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# Novel fermentations integrate traditional practice and rational design of fermented-food microbiomes

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## SUMMARY

Fermented foods and beverages have been produced around the world for millennia, providing humans with a range of gastronomic, cultural, health, and scientific benefits. Building on these traditional forms, a convergence of factors, including culinary innovation, globalization, shifts in consumer preferences, and advances in microbiome sciences, has led to the emergence of so-called 'novel fermentations'. In this review, we define novel fermentation as the confluence of traditional food practices and rational microbiome design. Using principles of microbial ecology and evolution, we develop a microbiological framework that outlines several strategies for producing and characterizing novel fermentations, including switching substrates, engrafting target species, assembling whole-community chimeras, and generating novel phenotypes. A subsequent analysis of existing traditional ferments points to gaps in 'fermentation space' where novel ferments could potentially be produced using new combinations of microbes and food substrates. We highlight some important safety and sociocultural issues presented by the repurposing and modification of microbes from traditional ferments that fermented-food producers and microbiologists need to address.

## Introduction

Fermented foods and beverages are widely consumed and have received increased attention in recent decades from home cooks[1–3], professional chefs[4,5], microbiologists[6–8], food scientists[9], and educators[10,11]. These foods are valued for their cultural significance[12], ability to provide unique flavors[13], potential health benefits[14,15], and as simple systems to understand principles of microbial ecology and evolution[6]. Fermented foods allow anyone to harness the power of microbial communities to provide inexpensive, low-tech, and easy modes of preservation, nutritional enhancement, and flavor development.

Traditional fermented foods and beverages use 'desired' microbial growth and metabolic processes to transform raw food substrates into food products with modified sensory and nutritional attributes[14] (Figure 1A). Most traditional fermentations began long before the development of modern microbiology or food science and may be made with limited technological interventions[16]. It is difficult to know exactly how many of the world's iconic fermented foods and beverages were developed intentionally[12,17], but it is likely that many fermented foods, or at least their precursors, emerged through fortuitous accidents and were subsequently developed to produce consistent, recognized products (Figure 1B). A particular human culture likely noticed that when a food was allowed to rot in a controlled manner, the outcome was sensorially exciting or had a longer shelf-life. Historical records from the Neolithic period suggest that cheese-making originated from the practice of storing milk in containers made from animal stomachs, where enzymes like rennet naturally present in these organs catalyzed the coagulation of milk proteins, giving rise to cheese[18,19]. Similarly, grapes stored in containers for preservation were accidentally fermented, resulting in the creation of wine, and cabbage was spontaneously fermented to give rise to a range of fermented vegetable products[20,21]. Such fermentation processes are ancient, ubiquitous, and documented throughout the animal kingdom[22–27].

More recently, against a backdrop of concerns about food-system sustainability, food security, nutritional deficiency, loss of biodiversity, and other interconnected global challenges, interest in and research into traditional fermented foods has dramatically increased[7,14,28,29]. The need to meet these grand challenges has also fueled a growing interest in engineering traditional fermented-food microbiomes to do new things. This work, unfolding across global networks of professional and amateur fermenters, chefs, scientists, and engineers, generally seeks to build on fermentation as traditional practice towards including a more rational design process. A growing body of work refers to these experiments as *novel fermentations*[30–34].

What are these so-called novel fermentations and how do they relate to traditional ones? Given the emergent nature of this field, we are not aware of a consensus on where to draw boundaries between novel and traditional fermentations. We are also not sure that such a line could ever be conclusively drawn; rather, we propose that multiple ways of drawing these boundaries could be equally useful and suited to different purposes. As our focus here is on fermented-food microbiomes and how they are modulated through current experimental fermentation practices, we provisionally define novel fermentation as an

 

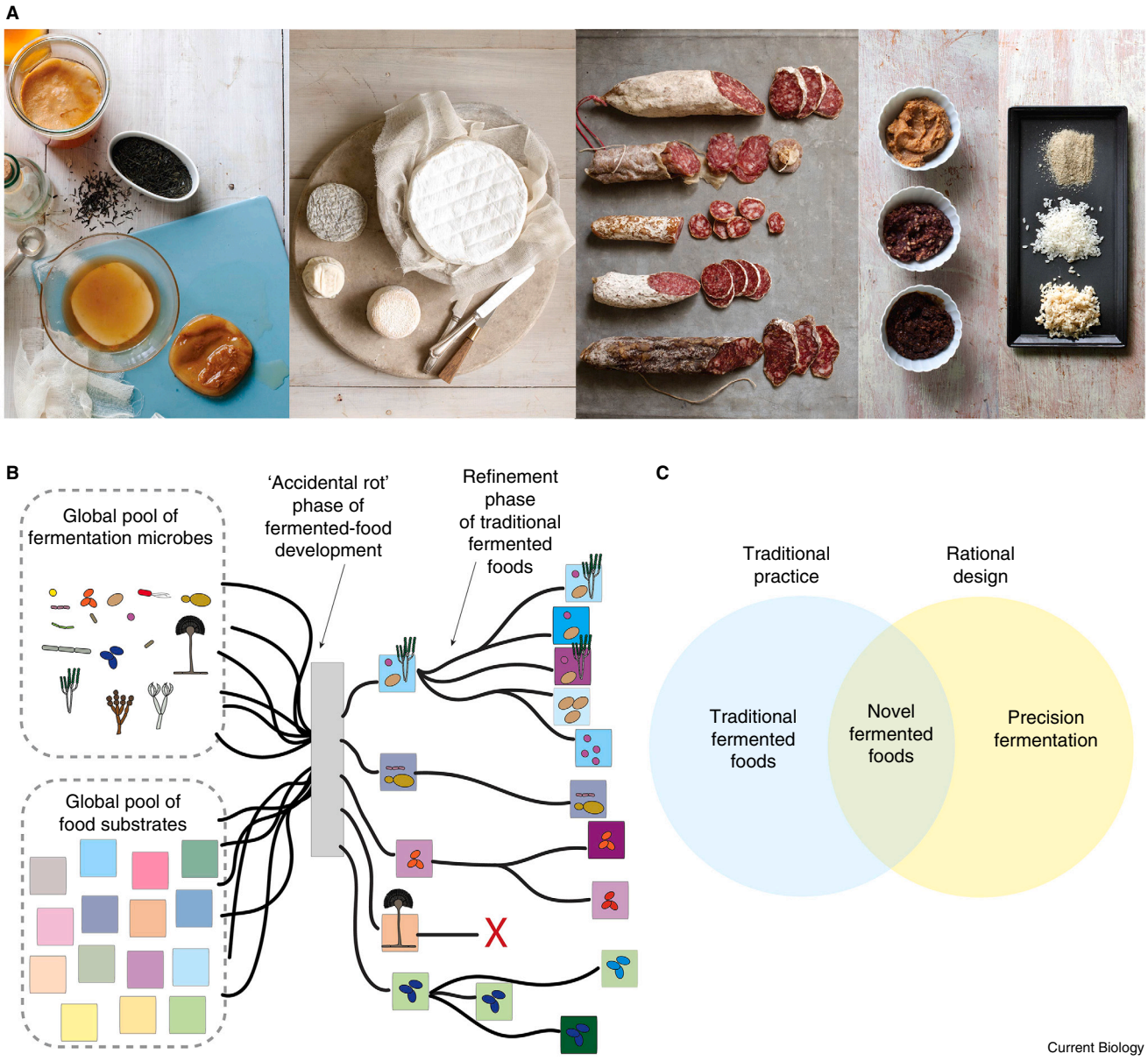


**Figure 1. Fermented foods, from traditional to novel.**
(A) Examples of traditional fermented foods with multispecies microbiomes. From left to right, kombucha, surface-ripened cheeses, salamis, misos, and kōji. Photos by Adam DeTour and used with permission. Food styling by Catrine Kelty. (B) A model of how traditional ferments may have developed serves as inspiration for the development of novel fermentations. The precursors of the traditional fermented products we now know likely began as fortuitous accidents that combined available microbes and food substrates. Unappealing ones would have remained 'accidental rot'; appealing ones, once noticed, would have been refined over generations into the products we know today. This refinement process has likely been gradual, generally not systematic, and heavily constrained by local substrate availability and environmental conditions. Through this refinement process, some combinations of microbes and substrates would have not worked or been deemed suitable by the selecting culture and been selected against (e.g. the red 'X'), while others would have been promising and perhaps even been further diversified. (C) More recently, the emergence of rational design principles from science and engineering offers a more systematic approach to designing and testing combinations of substrates, microbes, and growth conditions in historically unprecedented ways. The intersection of traditional practice and rational design is where we situate novel fermentations.

approach to fermentation that uses principles of rational design to develop traditional fermentation practices in new directions. Or in short: novel fermentation is the confluence of traditional practice and rational design (Figure 1C).

Rational microbiome design is growing and takes different forms. A common form seeks to shift away from traditional practice entirely, moving toward purely rational design processes. For example, so-called *precision fermentation* uses the growth of specific strains of microbes in bioreactors to produce specific molecules[35,36]. As this approach does not aim to build on traditional whole-food-based fermentation practices, we do not include it in our discussion of novel

fermentations — those where traditional practice and rational design coincide.

The kind of rational design we consider here uses science and technology for innovation, often employing a clear experimental framework and modern tools of microbiology, chemistry, and food science[27,29,33–35]. But we also note that novel fermentations can be developed by food producers without directly collecting data or conducting experiments to understand the mechanisms underlying the resulting features of a novel fermentation[4,37]. Indeed the origins of many novel fermentations, as with fermentation in general, often lie in a more practice-based, sensory approach, such as that found in home and professional kitchens and fermentaries[5,37]. We thus understand 'rational design' to mean the systematic, deliberate approach to experimenting with substrates, microbes, and fermentation conditions with the goal of producing novel outcomes. This approach can be pursued to a greater or lesser degree, depending on one's scientific inclinations and training, and access to resources.

Although it is common to see tradition and innovation as contrary forces, we understand them to have a more complementary relationship when considering novel ferments: innovation is the engine by which traditions develop, and tradition is the accretion of innovations that succeed[38]. Indeed, any traditional fermentation we could mention — cheese, wine, or sauerkraut as discussed above, or any other — exists because it has been iteratively innovated over centuries or millennia (Figure 1B). Still, we suspect it is useful to distinguish these from newer forms that we and others call novel. Some of the key differentiating features of novel fermentations have been facilitated by the globalized world in which they have emerged: the relatively rapid circulation of people, ingredients, microbes, and ideas has allowed this cosmopolitan, combinatorial, geographically discontinuous, deliberate, and even self-conscious approach to fermentation to emerge[37,39]. These contextual features, we propose, may help us distinguish 'novel' fermentations from traditional ones better than an arbitrary historical baseline. Understanding novel fermentation in this larger social, cultural, and historical context, in addition to painting a fuller, richer picture of it, can only help us better understand its scientific novelties.

The scientific value of these endeavors is both fundamental and applied: novel fermentations provide novel, tractable sites for better understanding and testing fundamental biological principles, as well as offering ways to address pressing global challenges. To address these complementary goals, and for novel fermentation microbiomes to be successfully developed and deployed, we identify some key questions we need to answer. First, what are the ecological design principles that guide the assembly and function of traditional ferments and how do these translate to novel fermentations? Second, what are the main approaches that are currently being used or proposed to generate novel fermentations? Third, what types of novel ferments can be developed using these techniques, based on potential substrate–microbe combinations that have not been considered? Fourth, what are some potential challenges of making novel ferments? Lastly, how can the use of microbes from traditional ferments be applied in novel contexts, while still respecting the traditional cultures where the microbes were originally deployed and/or cultivated? The aim of this review is to provide some forward-thinking answers to and reflections on these questions. Our focus will be on the microbiology of novel fermentations, but to adequately address the breadth of this topic we will also weave in themes and approaches from other fields to develop an interdisciplinary view of this emerging field.

Our review builds on some excellent recent reviews that have explored specific aspects of translating traditional fermentations into novel formulations[31,34,40]. These past reviews have tended to focus on specific types of novel ferments and individual microbes. As far as we are aware, none of these papers has tried to define and develop a framework for understanding novel fermentations in general. Our goal in this review is to develop such a framework, taking a community-level and cross-system view of traditional-to-novel fermentation transitions that is relevant and accessible to biologists, fermentation enthusiasts, and food producers.

## Microbiome assembly processes that could be used as design principles for novel ferments

For thousands of years, humans have been shaping the ecology and evolution of fermented food microbes and microbial communities through the iterative development of these products. A range of microbes are found in traditional ferments, including yeasts, lactic acid bacteria, acetic acid bacteria, bacilli, and filamentous fungi (also referred to as molds). The diversity of fermented-food microbiomes has been described in detail elsewhere[9,29,41–43] so we will not review that here. Instead, we provide a brief overview of a widely recognized framework[44] for understanding the assembly of ecological communities as it applies to fermented-food microbiomes, to highlight how these processes could help design novel fermentations (for a more detailed exploration of this topic, see Louw *et al.*[7]).

The first ecological process in building a fermented-food microbiome is *dispersal* (Figure 2). When considering dispersal processes in fermentation, it helps to think of fermented-food microbiomes as being made up of different parts (that is, different taxa or functional groups). We can then ask a simple question: *what microbial 'parts' are available to build a fermented-food microbiome?* Fermented-food producers can shape the dispersal of microbes in their ferments by using starter cultures that contain known individual strains or communities of microbes (for example, lactic acid bacteria added to yogurt fermentations) or undefined communities (such as a kombucha culture that contains bacteria and yeasts, often with unknown identities). In some ferments, producers maintain a particular environment to cultivate a collection of desirable microbes that can disperse to the fermented food, such as the caves or other environments used to age cheeses[45,46]. Dispersal also plays an important role in spontaneous fermentations such as fermented vegetables that rely on microbes naturally present in the raw materials for fermentation to proceed[47,48].

A second ecological process that occurs in traditional ferments and is relevant to novel ferments is *selection*. Selection poses another relatively simple microbiome assembly question: *how do the microbial parts that disperse and establish in a ferment interact, both with their environment and with each other?* One of the most important ecological controls in fermentation is how microbial species interact with and are shaped by their environment, or *abiotic selection*. Fermented-food producers create specific environments to favor the growth of

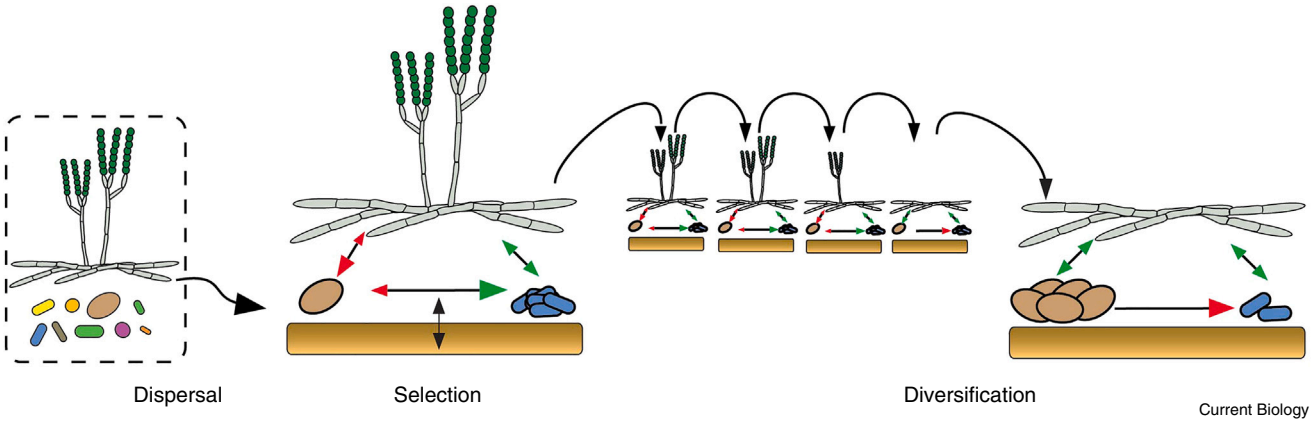


**Figure 2. Ecological and evolutionary processes shaping fermentation-microbiome assembly.**
Three main ecological and evolutionary processes — dispersal, selection, and diversification — can shape the composition and function of fermented-food microbiomes. Arrows with red and green tips indicate different types of biotic interactions between microbes (red = negative interaction, green = positive). The series of arching arrows indicates the process of repeated community assembling in a fermented-food production environment. During this process, diversification of microbial species and communities can occur.

some microbes over others, which subsequently shapes the composition of microbial communities in a ferment. These environmental controls include oxygen availability, pH, salinity, temperature, and other ways to manipulate the environment. Many food producers also indirectly manipulate *biotic selection* in fermentations, where microbe–microbe interactions can affect community composition and function. For example, some strains of microbes used in ferments can inhibit undesirable microbes[49,50] or can alter the morphology or behavior of co-occurring microbes to produce unique flavors and aesthetics[51,52].

A third process that shapes the diversity of traditional ferments is *diversification*. With diversification, we can ask the question: *how do microbial parts within a ferment change over time and space?* Over a range of time scales, fermentation has led to the evolution of food-adapted microbial lineages from 'wild' ancestors, just like dogs were domesticated from wolves[53,54]. As fermented-food producers have grown microbes on food substrates for millions of generations over centuries or millennia, the genomes and phenotypes of fermented-food microbes have diversified into a wide range of metabolisms, appearances, and flavor profiles. A variety of comparative-genomic approaches have described the diversity of domesticated fermented-food microbes and pointed to potential pathways of microbial domestication[54–58]. At shorter timescales, such as within a production year or even across several batches of ferments, microbial genomes and traits may also quickly change. Several different experimental evolution approaches have highlighted the potential for rapid evolution of fermented-food microbes[59–61], and some *in situ* time-course studies are being developed to demonstrate how microbes diversify within fermented-food environments[62].

By varying recipes, raw materials, environmental controls, local microbial communities, and starter cultures, fermented-food producers around the world manipulate the ecological and evolutionary processes described above. Underlying their top-down control through food production are the bottom-up microbiological phenomena that generated the diversity of traditional ferments we have today. The relative importance of different processes can shift the abundance of different types of microbes across traditional ferments. Manipulating each of these processes provides the 'ecological levers' to generate novel ferments.

## Approaches to making novel fermented-food microbiomes

Based on our systematic evaluation of the published literature, as well as considering conversations with food practitioners and chefs, we highlight four major ways that fermented-food producers and scientists have manipulated (or could, but have not yet tried) basic ecological processes to develop novel fermentations: switching substrates, engrafting target species, assembling whole-community chimeras, and generating novel phenotypes (Figure 3).

### *Switching substrates*

The most straightforward approach for making novel fermentations is by taking the microbial community of a traditional ferment and placing it on a novel substrate (raw food material): what we call *switching substrates*. The goal with this approach is to have the traditional microbial community perform some of the normal functions of the traditional ferment (for example, acidify the medium for preservation), while also potentially creating new flavors that are not necessarily found in the traditional ferment (Figure 3). These novel flavors could come from the microbial community utilizing new resources present in the novel substrate, from shifts in physiology and/or metabolism induced by the novel substrate, or by changes in community composition that lead to altered community functions.

Here we can identify different approaches to substrate switching, according to whether the microbes are inoculated — that is, intentionally introduced with the hope that they become part of, if not dominant, in the community — or allowed to spontaneously assemble. Inoculated novel ferments can be created in three main ways: with pure cultures, through backslopping (addition of existing, microbially active ferments to new batches to jump start the process), or by addition of microbially rich ingredients chosen for their desired microbial communities rather than their

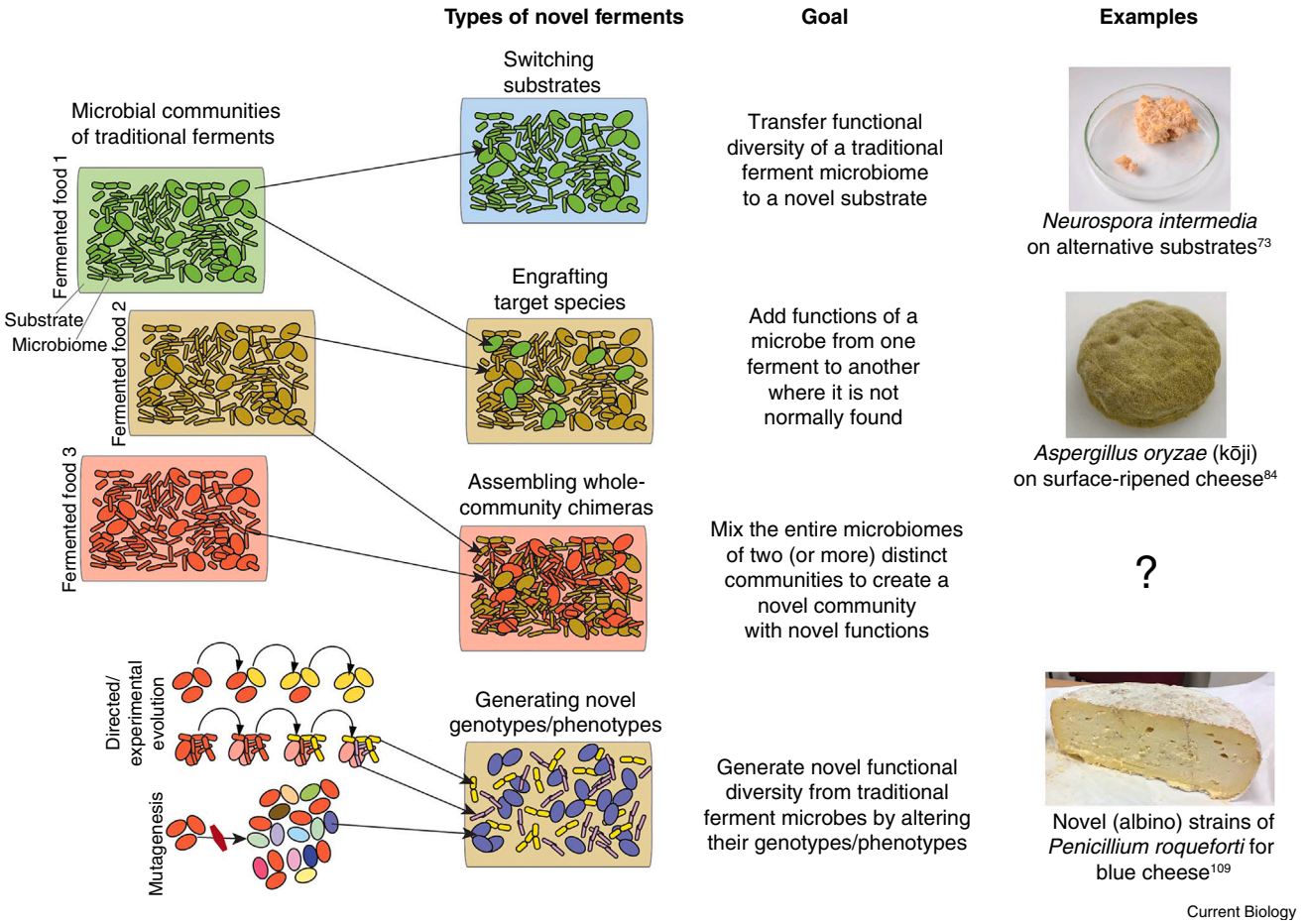


**Figure 3. Four approaches to making novel fermented foods and beverages.**
Microbial cells and communities are simplified for visual clarity, and do not represent the diversity of microbes found in ferments. Switching substrates involves taking the microbial community from one traditional food and using it to ferment novel substrates. Engrafting target species uses the addition of distinct microbial species to ferments where that species is not normally found. Assembling whole-community chimeras mixes two distinct fermented food communities to generate a novel community derived from the two parent communities. Generating novel phenotypes uses experimental evolution or mutagenesis to generate novel genotypes that provide new phenotypes in traditional fermentation microbes. The "?" for whole-community chimeras indicates that we are unaware of documented examples of this approach for novel ferments, though we suspect this happens often in kitchens and food production facilities around the world. *Neurospora* photo by Kåre Knudsen Squindo of Alchemist Restaurant and used with permission. *Aspergillus* photo by Kaory Sato and used with permission. Albino cheese photo by Paul Dyer and used with permission.

substrates or flavors. Examples of novel ferments generated with pure cultures include the use of lactic acid bacteria to make plant cheese, or *Neurospora* fungi grown on nuts to make meat alternatives (discussed further below). Recent uses of backslopping include transferring kombucha to novel teas or other liquids, like herbal infusions, vegetable juices, or even soymilk whey[63–65], or transferring a sourdough starter to a new kind of flour. Microbially rich substrates like fruits and other plants have been used by chefs and home fermenters to initiate novel alcoholic fermentations, as has been traditionally done with some kinds of mead, beer, and wine, or sometimes to create new sourdough starters. Spontaneous novel ferments can be created in two main ways: when the microbes come from novel substrates that are assembled to mimic a traditional process; and when the microbes originate from an ingredient that is spontaneously fermented without an existing product template in mind, which is then developed into a new product based on the outcome. Examples of the former strategy include novel misos, and an example of the latter is a novel endive-root tonic, both of which we discuss further below.

The current pursuit of plant-based substitutions for traditional dairy ferments has created a flurry of activity in this novel fermentation space and offers an illustrative example of substrate switching using inoculation with pure cultures. Numerous studies have explored how microbes from traditional fermentations could be used to create plant-based analogs of dairy products such as yogurts and cheeses[66,67]. Substrates for these ferments include soy, coconut, oats, and many other plant materials. Much of this research and product development has been happening within the food industry, so the identity of the microbial communities in these products is poorly characterized in the literature. Some dairy-derived, lactic acid bacteria, such as *Lactobacillus delbrueckii* subsp. *bulgaricus* and some strains of *Lactococcus lactis*, are likely highly adapted to grow in milk, and may not perform well in plant-based substrates[68,69]. But many of the other, typical dairy fermentation microbes are often

detected in these plant-based products[70]. In a recent study of plant-based cheese analogs, typical cheese bacteria and fungi were detected, including the bacteria *L. lactis* and *Leuconostoc mesenteroides* and the fungi *Geotrichum candidum* and *Penicillium camemberti*; in addition, some atypical bacteria detected may have originated from plant materials[71]. Microbial fermentation is just one aspect of making these novel products. Other ingredients not found in the traditional ferments are often added to create a similar consistency or flavor, all of which would be expected to shape the microbial community in different ways through abiotic selection.

Beyond the widely commercialized plant-based dairy products, many other novel substrate-switched ferments have been emerging. For example, there are recent reports of making sourdough by adding agave bagasse (waste from the production of tequila) to wheat flour[72] and inoculating it with lactic acid bacteria; this experiment revealed similar yeast and lactic acid bacteria dynamics to those found in traditional sourdoughs[72]. Another group recently grew the mold *Neurospora intermedia* from the Indonesian soymilk-residue ferment red oncom on novel substrates such as cashews and pine nuts to make meat alternatives[73]. These substrates may not be part of the food cultures where oncom has been made for many generations, but the fungus can easily grow across many nuts and legumes.

In other types of novel fermentation through substrate switching, a microbial species or community from a traditional fermented food may not be transplanted onto a novel substrate through inoculation. Instead, microbes associated with a novel raw food material (such as lactic acid bacteria that can grow anaerobically, produce organic acids, etc.) may form a novel microbial community spontaneously. Lactic acid bacteria are commonly found living on many plant materials and may contribute to the fermentation of many novel plant ferments[74]. The production of misos at the restaurant Noma in Copenhagen is an excellent example of this approach[75]. Novel substrates such as lupin seeds, fava beans, and regional varieties of lentil and pea were used in a traditional miso recipe. *Aspergillus oryzae*, which is used in conjunction with rice or soybean in traditional miso ferments, was instead inoculated into and grown on pearled barley to make kōji (see below for further discussion of kōji). The kōji was then mixed with the novel substrates to ferment and allowed to develop from whatever microbes were associated with the raw materials and/or from the fermentation environment. Although the kōji shaped the resulting bacterial and fungal community via abiotic selection through the liberated sugars, amino acids, and enzymes it provided, the salt and anoxic conditions in the developing misos select against the *A. oryzae*, instead favoring the growth of more salt-resistant and anaerobic taxa. Many typical miso microbes were detected in the finished novel misos, including *A. oryzae* and various genera of lactic acid bacteria. In addition, a rarer bacterial genus, *Exiguobacterium*, not before found in miso, was also detected in one novel miso, and seemed to be related to the treatment that the substrate had undergone before fermentation. This is another illustration of abiotic selection, and specifically how different substrates and culinary techniques can select for different microbial taxa and communities. Other studies have also explored substrate switching in miso, for example using quark (a type of fresh dairy cheese) instead of soybeans to make something the authors called 'dairy miso'[33].

Studies producing a cashew ferment and an endive-root ferment also found some typical lactic acid bacterial communities on these atypical substrates[72,76]. When novel substrates are not inoculated with an established set of cultures from a traditional ferment, the dispersal of microbes and modes of selection rely on the autochthonous microbes — that is, those microbes naturally associated with raw materials or in production environments. These organisms will play a critical role in determining fermentation success (acidification, elimination of spoilage microbes, etc.)[47]. The endive-root ferment is a good example of making a spontaneous ferment without an existing product in mind. In this case, the endive root was fermented in different batches, some with pure cultures of yeasts and bacteria, and some spontaneously, under different conditions. The spontaneous one exhibited distinct citrus aromas and, as a result, a novel tonic water was developed based on the fermented root's similarity to the profile of traditional tonic water.

One of the major challenges with the substrate switching approach is determining whether traditional fermentation microbes and microbial communities have the ability to grow and assemble on the novel substrate. For example, the microbial cultures used to produce dairy ferments for many decades have been selected or domesticated to perform well on animal milk. These microbes may not have the full capacity to degrade the plant substrates present in these novel ferments, and plant substrates may also have very different nutritional profiles to support microbial growth. Carbohydrates control the fermentation dynamics of lactic acid bacteria and different taxa have evolved to specialize in the fermentation of different carbohydrates[77]. The types of carbohydrates available for fermentation vary widely from cow's milk (only lactose) to plant milks (a mix of sucrose, fructose, glucose, and more complex carbohydrates such as starch, raffinose and stachyose)[78].

Even if the microbes from the traditional ferment can grow on the novel substrate, there may be substantial shifts in community composition due to abiotic selection and/or shifts in biotic interactions. These changes in microbial community composition could lead to major shifts in fermentation function. We are not aware of studies that have carefully compared the microbial community composition and function of traditional and novel ferments. Indeed, a robust framework to conceptualize these different fermentations is probably needed to design and conduct such empirical studies. This is an important area of research to ensure the success of novel substrate-switched fermentations and to understand the microbial ecology of these new foods.

### *Engrafting target species*

A second approach to novel fermentation is to engraft a target species found in one traditional ferment into another ferment where the species is not usually found. The resulting novel ferment will have the functional capabilities of the traditional ferment, but also should have novel functions due to the addition of the engrafted species (Figure 3). This approach is similar to the engraftment approaches used for probiotics in the human microbiome[79]. The difference between target-species engraftment and substrate switching is that in the latter, one or multiple species are added to a substrate to which they are not typically associated, whereas in the former, a species not normally

present in a traditional ferment is added to a community grown on its normal substrate. In other words, substrate switching holds microbes constant and varies substrate, while engraftment holds substrate constant and varies microbes through addition of species and/or strains.

Some of the most widely engrafted fermented-food microbes in novel fermentations may be the kōji molds *A. oryzae* and *Aspergillus sojae*. Kōji molds are traditionally used in Asian fermented foods such as miso, soy sauce, and sake[80]. They are grown on rice, soybeans, barley, and wheat and produce a suite of enzymes that then play roles in downstream fermentation processes. For example, in sake production, kōji molds liberate sugars and other nutrients from rice through enzymatic activities. These nutrients are then used by yeasts for the second phase of alcoholic fermentation[81]. One striking engraftment of *A. oryzae* in a novel ferment is as a surface-ripening mold in cheese production. In camembert and other mold-ripened cheeses, *P. camemberti* and other white molds are often used to grow the characteristic white and fuzzy rind[82]. The fungus breaks down the cheese through enzymatic activity and releases various compounds that people from cheese-eating cultures perceive as typical ripened cheese flavors including nutty and mushroom-like flavors[83]. Microbiologists in Japan have been working on swapping typical cheese fungi like *P. camemberti* for *A. oryzae* to make kōji versions of surface-ripened cheeses[84–87] (Figure 3). These fungi can fill a similar niche as the *Penicillium* molds, and based on chemical profiling can produce unique potential flavor molecules that may not be found in traditional *Penicillium* surface-ripened cheeses[84]. Other examples of species engraftments include the fungus *Monascus purpureus* (red kōji) to make surface-ripened cheese[88] and an internal mold-ripened cheese (similar to blue cheese)[89].

One challenge with the engraftment approach is the potential for biotic interactions between the traditional fermentation microbes and the engrafted species to limit the growth and functional potential of the latter. Biotic interactions play important roles in determining the structure and functions of many fermented-food communities[90–93]. If antagonistic interactions limit the establishment of novel species, the resulting ferment will simply be the traditional ferment with a failed engraftment. For example, bacteriophages can strongly inhibit the growth of lactic acid bacteria in some fermentations[94], and the presence of a bacteriophage in the traditional fermentation may severely constrain the success of an engrafted lactic acid bacteria species. The timing of microbial inoculation, known as priority effects in ecology, may help overcome some of these issues by introducing desired engraftment species early in the process[95,96]. Varying the microbial dispersal rate by increasing the number of cells of the engrafted species may also lead to higher establishment rates[97]. Most previous studies of microbial interactions in fermented foods have generally only considered microbial interactions *within* ferment types. To better understand the constraints on engraftment to create novel ferments, future studies should also explore microbe–microbe interactions across fermentations and across different substrates.

### Assembling whole-community chimeras (community coalescence)

What if, instead of just engrafting a single target species into a ferment, two whole communities from fermented foods or other raw materials are mixed together to create a novel community? This approach is more broadly known as *community coalescence* in microbial ecology[98]. The goal of this approach would be to mix the species and functions of two established microbial communities together to yield a completely novel combination of microbes and functions (Figure 3). The two communities could be mixed together and then added to one or both of the two original ferment substrates. For example, a sourdough microbial community could be mixed with a miso microbial community and then used to make either sourdough bread or a miso. Alternatively, two distinct communities could be mixed together and then introduced to a novel substrate. For example, a sourdough microbial community and a sauerkraut microbial community could be combined and inoculated into tea to ferment a new kombucha, or the sourdough–miso chimera above could be used to inoculate a jiang, a fermented savory paste from China (and likely historical precursor to miso). Fermented foods often share broad functional groups of microbes (like the lactic acid bacteria, acetic acid bacteria, yeasts, etc.) in addition to having measurable and alterable ecosystem functions (such as acidification and flavor production), which make them well suited systems for this approach to novel fermented-food development.

The microbial outcomes of community coalescence can be understood within an ecological framework that considers both the proportion of microbes that persist from each initial ferment after mixing and also their interactions (Figure 4)[99]. The resultant community is termed more *symmetric* if the two initial communities are present in similar abundances post-mixing and more *asymmetric* if only one of the initial communities is abundant after mixing. Interactions in coalesced microbiomes can be more *modular*, where interactions are preserved among species from the same initial communities, or more *chimeric*, where there is a greater number of novel interactions that have developed between the two initial communities.

The symmetric–asymmetric and modular–chimeric axes for classifying community coalescence outcomes are continua. Outcome communities that are not easily categorized (for example an outcome community with about 75% abundance of one parental community and 25% of the other) exist in between. In designing novel ferments, the desired placement on both the symmetric–asymmetric and modular–chimeric axes will depend on the target traits of the novel ferment. Physically achieving the desired placement may involve modifying mixing ratios and mixing frequency of input communities, spatial positioning of communities during mixing, as well as the communities' abiotic and biotic adaptations to the environment and each other.

We are unaware of studies that have documented what happens when two ferment microbiomes are mixed, but theory and examples from outside of food science suggest a few potential outcomes. For example, *Clostridium difficile* infections in the human gut are treated by coalescing the patient's resident microbiota with a donor's gut microbiota with the aim of displacing the resident gut microbiome (a therapy referred to as a fecal microbiota transplant). In this example, a successful outcome is both asymmetrical and modular, whereby the donor microbiome displaces the resident[100]. In other studies, microbiome mixing has resulted in selection for rare taxa[101], and the co-selection of dominant taxa and their syntrophic partners[102]. Both

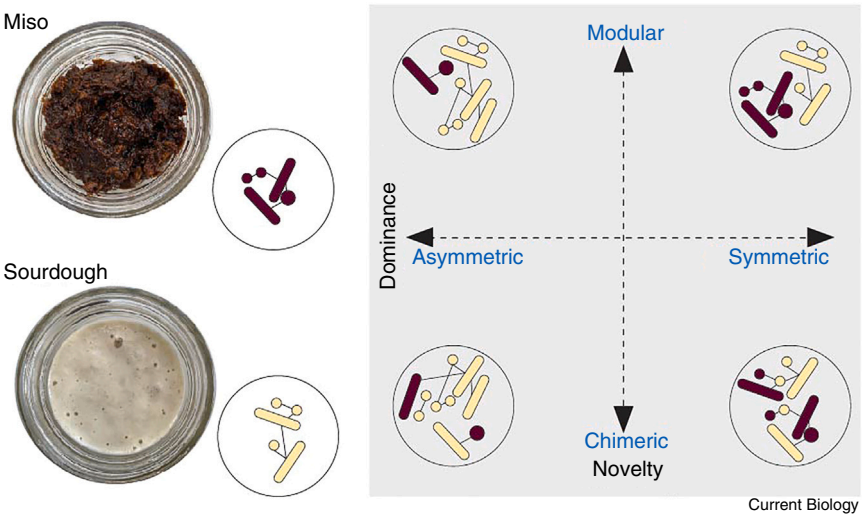


**Figure 4. A community coalescence framework for generating chimeric fermented-food communities.**
Distinct microbial communities from traditional ferments can be mixed together in different ways to yield novel community compositions and functions. Without any published fermented-food community coalescence examples, we use miso and sourdough as a hypothetical example. Depending on mixing ratios and how novel interactions develop in mixed communities, the composition and functioning of the mixed communities can range in dominance and novelty. The dominance–novelty framework is adapted from Castledine *et al.*[99].

processes result in novel microbiomes that are likely to have distinct functional traits. These examples suggest it is possible that community coalescence could be used as a tool to selectively increase the abundance of desired rare taxa in fermented foods.

There are many different ways that fermentation practices could promote the coalescence of two or more fermented-food communities. Many sourdough bakers report adding fruits to their starter to introduce microbes that contribute to the fermentation. Cheesemakers sometimes wash their cheeses with microbial communities from alcoholic fermentations. Beer brewers also make 'wild' ales, where their wort is intentionally exposed to the air to facilitate inoculation by wild yeasts and other microbes that comprise the aerobiome. These examples suggest the value of community coalescence theory not only as a framework for biological study, but also to inform fermentation practice.

The above examples of community coalescence in fermentation only consider the mixing of two distinct communities. But species pools outside of the fermented-food space may also serve as sources for development of de novo fermentation microbiomes. For example, insects can be a rich source of lactic acid bacteria and/or yeasts that may be able to coalesce with established fermented-food communities[103,104]. Other environmental microbiomes such as seawater or plant leaves may also be a source of microbes with the ability to ferment and form novel microbial communities[105]. This second kind of whole-community chimera based on non-fermented sources of microbes is still characterized by the intention to use these sources for their microbial communities. This is what distinguishes the chimera approach from simply the passive contributions of microbes from the air, equipment, ingredients and fermenters in, for example, spontaneous approaches to substrate switching.

Though we have proposed a variety of potential avenues to explore novel fermented-food development through community coalescence, this approach, too, comes with challenges. Only recently has community coalescence theory been studied in laboratories for practical use across ecological disciplines and industries. As an inherent part of this approach, one or more communities of microbes enter a new environment, and certain members may ultimately be unable to adapt to the biotic and or abiotic environments, leading to loss of taxa in the outcome[101,106]. Although such an outcome could be potentially useful in some contexts, coalesced communities lacking certain taxa may not be what the producer or scientist intended to achieve in the novel ferment. Biotic and abiotic growth constraints can thus present barriers for development. We hypothesize that some growth barriers could be circumvented through adjusting the physical parameters of mixing (for example, mixing ratio or frequency of mixing) and/or through experimental evolution in the conditions preventing colonization; that is, adaptation in response to, for example, an antagonistic microbe or nutrient-limited substrate. However, extensive experimental work is needed to support or disprove our hypotheses. Another challenge that arises is the tracking and management of similar species of microbes coming from both parental communities. Sequencing-based approaches could potentially be used to track strain level variation, but we encourage further investigation into coalescence events and outcomes on the strain level.

Again, as we have not come across any works studying the functional effects of coalescence in fermented foods, we can only speculate as to what the various degrees of coalescence outcomes might mean for the properties of fermented foods. We suspect that no one dominance–novelty pairing (e.g. symmetric–chimeric) will be the consistent solution for development, but rather the ideal microbial consortium to produce a consumable and marketable novel fermented food will be highly dependent on the input community's structure, evolutionary history, and physiology as well as the compositions of substrates involved. As community coalescences are studied and documented across systems (in fermented foods and beyond), predictive frameworks for community outcomes may emerge, further informing the rational design of novel fermented foods.

### *Generating novel genotypes and phenotypes*

A fourth way to dramatically alter the microbial properties of a traditional ferment and translate those properties to a novel ferment is through generating novel genotypes and phenotypes of the microbes or microbial communities used in fermentation (Figure 3). The use of genetic engineering in foods remains a complex and hotly debated issue globally, with different social

attitudes and regulatory approaches in different countries; however, there are several other tools and approaches that can be used to modify the genotypes (and subsequent phenotypes) of fermented-food microbes.

One approach is to guide the diversification processes described above to generate novel phenotypes in the lab. Experimentally evolving microbes in the lab to have new properties not found in traditional ferments provides potentially new flavors and other functions. Although there are numerous examples in which researchers have evolved fermented-food microbes in the lab and observed novel phenotypes that could alter fermentation qualities[59–61], we are not aware of documented cases of these potentially novel strains then being used to make a new fermented food. This is an exciting direction for future research and development.

In addition to evolving novel traits on traditional substrates, experimental evolution could be used to adapt microbes from traditional ferments to grow on novel substrates. In one recent study, authors evolved a dairy strain of *L. lactis* in oat milk and were able to produce an evolved strain that had higher production of a butter aroma in the novel substrate[107]. There may be some important challenges that emerge using this directed evolution approach. For example, traits that ancestral strains have before domestication may be lost as they adapt to a novel substrate. A hypothetical example can help illustrate this point. Getting miso yeasts to grow on camembert cheese would provide an exciting opportunity to blend flavors from two traditional ferments. But the miso yeasts, which have adapted to utilize mostly plant substrates, may shift their metabolism dramatically as they adapt to grow on cheese. The yeast may also make new byproducts of metabolism after cheese adaptation that could be deleterious to human health. Future studies of cross-substrate experimental evolution of fermented-food microbes will help pinpoint the metabolic and phenotypic tradeoffs that can occur during adaptation to novel substrates.

Another approach to generating novel phenotypes of traditional fermented-food microbes is through random mutagenesis. Through the application of some DNA damaging treatment, such as ultraviolet light or chemical mutagenesis, random mutations across the genome can create strains with novel and desirable properties. Despite being a direct modification of the genome (albeit random and untargeted), organisms created through random mutagenesis may not be considered 'genetically modified' by some regulatory bodies[108], and can therefore be used in fermented foods where genetically modified organisms are not typically accepted. An excellent example using this approach comes from the blue mold *Penicillium roqueforti* used to make blue cheese. Fungal biologists in the United Kingdom recently identified mutants of *P. roqueforti* created through ultraviolet mutagenesis that had altered pigment profiles, including a white (albino) mutant[109]. When used for production of blue cheese, these novel strains created a 'blue cheese' without the characteristic blue veins (Figure 3). Whether consumers would want to eat a blue cheese that has white veins is an interesting question for future research. Either way, this proof of principle provides one way forward for developing novel genetic variants of traditional fermentation microbes that might lead to novel fermented foods. Ultraviolet mutagenesis could also be used on whole microbial communities instead of just single species, creating a huge range of communities with potentially useful genetic novelty.

Regardless of the tool that is used, it is important that the novel microbial phenotypes that are generated are stable and do not further evolve to alter the trait of interest. This means that laboratory and *in situ* food testing will be required to clearly identify the genetic mechanism(s) underlying the novel traits and to ensure that unintended genomic or phenotypic changes that can affect food safety or quality have not occurred.

With these four approaches in mind — substrate switching, target species engraftment, whole-community chimeras, and generation of novel genotypes and phenotypes — there are some important caveats to note. First, these four distinct processes are not mutually exclusive. For example, one could create a novel phenotype of a traditional fermentation microbe (*P. roqueforti* for example) and then grow it on a novel substrate (almond milk cheese, for example). One such documented example exists, in which a strain of *L. lactis* was experimentally evolved to produce more butter aroma, and then introduced to plant-based milks[107]. Second, we consider the processes described above as distinct from designing custom microbiomes for a traditional ferment using species and strains already found in that type of ferment. For example, in many fermented foods, specific starter cultures can be and already are mixed in a highly controlled manner to create unique community compositions to attempt to alter the flavor profile or other functions of the food[110]. But these approaches are only creating specific combinations of microbes that are already found within the diversity of microbes within a specific ferment. They are not creating novel functional properties that are found outside of the potential of the traditional ferment. With these qualifications, we see great potential in exploring and combining these different approaches to novel-fermentation microbiology.

## What are the gaps of 'fermentation space' that could be filled with novel fermentations?

Despite the enormous diversity of existing fermented foods and beverages, there are likely still novel fermented foods yet to be developed. Throughout history, happy accidents followed by human tinkering and further microbial surprises have given us the spectrum of fermented foods we have today. Humans developed fermented foods and beverages in different parts of the world based on the availability of food substrates and out of a desire to preserve these foods for longer shelf-life, enhanced nutrition, more desirable textures, and enjoyable flavors. Yet because the foods that could develop were constrained by locally available substrates, microbes, and environmental conditions, it is likely that new combinations are waiting to be discovered. Is it possible that some novel microbe and substrate combinations have not come together simply because they have not yet happened to meet? What might these combinations be?

We can begin to systematically explore these new possibilities by mapping out the current 'fermentation space' of foods and beverages. By fermentation space we mean the set of all substrate, microbial community, and recipe/process combinations that yield viable fermentations, both actual and potential. This space should organize foods based on the substrate and microbial community similarities and should also highlight gaps where novel ferments could be developed by the various approaches

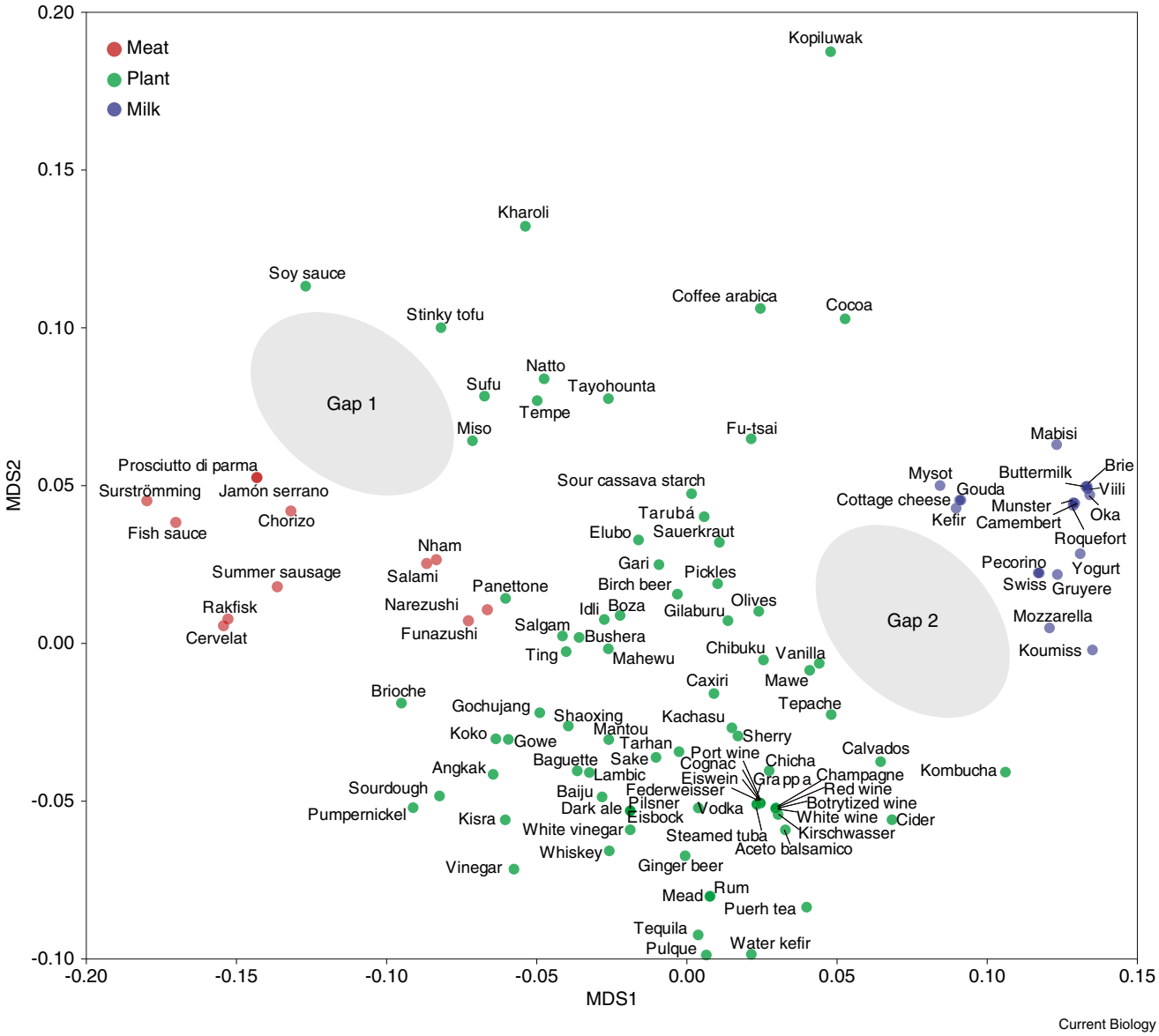


**Figure 5. Mapping 'fermentation space' to identify potential gaps for novel ferments.**
Using substrate and fermentation-organism data from Gänzle *et al.*'s periodic table of fermented foods[31,41], we used non-metric multidimensional scaling (NMDS) to map traditional fermented foods. We made a presence/absence matrix (Data S1 in Supplemental information) and coded it with 1 or 0 for each of three types of data: broad substrate categories (pulses, roots and tubers, seeds, fruit, leaves/stem/bark, plant-derived sugars (honey, agave, sugarcane), grain, meat, or milk), the main raw food ingredients (too many to list — see Data S1), and the dominant microbes that were noted in the periodic table (too many to list — see Data S1). We then used a Sorensen's dissimilarity matrix as the input for the NMDS. This analysis was conducted using Past4. Fermented foods with origins listed as 'novel' (five products) and fermented foods lacking data on fermentation organism species (three products) were excluded. This is a qualitative and preliminary exploration of fermentation space. We acknowledge that many important fermented foods are missing from this dataset (see text for a discussion of other caveats and limitations).

described above. To make a first estimate of the structure of fermentation space, we used Gänzle *et al.*'s 'periodic table' of fermented foods as a data source[31,41]. We used non-metric multidimensional scaling (NMDS) to map the multivariate space filled by current fermented foods based on their substrates and typical microbial membership.

From this qualitative approach, some interesting patterns emerge (Figure 5). As an indicator that this approach is effective and useful, we see clear structure in the NMDS plot based on the major types of substrates used in fermentation. Dairy ferments cluster together, meat and fish ferments cluster together, and plant ferments are scattered in between the two. This pattern makes sense given that milks have lactose as a sugar source, plants have a variety of sugars for fermentation, and meats typically have low carbohydrates. This variation drives unique microbial communities to form based on the resources available. This pattern has also been observed using a more quantitative analysis of fermented-food microbiomes[111].

Another important outcome of this activity is the appearance of major gaps in fermentation space. These spaces suggest rich new territories where we can begin to imagine the development of novel ferments. For example, between the dairy cluster and the vegetable ferments (on the side with lactic and alcoholic ferments) there is a considerable space (Gap 2). Are there combinations of microbes and substrates that could fill this space? Another interesting gap exists between the meat ferments and the pulse/bean ferments (Gap 1). Could some of the microbes typically found in salami or other fermented meats be used to create a novel bean ferment?

Our goal with this exercise is to consider where and how novel ferments could fill in the existing global diversity of fermented foods. We acknowledge that there are many caveats and limitations of this relatively crude and qualitative approach (as Michael Gänzle has already pointed out[41]). For example, the dataset we used only includes 'typical' microbes within each ferment, even though we know from many papers (including our own) that there is considerable variation in community structure and function within any ferment[112–115]. We also acknowledge that this dataset does not include all fermented foods made in all parts of the world, and that such a dataset would almost certainly suggest the existence of many more gaps in fermentation space waiting to be explored.

The results of this exploration of fermentation-space can only be as useful as the data used to map the space, as the structure of the space emerges from the data. Yet rather than a disqualification of the method itself, we see this limitation as an invitation to create better, more inclusive datasets on the global diversity of fermented foods and beverages, including their substrates, microbes, methods, and cultural contexts. Further directions of research on fermentation space might also involve machine learning to predict novel substrate–microbe combinations.

## Challenges, opportunities, and sociocultural dimensions of novel fermentations

Hopefully we have convinced you that the future of fermented foods is exciting and filled with opportunity. We can build on past food traditions, combining them with each other and with modern microbiological approaches to potentially create entirely new foods that provide consumers with new culinary and cultural experiences. We have outlined several approaches to making novel ferments and highlighted gaps that could be filled with these approaches. Despite these possibilities, we acknowledge that there may also be some broad challenges as food producers, chefs, and scientists begin to tinker with established ferments that have developed over many years of fine tuning.

As microbes are moved to novel substrates or as they interact with other microbes in new ways, there is potential for them to make undesirable metabolites. Despite the safe use of many existing microbes in fermented foods, we have a limited understanding of the vast trove of metabolites that they produce. Chemicals with preservation or potential health-promoting benefits have been well-characterized[116], but this is likely just the tip of the metabolomic iceberg. For example, there is a huge suite of potential metabolites made by filamentous fungi that have not been systematically characterized in most fungal ferments[52,117]. Some food-associated *Penicillium* or *Aspergillus* species, for example, have the potential to make mycotoxins depending on the environmental conditions[118]. Future studies should explore the metabolite profiles of novel ferments and identify if there are safety considerations that emerge from new microbial communities or microbe–substrate combinations.

Given the potentially unrecognizable or striking aesthetics and functions of novel ferments, producers of novel ferments may also face some regulatory hurdles. Most food regulations are based on traditional foods that have existed and been consumed for extensive periods of time[119]. Regulators may be unsure of how to inspect or understand the critical control points for a food that does not fit within the bounds of their expectations or past experiences.

There are also potential social and cultural issues that food producers and microbiologists should consider as they work to develop novel ferments. If we are taking microbes from a traditional ferment that has value for a particular culture and using them in a novel ferment, how do we make sure we respect the culture that developed the traditional ferment? Are there issues of appropriation? Who 'owns' the microbes in fermented foods and the traditional processes for working with them? Could local microbial communities and fermentation processes be co-opted without compensation to the communities that have maintained these practices for many generations? And are there more proactive, creative, participatory, and reciprocal ways that we as scientists can offer something back to these cultures and communities beyond due crediting, doing our homework, and basic respect and sensitivity?

A related and long-standing issue in fermented-food microbiology is the often-limited access to the microbiological techniques, knowledge, and resources to learn about fermented-food microbiomes. Some work in participatory microbiology has sought to address this issue by bringing non-expert participants into the process of doing science[120,121]. We hazard that even more work can be done in this direction, with benefits for both science and society. For example, many fermented foods, traditional and novel, are made by small-scale practitioners or in local communities where access to modern microbiological techniques may be limited. These practitioners often hold profound knowledge of fermentation craft and can offer unique perspectives and knowledge about the most interesting aspects of their products and how to study them. As we innovate to create novel fermentations by combining local fermentation traditions and microbes with rational design principles, we anticipate that the most interesting, successful, and delicious results will happen whenever we find ways to connect, share, and collaborate with fermentation practitioners. By opening up access to our sequencing technologies and our microbiome knowledge and combining it with the creativity and skill of fermentation practitioners, who knows what new ideas for the future of fermented foods might emerge.

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## DECLARATION OF INTERESTS

The authors declare no competing interests.

## SUPPLEMENTAL INFORMATION

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