frontiers in Sustainable Food Systems

REVIEW
published: 28 June 2021
doi: 10.3389/fsufs.2021.678045

Linking the Diversity of Yeasts Inherent in Starter Cultures to Quorum Sensing Mechanism in Ethnic Fermented Alcoholic Beverages of Northeast India

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Specialty section:
This article was submitted to Sustainable Food Processing, a section of the journal Frontiers in Sustainable Food Systems

Received: *08 March 2021*
Accepted: *24 May 2021*
Published: *28 June 2021*

Citation:
Nath BJ, Parasar DP and Sarma HK (2021) Linking the Diversity of Yeasts Inherent in Starter Cultures to Quorum Sensing Mechanism in Ethnic Fermented Alcoholic Beverages of Northeast India. Front. Sustain. Food Syst. 5:678045. doi: 10.3389/fsufs.2021.678045

In this review, the relevance of diversity of yeasts and their interactive association in household ethnic fermentation are discussed. The longstanding traditional household fermentation practice involves preparation of fermented product such as alcoholic beverages from various indigenous agricultural products with the help of microorganisms cultivated from local environment and perpetuated for hundreds of years through generations indoctrinating an indigenous knowledge system. Northeast India is known for its rich physiographic and geo-demographic diversity and is home to several ethnicities who follow unique practices of household traditional fermentation. The diversity of yeasts present within the microbial inoculum used for fermentation by different indigenous communities has been keenly studied and reported to be unique in spite of their common source for starter substrates. *Saccharomyces* yeasts are primarily involved in alcoholic fermentation, whereas non-*Saccharomyces* yeasts, which are reportedly confined to a particular geographical region, have been reported to contribute toward the final outcome of fermentation produce. During fermentation, interaction among these large microbial communities and their resulting physiological expression within the fermentation micro-environment is believed to affect the final quality of the product. Mechanism of quorum sensing plays an important role in these interactions in order to maintain proportionality of different yeast populations wherein the quorum sensing molecules not only regulate population density but also effectively aid in enhancement of alcoholic fermentation. Additionally, various secondary metabolites, which are secreted as a result of inter-species interactions, have been found to affect the quality of beverages produced. This review concludes that diverse species of yeasts and their interaction within the fermentation micro-environment influence the sustainability and productivity of household ethnic fermentation.

Keywords: ethnic fermentation, yeast, diversity, quorum sensing, alcoholic beverage

INTRODUCTION

Yeasts are single-celled eukaryotic microorganisms known to be the key players in the age-old practice of alcoholic fermentation for thousands of years. The practice of fermentation involving yeasts is one of the oldest human technologies dating back to the Neolithic period when spontaneous fermentation was carried out from plant sources such as grape must (Compagno et al., 2014). Due to their ability to ferment sugary substances into ethanol, yeasts are incorporated during formulation of inoculum or starter materials, which are used for preparation of fermented beverages in household fermentation worldwide (Hesseltine et al., 1988). This ancient practice of household ethnic fermentation in Southeast Asia involving yeasts is believed to have been originated from China, which spread across most of the neighboring countries with time (Limtong et al., 2002). Apart from the Asiatic region, the tradition of fermented product preparation is widespread among most of the indigenous communities belonging to different regions all over the world (Kabak and Dobson, 2011). These longstanding systems of alcoholic beverage preparation from various agricultural products with the aid of locally perpetuated fermentative agents have been in practice for generations indoctrinating indigenous knowledge system (Parasar et al., 2017; Nath et al., 2020a).

Methods of preparation of starter culture cakes among various communities is almost similar with minor variations observed in the methods followed and plant condiments added (Anupama et al., 2018). Household fermentation is recognized to be a popular practice among home brewers of indigenous communities in the entire Southeast Asia (Tsuyoshi et al., 2005) that reflect the ethnic heritage of existing communities, and northeast India is not an exception. Interestingly, in spite of a common source of ancestry of the indigenous communities of northeast India and usage of similar methods for ethnic fermentation, the diversity of yeasts perpetuated through those natural and spontaneous fermentation processes and maintained by the communities have been found to be unique (Buragohain et al., 2013; Tiwari et al., 2014; Parasar et al., 2017). Furthermore, since each community produces fermented beverage of distinct quality, the role of these genotypically diversified yeasts in both intra- and intercommunication is a question to be inquired, and their precise role in attributing quality characteristics in the final products of the fermented beverages needs to be understood. In addition to the interaction among yeasts in a consortia, the role of added plant condiments during starter material preparation may also play an important role in generating quality attributes as well as resuscitation of microbes within the starter cake/material propagated generation after generation (Nath et al., 2019).

In a fermentative micro-environment, intra- and interspecies interactions occur between co-existing yeasts and other microbes (Fleet, 2003) where the final quality of fermented beverage is believed to be affected due to the interaction among these large microbial communities and their resulting physiological expression (Ciani et al., 2016). Apart from the formation of ethanol, certain yeast species produce secondary metabolites such as fatty acids and killer toxins that act as growth inhibitors for other yeast species that eventually kill vulnerable yeasts (Pérez-Nevado et al., 2006). Direct physical interaction among different yeasts or with other microbes was also believed to be the limiting factor for the growth of certain non-*Saccharomyces* yeasts that spawn and proliferate during initial stages of fermentation (Nissen and Arneborg, 2003; Nissen et al., 2003; Renault et al., 2013). Noticeably, death of desirable yeast cells is triggered when unwanted yeast population reaches high cell density threshold during progressive fermentation (Nissen and Arneborg, 2003; Pérez-Nevado et al., 2006). These findings therefore suggest the importance of yeast interactions during both spontaneous and induced fermentation.

Apart from the above, it has been confirmed that quorum sensing molecules (QSMs) expressed by yeasts also play a key role in the expression of various population density-dependent characteristics that can affect the quality of a fermented product. QSMs are hormone-like molecules that accumulate in the external environment in proportionality to cell density population (Sprague and Winans, 2006) and either activates or represses certain genes when a particular threshold level of the molecules is obtained (Fuqua et al., 1994). The two fungal QSMs, viz., tryptophol and phenylethyl alcohol, were first recognized in *Candida albicans* (Lingappa et al., 1969) followed by the discovery of three additional QSMs, viz., farnesol, tyrosol, and farnesoic acid (Hornby et al., 2001; Oh et al., 2001; Chen et al., 2004; Hornby and Nickerson, 2004). These QSMs have further been examined by several researchers and their multifarious role in controlling morphogenic transition of yeast to filamentous form and vice versa has been established in the preceding years. Moreover, the QSM tyrosol has been reported to induce the upregulation of genes associated with DNA replication (Chen et al., 2004), thereby implying the probable enhancing effect of the molecule on cellular growth. This assumption was found to be true as was noted in our recent investigation where tyrosol significantly increased the population density of *Candida tropicalis*, *Wickerhamomyces anomalus*, and *Saccharomyces cerevisiae* (Nath et al., 2020b) during alcoholic fermentation.

Due to the involvement of diverse yeast species in the production of fermented goods, it is necessary to explore the link between their interactions and product outcome. There has been extensive research on determining the diversity of yeast conglomerates in fermentative cakes from northeast India, but unfortunately no clear explanation of yeast–yeast interferences or intercommunication within these starter cakes as well as fermented products could be inferred until the preparation of this report. As mentioned earlier, each indigenous community of northeast India produces fermented beverages with distinct quality attributed by specific yeast lineages tamed and cultivated by the individuals of these communities who exclusively preserve and perpetuate starter materials that are unique to each community type. It therefore becomes important to document the diversity of yeasts persisting within the starter materials, and it is pertinent that subtle differences in genotypes and phenotypes of diverse yeasts and the subsequent interactions among them are key factors that determine the oenological properties of final output in fermented beverages (Granchi et al., 2002). Keeping in view about the importance of cell–cell interactions during fermentations, we extrapolate that the diversity of yeast species in starter cultures of northeast India should be explored and the inherent oenological properties be evaluated to understand the complexity of traits unique to the region. The volatile profiles of higher alcohols, esters, carbonyls, and sulfur compounds have not been studied and the prospects of delineating yeasts that produce secondary alcohols, acetic acid, acetaldehyde, ethyl acetate, acetoin, and glycerol have never been accessed (Steward, 2017). We assume that the quality traits need appreciation so that the prospective yeasts can be commercialized for large-scale production of chemicals and metabolites. Earlier, we had examined the factors that determine the persistence of yeast communities within the fermentation micro-environment but a larger view of the entire repertoire of yeasts from the region is still lacking. Moreover, the role of QSMs during fermentation does interfere and alter the quality of final products (Nath et al., 2020b), and henceforth, the array of QSMs expressed by the native yeasts of the region has to be deciphered to validate unique combination of yeasts with profound benefits.

BIBLIOMETRIC INFORMATION

The importance of traditional and sustainable food has received tremendous attention in recent years due to several reasons including their benefits to health, environment friendly methods of preparation, natural origin, absence of toxic effects, and prospects of commercialization. The exploration of indigenous knowledge systems inherent in cultures and traditions practiced through ages have helped in the conservation of innumerable diversity of both conventional and non-conventional food that have not been fully explored in the context of the Indian subcontinent. India is home to 550 ethnic communities (Schedule Tribes in India, jagranjosh.com) with a major proportion residing in the northeastern part of the country. Traditional brewing and household preparation of fermented food and drinks has been a major source of activity inculcated in their customs and traditions. The diversity of yeasts and other microbes inherent in these traditional brewing methods have been studied only recently, and we could find literature from 1994 onwards. In this review, all bibliographic literature available in PubMed, Web of Science, and Scopus indexed journals were consulted (1994–2020). A good number of research publications on the diversity and identity of yeasts during fermentation have been published since 1990 to date (PubMed 1,008 papers). To get a clear view of the extent of work conducted on the subject, we searched various scientific engines and found that the approximate number of papers published for the last 10 years stands at 1,432, which were retrieved from PubMed using various keywords/phrases [(1) Yeasts in traditional fermentation, (2) Traditional fermentation from northeast India, (3) Yeasts from northeast India, (4) Quorum sensing in yeasts, (5) Quorum sensing in traditional fermented yeasts, (6) Quorum sensing of *Saccharomyces* and non-*Saccharomyces* yeasts, (7) Quorum sensing in non-conventional yeasts, etc.], which reflected that the extent of research is not very pronounced. The search query found that the maximum number of documents (1,008) were related to the general term "yeasts in traditional fermentation" where a lot of literature on a global scale was available. This was followed by the term "quorum sensing in yeasts" where an appreciable number of publications (382) could be retrieved and 80% of the publications were related to *Candida* and *Cryptococcus* spp. that cause fungal infections in human. We could retrieve only nine publications related to the term "quorum sensing of *Saccharomyces* and non-*Saccharomyces* yeasts," which suggests that the area remains unexplored and very little attention is drawn toward quorum sensing among yeasts and their subsequent impact on fermentation/traditional fermentation, which therefore remains as a major gap. Bibliometric analysis enabled us to understand the global context of the subject, themes that have not been addressed yet and also the major drawbacks of the extent of research impact (Ashraf et al., 2021). The data, when analyzed, showed that the available knowledge on the subject is still limited and the milestones achieved are yet to be acknowledged, which has hindered the prospects of commercialization of ethnic foods on a scientific basis.

DIVERSITY OF YEASTS IN STARTER CULTURES OF NORTHEAST INDIA

The northeastern part of India includes a biogeographic realm with a characteristic biome and encompasses unique features in terms of rich biodiversity and multiple ethnicities of its people. The indigenous communities follow their own practice of household traditional fermentation. Each community harbors unique distribution of yeast species, which have been perpetuated throughout generations (Buragohain et al., 2013; Tiwari et al., 2014; Parasar et al., 2017) and this has resulted in the variety of alcoholic beverages assorted and produced by the communities through traditional fermentation practice. In household fermentation practiced by the communities of northeast India, solid-state starter cultures in the form of "flat cakes" or "spherical balls" are prepared from starchy substances such as rice, millets, maize, or wheat that are powdered and mixed with microbial inoculum (Nath et al., 2020a). These "cakes" supplement carbon constituents for the growth of yeasts that initiate fermentation. In the Rabha community, fermentative starter cake (known as *bakhaor*) is prepared in the form of "flat globules" by mixing soaked rice granules (*Oryza sativa* L., land variety sali and ahu) with considerable amount of old starter cakes (containing fermentation yeasts) and various plant condiments (Deka and Sarma, 2010). In order to prepare a consumable beverage, rice is tightly cooked and air cooled over bamboo mats, which act as substrate for rice beer. Starter cake is powdered (inoculum) and mixed with boiled rice. Later, this mixture is placed inside earthen pots while a special cylindrical structure made of bamboo (*janthi*) is placed inside and the mouth of the pots are tightly closed with banana leaves. After a few days (4–5 days in summer, 7–8 days in winter), fermented rice beer accumulates inside the *janthi*. This beer is further fermented using water and starter cakes, followed by distillation using series of earthen or metallic pots. Finally, a strong, consumable fermented beverage is produced (Deka and Sarma, 2010).

The presence of non-*Saccharomyces* species along with chief fermentative yeasts in starter cakes of various indigenous communities has been observed universally. The microbial inoculum in starter materials has been maintained for generations. However, in spite of extensive perpetuation for hundreds of years, the quality and consistency of the fermented produce have not varied much and appear to be constant across continued generations without any noticeable change in their fermentation efficiency. This consistency in fermentation outcome indicates the steady maintenance of yeasts and their stable genetic features. Amylolytic yeasts presumably play a crucial role in fermentation by enabling the breakdown of high carbon materials such as starch into simpler glucose molecules while fermentative yeasts thrive and carry out fermentation on those ready-made energy sources. Competition over common resources arises when two or more species of yeasts compete to thrive within a specified fermentation environment. However, cooperation between amylolytic and non-amylolytic yeasts always prove to be a beneficial trait when the population has to rely on starchy carbon source (Nath et al., 2020a). To note, non-*Saccharomyces* yeasts such as *W. anomalus* produces volatile compounds that enhance the aroma characteristics of wines, thereby enabling better quality yield of fermented beverage (Ye et al., 2014).

Fermented products are categorized into solid or semi-solid fermented food and fermented beverages. The diversity of yeasts in fermentative sources has been well-documented from Southeast Asia (Boekhout and Robert, 2003). The documentation of diversified yeasts from fermentative foods of northeast India have also been done from time to time. Buragohain et al. (2013) had reported the presence of *S. cerevisiae*, *Debaryomyces hansenii, W. anomalous*, and *Candida glabrata* in starter cakes collected from the tea ethnic community, Ahom, Nepali, Bodo, Adivasi, Karbi, and Dimasa communities of Assam, Meitei community of Manipur, Angami community of Nagaland, Apatani community of Arunachal Pradesh, and the Khasi community of Meghalaya. The presence of *Candida parapsilosis* and *Geotrichum candidum* in *kinema* fermented food of the Gorkha and Nepali communities was reported from the state of Sikkim (Sarkar et al., 1994). Dewan and Tamang (2006) had reported about the presence of *Saccharomycopsis fibuligera* and *Candida* spp. from *chhu* or *sheden* ethnic fermented milk products of the Bhutias, the Lepchas, the Monpas, the Sherdukpen, the Khambas, the Membas, and the Tibetan people living in the higher altitudes of the eastern Himalayas. The persistence of the yeasts representing *Saccharomycopsis* and *Candida* have also been reported from *dahi* (curd) from the entire northeast India (Dewan and Tamang, 2007); *Candida* spp. from *goyang* fermentation of the Sherpa community in Sikkim (Tamang and Tamang, 2007); *S. cerevisiae, Pichia burtonii*, and *Candida castellii* from *maseura* or *masyaura* fermentations (Chettri and Tamang, 2008); and *S. cerevisiae, Saccharomyces kluyveri, D. hansenii, P. burtonii*, as well as *Zygosaccharomyces rouxii* from *selroti* fermented product of the Gorkha community (Yonzan and Tamang, 2010). Chettri (2012) had described about the presence of *S. cerevisiae*, *D. hansenii*, and *P. burtonii* in *tungrymbai* fermented food of the Khasi community from Meghalaya as well as from *bekang* fermentation of Mizoram. Tamang et al. (2016) reportedly marked about the presence of *Saccharomyces* and *Torulopsis* yeasts in *soibum* fermentation of the Meitei community from Manipur. On the contrary, Thapa et al. (2004) reported the predominance of *Candida* and *Saccharomycopsis* yeasts in *ngari* and *hentak* fermented drinks of Manipur, *Candida chiropterorum, Candida bombicola*, and *Saccharomycopsis* spp. from *gnuchi* of the Lepcha community of Sikkim while the presence of same yeasts had been reported from *suka ko maccha* and *sidra* fermentations prepared by the Gorkha community from Sikkim (Thapa et al., 2006).

Since solid-state starter cultures are primarily used as inoculum for fermented beverage production, these have a special mention in most of the published reports from the region, such as starter cake *marcha/murcha*, which is used to produce the alcoholic drink called *jaanr* in Sikkim and Himalayan terrains (Shrestha et al., 2002; Tamang, 2005, Thapa and Tamang, 2020). Incidentally, the persistence of the yeasts *S. fibuligera*, *Saccharomycopsis capsularis*, *Pichia anomala*, *P. burtonii*, *S. cerevisiae*, *Saccharomyces bayanus, W. anomalus*, and *C. glabrata* seem to be ubiquitously present along the eastern Himalayan landscape (Tamang and Sarkar, 1995; Thapa, 2001; Tsuyoshi et al., 2005; Sha et al., 2018). The ecology and distribution of yeasts in fermented products from the rest of the seven northeastern states have also been reviewed by several researchers. The supremacy of *S. cerevisiae* over other yeasts in consortia was observed in a starter material called *piazu*, which is used to prepare alcoholic brew called *zutho* by the Angami community of Nagaland (Teramoto et al., 2002). Similar observations were noted for the alcoholic brew called *litchumsu*, which is prepared by the Ao community of Nagaland (Das et al., 2012). *Zutho* in the state of Nagaland is also produced from another starter culture named *Khekhrii*, wherein the dominance of *W. anomalus* and *P. anomala* was observed (Sha et al., 2018). Similarly, existence of *S. cerevisiae*, *P. anomala*, *Trichosporon* spp., *C. tropicalis*, *Pichia guilliermondi*, *C. parapsilosis*, *Torulaspora delbrueckii*, *Pichia fabianii*, *Pichia kudriavzevi*, *Candida montana*, and *C. glabrata* was reported from *hamei* starter culture, which is employed in the production of *atingba* and *yu* alcoholic beverages by Meitei and Kabui community of the state of Manipur (Jeyaram et al., 2008, Sha et al., 2018, Wahengbam et al., 2020). In Meghalaya, starter cultures called *wanti* and *thiat* are used in preparation of alcoholic beverages (Anupama et al., 2018; Mishra et al., 2018). The starters of *wanti* are primarily composed of the yeasts *S. cerevisiae*, *Rhodotorula mucilaginosa*, and *W. anomalus*, which is used to prepare *chubitchi* beverage by the Garo community, *kyiad* beverage by the Khasi community, and *sadhiar* beverage by the Jaintia communitiy of Meghalaya (Mishra et al., 2018). The starters of *thiat* contain yeasts belonging to *S. fibuligera, W. anomalus*, and *Pichia terricola*, which is used to prepare alcoholic beverages by the Khasi community (Sha et al., 2018). Earlier investigations revealed the presence of *W. anomalus* in *epo* starter culture perpetuated by the Apatani community and *phut* starter cake of the Monpa community of Arunachal Pradesh (Tanti et al., 2010; Buragohain et al., 2013; Anupama et al., 2018; Sha et al., 2018). In the state of Mizoram, beverages such as *zupui, zufâng*, and *rakzu* are prepared by Mizo community from a starter culture called *dawdim,* where the occurrence of *W. anomalus*, *C. glabrata, P. anomala*, and *S. fibuligera* were found to coexist as a consortia (Sha et al., 2018; Thanzami and Lalhlenmawia, 2020). In the state of Tripura, production of local alcoholic drinks like *gora bwtwk* and *chuwak* are customary traditions carried out by the Kalai, Jamatia, Debbarma, and Molsom communities who conserve and perpetuate a starter culture called *chowan*, where the dominance of *C. glabrata* and *W. anomalus* was reported (Anupama et al., 2018; Sha et al., 2018; Majumdar, 2020). In our previous investigations (Parasar et al., 2017), we analyzed the starter cultures conserved by the Bodo, Karbi, Rabha, Mishing, Ahom, and Kachari communities of Assam. The starter culture *emao/amao* of the Bodo community was found to be dominated by *P. burtonii, P. anomalus*, and *S. cerevisiae* while another starter culture called *thap* of the Karbi community was dominated by *S. cerevisiae* (Parasar et al., 2017). The Ahoms perpetuate a starter culture called *xajar pitha*, which is enriched with *C. tropicalis* and *C. glabrata*, an unusual observation with a great deal of research interest since no *Saccharomyces* isolates could be retrieved from the starters (Parasar et al., 2017). The Mishing community of Assam prepare and preserve *apong kusure/apop pitha* starter cake where the unusual yeast *Rhodotorula taiwanensis* was found to predominate (Parasar et al., 2017). The Rabhas, another major ethnic community, perpetuate starter cultures called *bakhor* where the persistence of *Meyerozyma carribica* was reported (Tanti et al., 2010; Narzary et al., 2016; Parasar et al., 2017; Barooah et al., 2020). The Kachari community of Assam prepare *modor pitha* starter cultures that contain a consortia of *S. cerevisiae, W. anomalus,* and *C. glabrata* (Parasar et al., 2017; Anupama et al., 2018). To our utter surprise, the entire spectrum of starter cultures studied from the region revealed the presence of *W. anomalous* except for the starter cultures collected from the Ahom community (Parasar et al., 2017; Nath et al., 2020a). Occurrence of dominant yeasts in starter cultures are summarized in **Table 1**. Additionally, the distribution of ethnic communities of the region, the starter materials used in traditional brewing, and the names of resultant beverages are summarized in **Figure 1**. Here, we have mentioned only those starter cultures whose detailed studies are available in literature and which have been investigated by researchers from the region. The repertoire of cultures is colossal and shall require far more intricate research plans to reach a final conclusion regarding the origin, distribution, and diversity of yeast types and the array of traditional fermentation procedures practiced in the region (Parasar et al., 2017; Nath et al., 2020a). Our recent findings regarding distribution of yeasts in starter cakes (Parasar et al., 2017; Nath et al., 2020a) are illustrated in **Figure 2**.

YEAST–YEAST INTERACTION AND INVOLVEMENT OF QSMs IN FERMENTED BEVERAGES

Microorganisms exist in diverse communities in both natural and man-made ecosystems. Interactions among these microbes define the complexity of food and beverages (Avbelj et al., 2016). Such intra- and interspecies interference could be observed between yeasts and other microbes that coexist in wine micro-environment (Fleet, 2003). Essential metabolic interactions and complementation physiognomies have been reviewed in food ecosystems (Ivey et al., 2013). Positive interactions such as mutualism and synergism allow the participating microbes to derive benefit from the interactions. For example, during alcoholic fermentation of starchy material, two types of yeasts have been found to play the principal role of fermentation that include amylolytic yeasts that degrade starch into simpler carbohydrates while alcohol-fermenting yeasts grow on the resulting simpler carbohydrates to yield ethanol (Tsuyoshi et al., 2005). This was further analyzed in our recent experiments and was observed that utilization of starch and subsequent ethanol production was higher when *S. cerevisiae* (non-amylolytic) was combined with *C. tropicalis* (amylolytic) in co-culture combination compared to tested combinations of *S cerevisiae* with other non-amylolytic yeasts (Nath et al., 2020a). Cooperation of yeasts with other species has also been found to be beneficial for the production of quality fermented product. For example, production of Japanese alcoholic drink *sake* employs fermentation by *S cerevisiae* var. *sake* along with *Aspergillus oryzae*, wherein *Aspergillus* break down rice starch into simpler sugars while yeasts convert resultant sugars into ethanol (Jay, 1991; Azumi and Goto-Yamamoto, 2001). Furthermore, such interactions also do enhance unique characteristics by producing secondary metabolites, higher alcohols, and ethers that produce pleasant aroma and quality texture (Hosaka et al., 1998).

Contrarily, negative interactions such as amensalism adversely affect the growth of competitive microbes. Two good examples can be cited for amensalism wherein the production of ethanol by *S. cerevisiae* eliminate all non-*Saccharomyces* yeasts present in the must during fermentation while nisin production by *Lactobacillus lactis* inhibits proliferation of other competing lactic acid bacteria (LAB) (Hutkins, 2007). Competition is another aspect of negative interaction, where the microbes compete with one another for nutrient uptake and for space to survive. Such examples can be seen during alcoholic fermentation, where *S. cerevisiae* engage in defensive mechanisms such as physical cell contact and secretion of antimicrobial peptides against other microbes that impart significant impact on wine profiles (Albergaria and Arneborg, 2016). Such microbial interactions influence the quality of the final product and impact critical parameters such as sensory quality, low toxicity, and shelf life of the fermented food or beverage (Rul and Monnet, 2015).

Application of the QSMs 2-phenylethanol, tryptophol, and tyrosol have already been reported in various biotechnological techniques, which include evaluation of wine quality (Garde-Cerdán et al., 2007; González-Marco et al., 2010) and enhancement of aroma in foods and drinks (Etschmann et al., 2003; Wang et al., 2011). In addition to enhancing food value, quorum sensing mechanisms have the potential to control food spoilage (Avbelj et al., 2016). Such observation has been reported during wine fermentation, where K2 and Klus-type yeast killer toxins were found to be responsible for

TABLE 1 | Dominant yeast species associated with starter materials from ethnic communities of northeast India.

State	Ethnic community	Starter material	Dominant yeast species	References
Sikkim	Nepali, Gorkha, Lepchas, Limboo, Bhutia,	*Marcha*	*S. fibuligera, Saccharomycopsis capsularis, P. anomala, P. burtonii, S. cerevisiae, S. bayanus, C. glabrata*	Tamang and Sarkar, 1995; Thapa, 2001; Tsuyoshi et al., 2005; Thapa and Tamang, 2020
Arunachal Pradesh	Apatani, Mongpa	*EpoPhut*	*W. anomalus*	Tanti et al., 2010; Buragohain et al., 2013; Anupama et al., 2018; Sha et al., 2018
Nagaland	Angami, Ao	*Piazu,Khekhrii*	*S. cerevisiae, C. glabrata, W. anomalus, P. anomala.*	Das et al., 2012; Buragohain et al., 2013; Sha et al., 2018.
Manipur	Meitei, Kabui	*Hamei*	*S. cerevisiae, P. anomala, Trichosporon spp., C. tropicalis, P. guilliermondi, C. parapsilosis, T. delbrueckii, P. fabianii, C. montana, P. kudriavzevi, C. glabrata*	Jeyaram et al., 2008; Sha et al., 2018; Wahengbam et al., 2020.
Meghalaya	Garo, Khasi, Jaintia	*Wanti,Thiat*	*S. cerevisiae, R. mucilaginosa, W. anomalus, S. fibuligera, P. terricola, S. fibuligera, W. anomalus, P. terricola*	Anupama et al., 2018; Mishra et al., 2018; Sha et al., 2018.
Mizoram	Mizo	*Dawdim*	*W. anomalus*, *C. glabrata, P. anomala*, *S. fibuligera*	Sha et al., 2018; Thanzami and Lalhlenmawia, 2020
Tripura	Kalai, Jamatia, Debbarma, Molsom	*Chowan*	*C. glabrata, W. anomalus*	Anupama et al., 2018; Sha et al., 2018; Majumdar, 2020
Assam	Bodo Karbi	*EmaoThap*	*P. burtonii, P. anomalus, S. cerevisiae, W. anomalu* *S. cerevisiae, W. anomalus*	Tanti et al., 2010; Narzary et al., 2016; Parasar et al., 2017; Anupama et al., 2018; Barooah et al., 2020; Nath et al., 2020a.
	Kachari	*Modor pitha*	*S. cerevisiae, W. anomalus, C. glabrata.*	
	Rabha	*Bakhor*	*M. carribica, W. anomalus*	
	Ahom	*Xajar pitha*	*C. tropicalis, C. glabrata*	
	Mishing	*Apong kusure/ Apop pitha*	*R. taiwanensis, W. anomalus*	
	Adivasi Dimasa	*DabaiHamao*	*C. glabrata* *D. hansenii, W. anomalus*	Tanti et al., 2010; Buragohain et al., 2013; Sha et al., 2018.

controlling proliferation of spoilage yeasts (Comitini et al., 2004; Rodríguez-Cousiño et al., 2011). Alternatively, quorum sensing inhibitors (QSIs) can be employed to control the proliferation of spoilage microbes thereby inhibiting the expression of undesired virulent traits (Sharma and Jangid, 2015). Recent studies reveal that different plant extracts harboring phytochemical constituents and essential oils inhibit biofilm formation of harmful yeasts/microbes, thereby rendering the product suitable for human consumption and henceforth these substances may be considered as effective QSI during wine fermentation (Avbelj et al., 2016). Likewise, a QS mechanism has been observed to control food spoilage by regulating the expression of enzymes such as cellulases, lipases, chitinases, nucleases, pectate lyase, and various proteases, thereby facilitating the management of quality control of processed foods (Skandamis and Nychas, 2012).

In traditional fermentations practiced by the communities of northeast India, different plant condiments are added during the preparation of starter cultures (Tanti et al., 2010). Metabolites and constituents from such plant additives/parts are believed to play an important role during fermentation (Nath et al., 2019). The phytohormone indole-3-acetic acid (IAA) is one of several metabolites that are known to promote rapid and long-term responses in plants (Cleland, 2010) and incidentally has also been observed to be expressed by certain yeasts inherent in traditional starters from the region (Nath et al., 2019). It is noteworthy that reports of yeasts capable of producing IAA are already available in published literature, which contemplates the importance of traditional yeasts to be exploited for producing phytohormones other than conventional metabolites (Nakamura et al., 1991; El-Tarabily, 2004; Nassar et al., 2005). Parenthetically, previous studies had reported that IAA stimulates growth and promotion of filamentous morphogenesis in *Saccharomyces* (Prusty et al., 2004), which was also supported by our recently published findings (Nath et al., 2019). From such observations, it can be presumed that IAA contributes toward the growth of yeasts while the addition of plant condiments supplements the necessary phytohormone for perpetuation and coexistence of the varied yeast species in starter cakes.

It is to be mentioned that tyrosol, the chief QSM expressed in yeasts, was reported to confer protection from oxidative stress induced by respiratory burst of neutrophils (Cremer et al., 1999) and ethanol (Nath et al., 2020b) apart from morphogenic transition and other QS-related activities. In an earlier report,

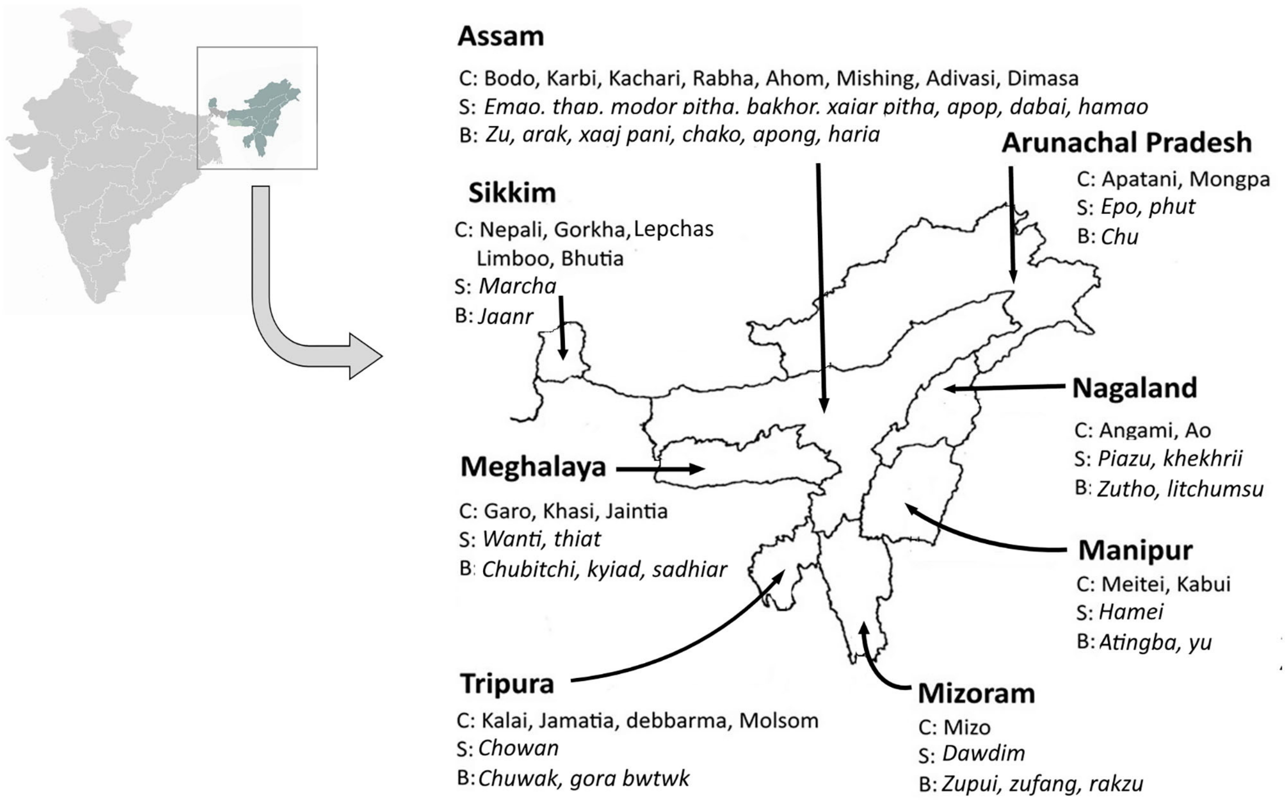

FIGURE 1 | Map of northeast India indicating ethnic communities (C), starter material/cake (S), and fermented beverages (B) associated with ethnic culture of the seven states. This illustration is based on reports by various researchers on yeast population harbored in the starter cakes and their beverages (Tamang and Sarkar, 1995; Thapa, 2001; Tsuyoshi et al., 2005; Jeyaram et al., 2008; Tanti et al., 2010; Das et al., 2012; Buragohain et al., 2013; Narzary et al., 2016; Parasar et al., 2017; Anupama et al., 2018; Mishra et al., 2018; Sha et al., 2018; Barooah et al., 2020; Majumdar, 2020; Nath et al., 2020a; Thanzami and Lalhlenmawia, 2020; Thapa and Tamang, 2020; Wahengbam et al., 2020).

tyrosol was reported to influence germ tube formation through upregulation of DNA replication and cell cycle maintenance (Chen et al., 2004). Such upregulations can presumably exert the growth-enhancing effect in yeasts concurrent with the increase in cell density. Evidently, our recently published work also demonstrated an increase in cell number under the influence of self-expressed and exogenously introduced tyrosol in both *Saccharomyces* and non-*Saccharomyces* yeasts (Nath et al., 2020b), and since ethanol production was found to be proportional to cellular density, an indirect involvement of tyrosol during fermentation could be well-justified. Nevertheless, such QS activity is believed to be limited by ethanol concentration and addition of external ethanol was found to inhibit the production of tyrosol by *S. cerevisiae*, a strong indication of an antagonistic role of ethanol on QS activity (Avbelj et al., 2015).

THE IMPORTANCE OF ASSOCIATION OF YEAST CONGLOMERATE AND QUORUM SENSING

This review was an attempt to provide an insight into yeast–yeast interrelation and the role of quorum sensing mechanism on the production of ethnic beverages during traditional fermentations. As mentioned earlier, diverse species of yeasts in fermentative cakes impart substantive effect on the shelf life and oenological properties in wines and beverages when cultured in consortium. Survival experiments of yeast isolates under co-culture conditions revealed the usefulness of non-*Saccharomyces* yeasts during fermentation and is now well-understood that apart from the enhancement of ethanol content, other metabolites also play important roles in the enhancement of quality attributes of the fermented products (Nath et al., 2020a). The unusual yeast *W. anomalus* was found to be ubiquitously present and dominant in most of the fermentative cakes representing several indigenous communities of Assam (Parasar et al., 2017), and is not a chief fermenting yeast, and yet, the species has been reported to produce volatile compounds that enhance the aroma profile of traditional wines (Clemente-Jimenez et al., 2005). Several investigations reported earlier stated that high-quality balanced wines can be produced when *W. anomalus* is mixed and co-cultured with *S. cerevisiae*, which often leads to the production of acetate esters, ethyl propanoate, phenyl ethanol, and 2-phenylethyl acetate that are known to enhance the aroma profile of wines (Rojas et al., 2003; Clemente-Jimenez et al., 2005; Swangkeaw et al., 2011, Passoth et al., 2006). Similarly,

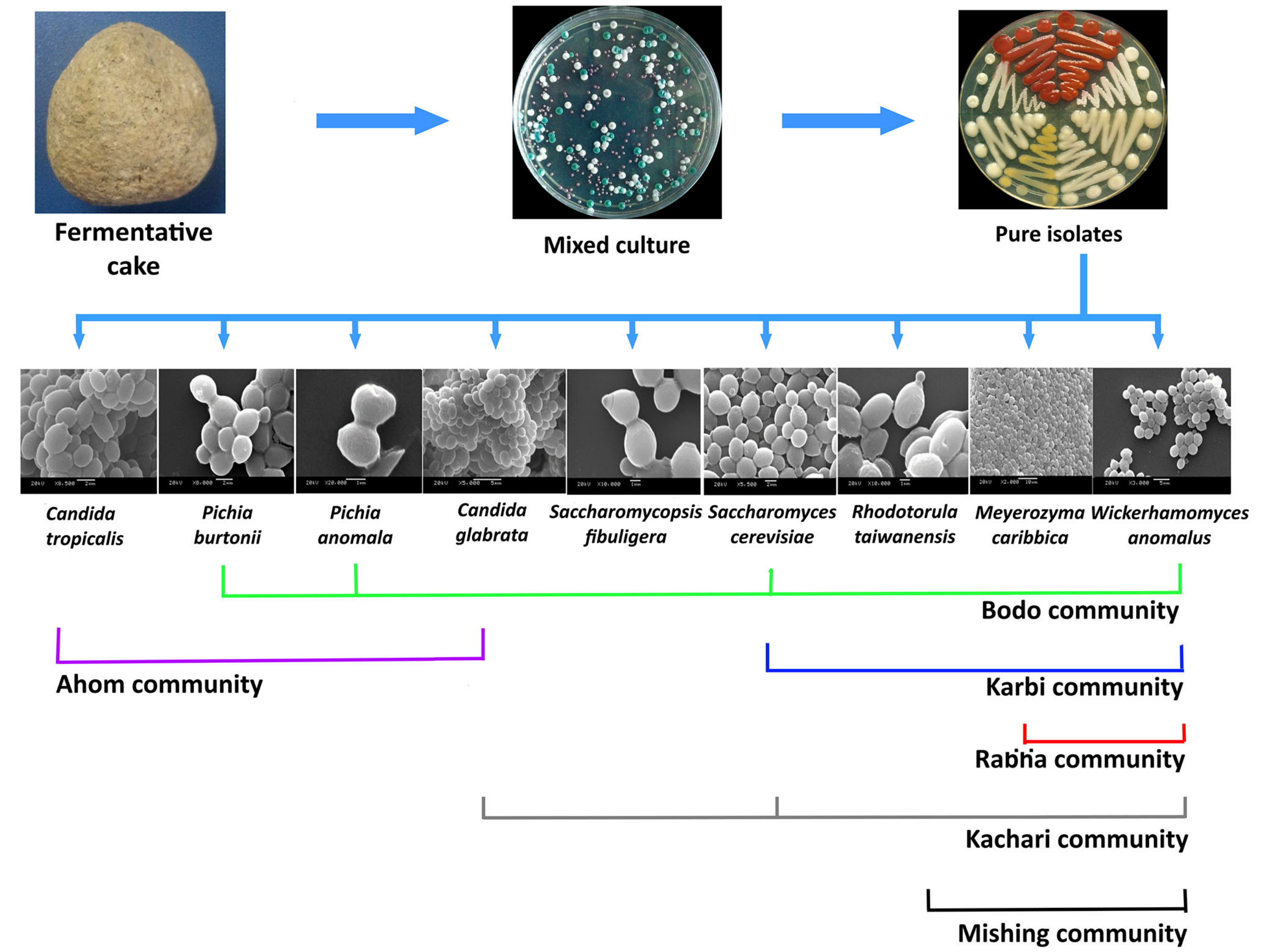

FIGURE 2 | Graphical depiction of distribution of yeasts in various starter cultures of indigenous community of Assam. The experimental data are derived from Parasar et al. (2017) and Nath et al. (2020a).

other unusual non-*Saccharomyces* yeasts like *Zygosaccharomyces bailii* (Gueguen et al., 1995), *D. hansenii* (Yanai and Sato, 1999), *P. anomala* (Manzanares et al., 2001; Swangkeaw et al., 2011), and *Hanseniaspora* (Swangkeaw et al., 2011) have been reported to express and produce several valuable metabolites, volatile compounds, and enzymes like β-glucosidase during fermentation of grape must (Rodríguez et al., 2004). It is now well-known that non-*Saccharomyces* yeasts saturate the fermentation culture during early stages of fermentation, and with an increase in ethanol concentration, the dominance of ethanol tolerant *S. cerevisiae* persists, which continues the process till the end of fermentation (Xufre et al., 2006; Lee et al., 2012a,b). Meanwhile, although the precise role of QSMs during the fermentation process has not received much attention, considering the effects of QSMs studied to date, the importance of molecules like tyrosol has proved to be beneficial, not only because of its cell growth-enhancing capability but also because it provides nutritional value to fermented products with quality traits that confers health benefits as tyrosol possesses incredible antioxidant property (Giovannini et al., 1999).

CONCLUSION

From the preceding discussion, it is evident that association of yeasts and their productive communication results in the production of beverages with distinct enological qualities inherent in fermented beverages/drinks prepared by various indigenous communities of northeast India. These unique characteristics are presumably observed due to the presence of distinct dominant species of yeasts and the addition of plant concoctions/condiments into the starter materials for perpetuation and cultivation of fermenting principle. However, several limitations such as bad odor, turbidity, inconsistency, presence of toxic metabolites, and variable texture contribute to uninvited traits rendering the fermented products unsuitable for commercialization (Tsuyoshi et al., 2005). Although genetic or chemical engineering approaches can eliminate such limitations, natural methods of co-culturing or sequential culture procedures could prove to be more cost-effective and user-friendly. To conclude, the aforementioned yeast–yeast association experiments and studies pertaining to the role of chemical communication by QSMs like tyrosol in controlling the quality of fermented products need to be thoroughly investigated, but unfortunately, records of such investigations are scanty from northeast India, which has an abundant microflora distribution and rich in cultural heritage of a huge congregation of ethnic indigenous people. Considering the immense potential of these traditional products, more and more applications of such natural interactions in fermentation should be prioritized so that the indigenous people could benefit from these household preparations and get an opportunity for choosing sustenance through commercialization of these indigenous products that will impart sustainable livelihood options.

FUTURE DIRECTIONS AND PERSPECTIVES

The mechanism of QS in both gram-positive and gram-negative bacteria are well-established (Rutherford and Bassler, 2012). This understanding has resulted in efforts to inhibit bacterial pathogenesis and design novel antimicrobial therapeutics. Unlike bacteria, where the role of autoinducing molecules in QS like lactones and oligo-peptides and the corresponding genes that express them have been deciphered, the fungal QS system is yet to be studied in detail, particularly with reference to the effects of QS on fermentation. Processes in QS include other activities like bioluminescence, sporulation, competence, antibiotic production, biofilm formation, and virulence factor secretion (Rutherford and Bassler, 2012) and such effects cannot be nullified in fungal quorum sensing too. Research on autoinducing molecules and transporters that release or transport these molecules in and out of cells shall complement their effects on the formation of final products as well as adduct secondary molecules that could prove to be industrially beneficial. Similarly, the effect of QSMs in starter culture perpetuation needs to be appreciated and should be studied to explicate the benefits of QS among yeasts in solid-state fermentation. At the same time, the differences of expression and activity of QSMs in starter cultures and during submerged fermentation need to be investigated. In starter materials, yeasts remain in dormant dry state that are activated upon contact with substrates. Proliferation of yeasts within starter materials without the involvement of fermentation is a question to ponder. Notwithstanding the fact that a large number of studies pertaining to the probable role of plant material concoctions in the enhancement of attributes of fermented beverages in spontaneous or traditional fermentation from starter cultures have been discussed (Nath et al., 2019), an authentic explanation to the definite role of these concoctions on QS activity concomitant to fermentation process has never been addressed. Besides these, the necessary information on the accessibility and roles of other QSMs other than tyrosol on fermentation (Nath et al., 2020b) is still missing and thus our knowledge on the array of QSMs remains limited, which needs to be addressed. More importantly, the ecology and behavior of traditional yeasts in fermentation have not been studied much and henceforth the queries on the key ecological aspects of these beneficial fungi in response to change in parameters and composition of substrates need to be studied. It has been reported that QSMs in yeasts like farnesol suppress the pathogenicity of certain pathogenic yeasts like *C. albicans* through morphogenesis (Hornby et al., 2001). Similarly, 2-phenylethanol and tryptophol regulates phenotypic changes in *S. cerevisiae* (Smukalla et al., 2008; Avbelj et al., 2016). The regulatory mechanisms of these QSMs are well-explained (Avbelj et al., 2016), but their direct involvement in fermentation is yet to be thoroughly explored. In addition, assessing the role of these QSMs during inter- and intra-species competition in a fermentation microenvironment needs validation. The role of QSMs in traditional fermentation is important to check the changes in parameters and the expression/production of both desirable and undesirable metabolites in culture. There are several future prospects of QS mechanism in the production of fermented foods. QSMs discovered to date have various health benefits (Nath et al., 2020b). As QSMs are produced in minute quantities, purification of these shall not be an economically viable option. Therefore, understanding the mechanism to develop fortified fermented food enriched with beneficial molecules could be one useful alternative. In anaerobic condition, increased production of 2-phenylethanol, tryptophol, and tyrosol was observed in *C. albicans* (Ghosh et al., 2008) and *S. cerevisiae* (Avbelj et al., 2016), implying the role of QSMs in the enhancement of fermentation during anaerobic conditions. Anaerobic condition suppresses biomass proliferation and increases more carbon conversion to end product (Huang and Tang, 2007). It is therefore envisioned that proper exploration and application of the regulating mechanisms of fermentation through QSMs can open new insights that will be beneficial in food and beverage industries. Furthermore, to the above, the interactions among yeasts, their presence, and their metabolic exchanges are key to the formation of products that will have economic value. As QS mechanism is a density-dependent phenomenon, regulation of cell population during expression of QSMs is anticipated (Nath et al., 2020b). It is evident that more experiments shall have to be conducted to reach to a conclusion as to how a fermented product is modified through QS mechanism. Co-culturing techniques could possibly help in determining the competitiveness among species, while genetic engineering approaches can facilitate in understanding the underlying molecular mechanisms of such interaction during fermentation.

AUTHOR CONTRIBUTIONS

All the authors have contributed equally in conceiving, designing, and writing the manuscript.

FUNDING

A part of this article has been comprehended from our previous work supported by a project (BT/303/NE/TBP/2012 dated 04/01/2013) funded by the Department of Biotechnology, Government of India. Some observations have also been generated from our ongoing Department of Biotechnology, Government of India-funded project on pigmented yeasts from northeast India (BT/PR25652/NER/95/1326/2017 dated 26/07/2018). BN was a recipient of NFOBC-UGC fellowship (F./2017-18/NFO-2017-18-OBC-ASS-61070/SA-III/Website) for PhD under HS. DP was a recipient of BSR-UGC fellowship (GU/UGC/BSR/P.J.Handique/2012/1183-87 dated 6.7.12) for PhD under HS.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.