis.

The uncertainty surrounding population stability obviously makes the preceding overlap analysis uncertain, and these questions, being yeast evolution in practice, must at the same time be at the heart of understanding yeast evolution. The greater is the pity that the issues are so little explored.

Farmhouse brewers in Norway, Latvia, Lithuania, and Russia, as well as outside Europe, are still brewing and actively using these cultures, providing researchers with the opportunity to perform studies on these landrace cultures as they evolve in their natural habitat. At least for the time being.

### 8.3. Strain stability

The speed at which yeast genomes change over time remains little known, although it is known that mutation rate is influenced by a number of factors, such as environmental stress. Thus, in addition to the question of population stability comes the question of strain stability.

For strains which can only reproduce asexually mutation remains the primary means of genetic change, but [1] finds evidence of a sexual cycle for farmhouse yeasts, suggesting they might reproduce sexually. If so, strain stability for these yeasts would be substantially lower than for modern industrial strains.

More precise data on the rate of genetic change for sexual and asexual brewing yeasts would obviously cast light on the history and evolution of *Saccharomyces cerevisiae*, allowing the genetic results now emerging in numerous studies to be connected with the historical development of brewing.

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