Biotechnology for Biofuels

REVIEW

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Bioethanolic yeasts from dung beetles: tapping the potential of extremophilic yeasts for improvement of lignocellulolytic feedstock fermentation

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Abstract

Bioethanol from abundant and inexpensive agricultural and industrial wastes possesses the potential to reduce greenhouse gas emissions. Bioethanol as renewable fuel addresses elevated production costs, as well as food security concerns. Although technical advancements in simultaneous saccharification and fermentation have reduced the cost of production, one major drawback of this technology is that the pre-treatment process creates environmental stressors inhibitory to fermentative yeasts subsequently reducing bioethanol productivity. Robust fermentative yeasts with extreme stress tolerance remain limited. This review presents the potential of dung beetles from pristine and unexplored environments as an attractive source of extremophilic bioethanolic yeasts. Dung beetles survive on a recalcitrant lignocellulose-rich diet suggesting the presence of symbiotic yeasts with a cellulolytic potential. Dung beetles inhabiting extreme stress environments have the potential to harbour yeasts with the ability to withstand inhibitory environmental stresses typically associated with bioethanol production. The review further discusses established methods used to isolate bioethanolic yeasts, from dung beetles.

Keywords: Bioethanol production, Dung beetles, Yeasts, Fermentation, Extremophilic trait

Background

Bioethanol and bioethanolic yeasts: gaps, limitations, and challenges

Bioethanol is an attractive alternative to petroleum fuels due to its numerous advantages [1–7]. Reduced reliance on non-renewable energy sources and a decrease in greenhouse gas emissions are the two major merits. Although fossil fuels meet our demand for energy, their contribution to climate change as a result of greenhouse gas emissions is a global dilemma. The transportation sector is the world's biggest contributor to greenhouse gas emissions due to its high dependence on fossil fuels [8–11]. The use of renewable fuel in this sector to achieve greenhouse gas emission neutrality is an imminent solution for sustainable and environmentally friendly energy sources. However, for bioethanol to be competitive against non-renewable fuel sources, there are many hurdles to overcome [11–13]. One of the most important hurdles is food security. First-generation bioethanol produced from edible food crops such as corn, rice, barley, potatoes, sugarcane, and other starchy food crops [14–18] has led to controversies due to competition with food production and land use. The competition for land use increases the demand and price of food crops [19–23]. Second-generation bioethanol using non-edible, inexpensive, and abundant lignocellulosic biomass

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such as woody and herbaceous biomass, forest residues, industrial and agricultural wastes, and other non-food crops [16, 18, 24] as raw materials address the food versus fuel challenge associated with the use of food-grade feedstocks. Although second-generation bioethanol processing generates far lower levels of greenhouse gases as compared to the first-generation alternative [25], it is not without demerits. Production costs associated with separate hydrolysis and fermentation (SHF) processes where each step is carried out under optimal pH and temperature conditions [26] are extremely high to achieve sustainability. Recently, however, Simultaneous Saccharification and Fermentation (SSF) is a method that has become increasingly attractive in the production of bioethanol from non-edible lignocellulosic feedstocks, as well as dedicated energy crops [13, 27, 28] as it produces higher bioethanol yields than SHF [2, 7, 29–31]. This method allows hydrolysis and fermentation undertaken simultaneously to reduce production costs. Lignocellulosic feedstocks are pre-treated using physical, chemical, and biological pre-treatments [32, 33]. Chemical pre-treatment exploiting either acid or alkali treatments [34–37] at high temperatures is the most preferred method. However, this pre-treatment process creates another hurdle, because there are limited robust yeasts strains that can tolerate the presence of inhibitory toxic compounds such as acetic acids, levulinic acids, furfural, 5-hydroxymethylfurfural (HMF), and ferulic acids [7, 16, 20, 38, 39] which are generated during this process (Fig. 1). In addition, the process exerts extreme osmotic and oxidative stresses [19, 32, 40, 41] (Fig. 1), which are extremely harsh for the conventional bioethanolic yeasts. These conditions can inhibit or reduce speed of growth and fermentation efficiency of yeasts [16, 17, 28, 36]. The use of biological treatments, such as thermotolerant cellulolytic enzymes (optimal temperature 45–80 °C) [42], is another option. One major drawback is the wide difference of temperature requirements for this treatment and those used for growth and fermentation of yeasts which ranges from 20 to 35 °C [26] if the process is to be simultaneous as a cost-cutting measure. Therefore, using fermentative yeasts with extreme stress tolerance attributes such as thermotolerance, ethanol tolerance, oxidative stress tolerance, osmotolerance, and tolerance to inhibitory substrates among others would be ideal to overcome these drawbacks. Currently, mesophilic yeasts are used to produce bioethanol. The most desirable yeasts are thermophiles fermenting at temperatures of 40 °C or higher as this reduces the costs of pumping and cooling as well as allowing for efficient saccharification [43]. Efficient saccharification subsequently increases the amount of available fermentable sugars, which improves the overall fermentation productivity. In addition, higher temperature fermentation minimises contamination risks among

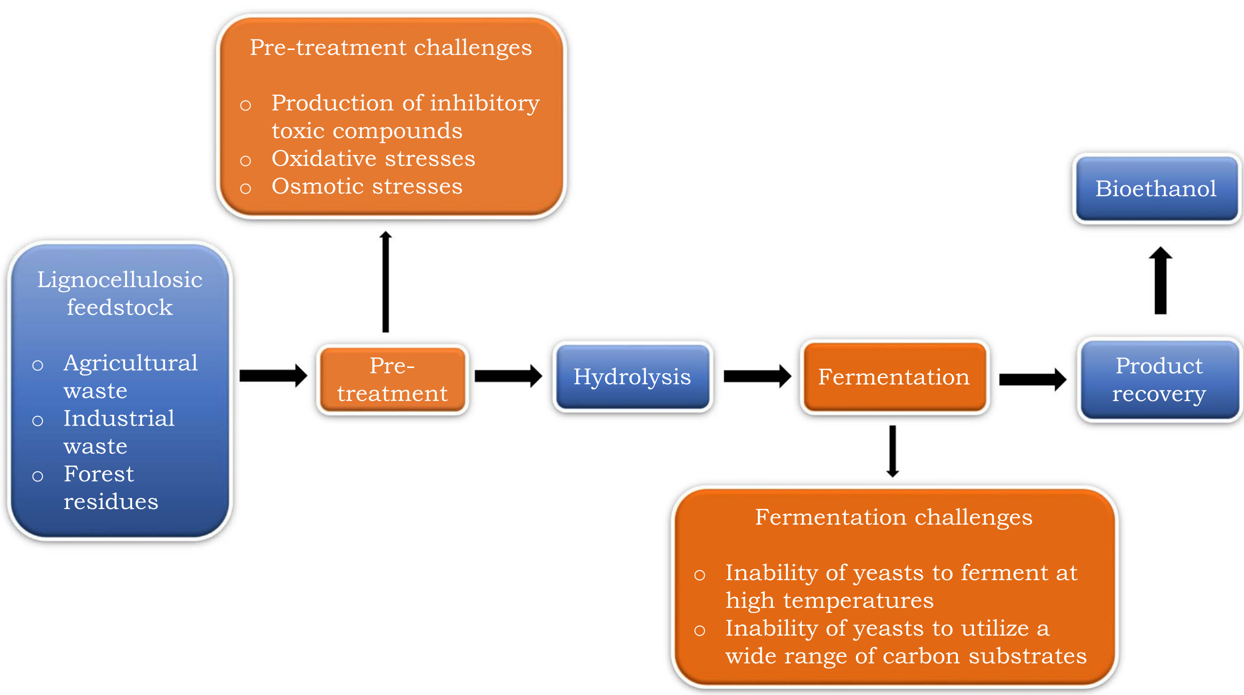

Fig. 1 An overview of challenges affecting bioethanol production in the pre-treatment and fermentation stages

other advantages. Examples of thermophilic yeasts such as *Issatchenkia orientalis* [44] and *Kluyveromyces marxianus* [45] are ideal, although they have their limitations such as lower ethanol yield from lignocellulosic feedstocks, poor tolerance to inhibitors and ethanol leading to a lower fermentation efficiency [46]. Hydrolysis of lignocellulosic feedstocks, which typically consists of cellulose, hemicellulose, and lignin, yields various fermentable sugars, such as pentoses (for example, xylose and arabinose) and hexose sugars (for example, mannose and galactose) [1, 16, 19]. A wide substrate utilization range is an essential characteristic of bioethanol production yeasts. The wild-type conventional/traditional yeast used in bioethanol fermentation, *Saccharomyces cerevisiae*, is incapable of fermenting pentose sugars, which subsequently reduces the efficiency of the process (Fig. 1). For example, this yeast cannot ferment xylose, the most abundant pentose sugar in lignocellulosic feedstocks [3]. The search for extremophilic and robust fermentative yeasts from dung beetles inhabiting extreme environments is one way to progressively increase productivity and subsequently the sustainability of bioethanol.

Dung beetles of the *Scarabaeidae* family and order *Coleoptera* are dependent on lignocellulose-rich animal dung for survival and reproduction [47, 48]. About 80% of dung is composed of indigestible carbon sources such as cellulose, tannin, and lignin with low nutritional content and quality [49–51]. Such a recalcitrant material for a diet suggests that symbiotic associations are obligatory for dung beetles to efficiently process lignocellulose within their guts. Such a diet requires immense specialisation for resident yeasts, which could serve as a unique ecological niche for novel yeasts with the ability to degrade inexpensive lignocellulosic feedstocks in bioethanol production processes. For decades, dung beetle research suggests that their guts possess microbial consortia, including yeasts which provide nutrition and assist in the digestion of such complex substrates [49]. The search for yeasts from dung beetles could be extended to those beetles inhabiting harsh environments like the hot deserts and tropical surroundings as extremophilic environments. Such ecological niches could be even more attractive as a source of multi-stress tolerant yeasts, which are likely to be found in association with resident extremophilic beetles. Robust stress tolerance is a phenotype of interest for the techno-economic feasibility of bioethanol production. Stressors such as weak acids and furans generated by hydrolysis of lignocellulosic feedstocks, ethanol, and high-temperature fermentation severely reduce the fermentative capacity of the bioethanolic yeasts.

This review presents an overview of challenges encountered during bioethanol production by conventional yeasts and the potentiality of dung beetles in harbouring novel yeasts with various attributes beneficial to the bioethanol industry.

Dung beetle as a source of extremophilic and ethanologenic yeasts

Symbiotic relationships between phylogenetically diverse insects and yeasts are well documented [52–55]. Insects mutually benefit from an association with yeasts; by attraction to food, whereas yeasts are vectored by insects from one food substrate to another [53, 54, 56]. Yeasts have a role to play in the nutrition of beetles, for example, secretion of enzymes for digestion of food [57–59], provision of essential organic acids, vitamins, as well as other products of their carbon metabolism pathway [58, 60, 61]. Well-documented examples of yeasts associated with *Drosophilid* insects suggest that yeasts provide essential vitamins (e.g., thiamin) and lipids needed for metabolism, and also assist with their reproduction by facilitating chemical communications and mating activities [54, 58, 62]. The growth and development of insects colonies such as honeybees are enhanced by yeasts inhabiting their gastrointestinal tract [54]. Yeasts found in termites play a role in the digestion of wood by producing relevant enzymes for xylose degradation [54, 63]. Furthermore, yeasts help to regulate various interactions among insect species. Yeasts are vectored by insects from one environment to another and are protected from adverse environments as well as resource depletion [53, 54, 58], as compared to their microbial counterparts, bacteria, and fungi, which can be dispersed through air; for example, flower beetle insects vector yeasts (e.g., *Kuraishia capsulata* and *Yamadazyma tenuis*) from one flower to another [54]. The environment within the insect gastrointestinal tract is conducive for yeast growth, reproduction, and survival. Yeasts inhabiting beetle intestines are provided with xylose sugar therefore enabling such yeasts to acquire xylose utilization and fermentative traits.

Yeast biodiversity in many insects like dung beetles for industrial applications has been poorly studied. About 1% of yeasts species is currently known and more are yet to be discovered [64]. Over 650 yeasts have been isolated from beetle guts [65]. *Candida sp, Hanseniaspora sp, Kluyveromyces sp, Metschnikowia sp, Pichia sp,* and *Saccharomyces sp* [65] are examples of yeast genera isolated from beetle guts that can be used for lignocellulosic feedstocks fermentations. A novel yeast *Trichosporon heliocopridis sp. nov* isolated from a dung beetle (*Heliocopris bucephalus* Fabricius) [66] was reported to assimilate a variety of carbon sources like glucose, sucrose, galactose, maltose, raffinose, trehalose, D-arabinose, and lactose to mention a few. The yeast was incapable of assimilating other carbon sources such as cellobiose, soluble starch, melibiose, D-xylose, L-arabinose, and L-sorbose. A major downside to this is that the yeast could not ferment glucose. However, the yeast's ability to ferment other sugars, as well as its thermotolerance ability are ideal background traits for strain development for example via evolutionary engineering [67]. Evolutionarily engineering of *Candida intermedia*, for example, enhanced xylose conversion, production of ethanol, and tolerance to lignocellulose-derived compounds [68]. Exploring robust fermentative yeasts capable of utilizing inexpensive and abundant carbon sources as well as exhibiting extremophilic stress tolerance traits from dung beetles that inhabit extreme and pristine environments could tremendously improve the economic feasibility of bioethanol.

Other than the ability to ferment multiple sugars, stress tolerance is an essential attribute for bioethanol fermenting strains. Yeasts from dung beetles inhabiting extreme environments with abilities to withstand stresses such as high temperatures, high salt, sugar, and ethanol concentrations could be isolated. Examples of such traits are listed in Table 1.

Fermentation of sugars found in lignocellulosic feedstock: a key trait sought for in dung beetle yeasts

Yeasts are facultative anaerobes that can shift to fermentation in the absence of oxygen, a process that allows them to break down sugars, producing ethanol as a byproduct. Some yeasts termed as Crabtree positive yeasts can ferment even in the presence of oxygen [69]. They inhabit sugar-rich environments such as fruits in nature. Bioethanol production yeasts can either be acquired from culture collections or commercial suppliers, developed using classical genetic methods as well-developed evolutionary engineering or can be isolated

Table 1 Possible yeasts with extremophilic traits for efficient bioethanol production

Trait	Yeast species	References
High ethanol productivity	*S. cerevisiae*	[98]
	Brettanomyces (=*Dekkera*) *bruxellensis*	[85, 99, 100]
	K. marxianus	[45, 101, 102]
Lignocellulosic-based carbon (e.g., cellulose, arabinose, xylose)	*P. stipitis, C. shehatae, and P. tannophilus, Schizosaccharomyces spp*	[103]
Thermotolerance	*K. marxianus*	[13, 18, 32, 86–88, 104–106]
	O. polymorpha	[87–91]
	P. kudriavzevii	[86, 107–113]
Osmotolerance	*Z. rouxii*	[86, 88, 91, 114–116]
	Torulaspora delbrueckii	[86, 116, 117]
	Z. bailii	[91, 115, 117, 118]
	Metschnikowia pulcherrima	[86]
	Wickerhamomyces anomalus	[24, 86, 119]
	Debaryomyces hansenii	[86, 117, 120]
	Schizosaccharomyces pombe	[86, 115, 117]
	P. kudriavzevii	[117]
Halotolerance	*Z. rouxii*	[88, 115, 116]
	T. delbrueckii	[86, 88]
	W. anomalus	[86, 88, 115]
	D. hansenii	[86, 88, 106, 115, 117]
Ethanol tolerance	*O. polymorpha*	[87, 89–91, 121]
	W. anomalus	[86]
	D. bruxellensis	[86, 91, 115, 122]
	S. pombe	[115]
	T. delbrueckii	[86, 123]
	Z. bailii	[86, 115, 120]
Furan derivative tolerance	*P. kudriavzevii*	[86, 91, 124, 125]
	W. anomalus	[24]
Acid tolerance	*Z. bailii*	[86, 91, 114, 115, 118, 126]
	W. anomalus	[115]
	P. kudriavzevii	[115, 125]

from their natural environments. Yeasts from nature are most exploited in bioethanol production, due to their ability to utilize various fermentable sugars and convert them into ethanol. High ethanol productivity is an indispensable attribute for bioethanol production.

Saccharomyces cerevisiae, the 'conventional' yeast, an extensive model fermentation organism used for bioethanol production [3, 19, 70, 71] monopolised the bioethanol industry before the use of inexpensive and abundant lignocellulosic feedstock. Lignocellulosic feedstocks contain a wide range of sugars, which cannot be fermented by *S. cerevisiae*. One reason could be the ecology and niche preferences, since *S. cerevisiae* is a fruit sugar yeast whose niches in ripening and rotting fruits do not contain lignocellulosic sugars. It evolved to ferment a wide range of hexose sugars found in fruits and subsequently producing ethanol as a niche engineering strategy [2, 32, 72]. Its high ethanol tolerance made it the most employed yeast for industrial ethanol production. In addition to this attribute, its GRAS (generally regarded as a safe microorganism) status by the US FDA Organization, its genetic amenability, and its well-established systems-level attributes made it an ideal organism, which also accounts for its monopoly. Pentose sugars and sugar polymers represent a significant proportion of sugars in inexpensive and abundant lignocellulosic feedstocks [32]. Xylose, arabinose, glucose, galactose, and mannose are examples of key sugars present in lignocellulosic feedstocks [73–75]. The ability of yeasts to assimilate even a small amount of a variety of all available sugars enhances the productivity of the bioethanol production process and subsequently increases its economic feasibility [32]. Some researchers have reported several yeasts such as *Pichia* spp, *Candida* spp, *Brettanomyces spp*, *Scheffersomyces* spp, and others that can ferment xylose albeit at lower yields for sustainable production [46]. Cofermentation of key hexoses and pentoses has been touted as attractive in the reduction of the uneconomical fermentation time when pentoses are fermented, after the exhaustion of hexoses. This strategy is known to increase the economic feasibility of bioethanol [32]. Numerous approaches to enhance bioethanol production by the introduction of pentose pathways into yeasts strains via metabolic engineering have been reported [39, 40, 76–79]. Another approach would be to scout for yeasts that can utilize and ferment a wide range of sugars from nature. Such strains can be used as they are, or their genetic novelty can be used for reverse metabolic engineering of robust strains.

Current sources of extremophilic yeasts for bioethanol fermentations

Yeasts with extremophilic traits are ideally important for the improvement of the efficiency of bioethanol production. Several extremophilic traits have been documented (Table 1). In general, stress tolerance is known among non-conventional yeasts. Some noticeable genera include *Saccharomyces spp* [15, 32, 80–82], *Schizosaccharoymces spp* [15, 32], *Dekkera spp* [15, 83–85], *Pichia spp* [32], *Pachysolen spp* [15], and *Kluyveromyces spp* [80–82]. Thermotolerance is one of the most desirable characteristics of a bioethanol production strain. Alcoholic fermentation during simultaneous saccharification and fermentation is carried out at elevated temperatures. This decreases cooling costs, lowers the risk of contamination, and increases ethanol yields [32]. *Ogataea* (*Hansenula) polymorpha, Pichia kudriavzevii* (=*Issatchenkia orientalis*=*Candida krusei*), and *K. marxianus* are well-known thermotolerant yeasts [86–88]. *O polymorpha* is a methylotrophic yeast with thermotolerant traits, whose ability to ferment xylose is advantageous in bioethanol fermentation [89–91]. *P. kudriavzevii* although an opportunistic pathogen, has been identified as a multi-stress tolerant yeast that can be used for bioethanol production. It can tolerate elevated temperatures, high sugar concentrations, furan derivatives, and weak acids (e.g., acetic acid) (Table 1). Thermotolerant yeast, such as *K. marxianus* (Table 1), can assimilate various sugars like xylose, cellobiose, lactose, and arabinose [91]. Osmotolerance is another desirable attribute of bioethanol fermenting yeasts. Non-conventional yeast species such as *Zygosaccharomyces rouxii* and *Zygosaccharomyces bailii* are known to possess outstanding osmotolerant abilities (Table 1), even though their ethanol production capacity is poor [32].

Other yeasts with beneficial traits have also been isolated. *Pichia stipitis, Candida shehatae,* and *Pachysolen tannophilus* have in common xylose fermentation abilities [16, 32, 92–94]. The recently described *Spathaspora passalidarum* also has xylose fermentation attributes [74, 90, 94–97].

Sources of yeasts currently used in bioethanol production

Yeasts currently used for bioethanol fermentation have been isolated from different sources (Table 2). However, these yeast strains have not sufficiently addressed the current challenges of stream-lined carbon substrate utilization range, poor stress tolerance, and low ethanol productivity.

Described methods and advances in isolation of yeasts from dung beetles

Dung beetles harbour yeasts in their guts in either a mutualistic or symbiotic relationship [143]. The precise roles of yeasts in specific sections of the dung beetle guts (foregut, midgut, and hindgut) could yield yeasts adapted to different niches whose potential in bioethanol

Table 2 Sources of potential yeasts for bioethanol production

Source	Yeast species	References
Wines	*D. bruxellensis*	[56, 99, 122, 127]
	W. anomalus	[128]
	Pichia kluyveri	[128, 129]
	T. delbrueckii	[128, 129]
Insects	*S. passalidarum*	[74, 95–97, 130, 131]
	D. bruxellensis	[54, 59]
	K. marxianus	[54]
	O. polymorpha	[54, 59, 132]
	W. anomalus	[132–134]
	P. kudriavzevii	[54, 133]
	M. pulcherrima	[58, 59, 133, 135]
Fruits	*M. pulcherrima*	[61, 135, 136]
	P. kluyveri	[136]
	P. kudriavzevii	[136]
Sugarcane juice	*P. kudriavzevii*	[137]
	O. polymorpha	[137]
	K. marxianus	[102]
Cocoa bean	*P. kudriavzevii*	[113, 138, 139]
	P. kluyveri	[139, 140]
Cheese	*P. kudriavzevii*	[113, 141]
	K. marxianus	[91, 141]
	T. delbrueckii	[141]
	D. bruxellensis	[142]
	W. anomalus	[141]

production needs to be explored. Isolation of yeasts from dung beetles was extensively studied by [65]. Dung beetles are starved for some days to reduce the microbial populations as well as removing contaminating organisms [144, 145]. As a strategy to exclude non-resident surface microorganisms, beetles are initially surface disinfected with ethanol and rinsed with saline to wash off excess ethanol before dissection [65, 144–146]. After dissection, removal of guts is carried out aseptically before chopping them into pieces for isolation of resident yeasts. Alternatively, the legs, wings, and elytra can be removed before grinding the remaining body parts to isolate yeasts [66]. Use of homogenised gut contents as inoculum for selective isolation of yeasts with a specific phenotype using enrichment media supplemented with targeted compounds, such as preferred carbon sources, nitrogen sources, vitamin sources, and compounds supplying trace elements, or a specific stressor environment is common. As with the norm in isolation of yeasts, inhibition of growth of contaminating bacteria and moulds is carried out using antibiotics as well as using media with growth inhibitory compounds such as dichloran or biphenyl [147]. Culturing yeasts by simply streaking into an appropriate medium, without enrichment or after serial dilutions and subsequent plating of the suspensions into selective media agar [52, 144, 145], has been well documented to be successful. Single yeast colonies can then be isolated and verified using morphological, physiological, and biochemical tests. With the advent of DNA sequencing and sequence analysis technologies, the use of molecular approaches has become the most preferred for rapid and accurate identification of yeasts.

Yeasts can be selected for their abilities to consume different carbon sources by growing them on Yeast Extract Peptone Dextrose (YPD) media and substituting the dextrose with other carbon sources. Similarly, to select yeasts with abilities to tolerate different stresses, they can be grown in YPD media containing stressors (e.g., acetic acid, furfural, formic acid, and ethanol) of varying concentrations.

To check for the ability of yeasts to ferment a variety of sugars, they can be grown in fermentation media as described by [67], in test tubes containing Durham tubes and incubating at 30 °C for about 5 days. The presence of a gas bubble in the Durham tube will indicate that the yeast ferments the sugar [67].

Conclusion and future of yeasts from dung beetles in producing bioethanol

Bioethanol has the potential to reduce greenhouse gas emissions. One noteworthy drawback of the petroleum fuel alternative is its economic feasibility due to the soaring costs of its production. One way to increase the feasibility of bioethanol development is a cost-effective bioprocess such as the utilization of inexpensive industrial and agro-industrial lignocellulosic feedstocks. However, there is a limited choice of robust yeasts with extreme traits needed to efficiently produce high ethanol titres for the feasibility of bioethanol commercialization. Due to the rich lignocellulose diet that dung beetles survive on, the isolation of specialised lignocellulosic degrading yeasts was proposed. Exploration of robust yeasts with novel traits from novel reservoirs needed to advance bioethanol production processes by reducing production costs, enhancing pre-treatment methods, and increasing ethanol yields is an attractive strategy that can be used to decrease greenhouse gas emissions. This augments the feasibility of conventional bioethanol production processes.

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NZ, TB, and KR conceived the idea to explore dung beetles associated yeasts with potential in bioethanol feasibility. AEN, KR, TB, and NZ wrote the paper. All authors read and approved the final manuscript.

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References

1. Pinaki D, Lhakpa W, Joginder S. Simultaneous saccharification and fermentation (SSF), an efficient process for bio-ethanol production: an overview. Biosci Biotechnol Res Asia. 2015;12(1):87–100.
2. Balat M, Balat H, Öz C. Progress in bioethanol processing. Progr Energy Combust Sci. 2008;34(5):551–73.
3. Olofsson K, Bertilsson M, Lidén G. A short review on SSF–an interesting process option for ethanol production from lignocellulosic feedstocks. Biotechnol Biofuels. 2008;1(1):7.
4. Petrova P, Ivanova V. Perspectives for the production of bioethanol from lignocellulosic materials. Biotechnol Biotechnol Equip. 2010;24(sup1):529–46.
5. Balat M, Balat H. Recent trends in global production and utilization of bio-ethanol fuel. Appl Energy. 2009;86(11):2273–82.
6. Soccol CR, Faraco V, Karp SG, Vandenberghe LP, Thomaz-Soccol V, Woiciechowski AL, Pandey A: Lignocellulosic bioethanol: current status and future perspectives. In: Biofuels: Alternative Feedstocks and Conversion Processes for the Production of Liquid and Gaseous Biofuels. Elsevier; 2019: 331–354.
7. Yuan H-w, Tan L, Kida K, Morimura S, Sun Z-Y, Tang Y-Q. Potential for reduced water consumption in biorefining of lignocellulosic biomass to bioethanol and biogas. J Biosci Bioeng. 2021. https://doi.org/10.1016/j.jbiosc.2020.12.015.
8. Santos GJTP. Road transport and CO2 emissions: What are the challenges? Transp Policy. 2017;59:71–4.
9. Shaheen SA, Lipman TE. Reducing greenhouse emissions and fuel consumption: sustainable approaches for surface transportation. IATSS Res. 2007;31(1):6–20.
10. Kang Q, Appels L, Tan T, Dewil R. Bioethanol from lignocellulosic biomass: current findings determine research priorities. Sci World J. 2014;2014:298153.
11. Wyman CE. Biomass ethanol: technical progress, opportunities, and commercial challenges. Annu Rev Energy Env. 1999;24(1):189–226.
12. Ramos JL, Valdivia M, García-Lorente F, Segura A. Benefits and perspectives on the use of biofuels. Microb Biotechnol. 2016;9(4):436–40.
13. Saini JK, Saini R, Tewari L. Lignocellulosic agriculture wastes as biomass feedstocks for second-generation bioethanol production: concepts and recent developments. 3 Biotech. 2015;5(4):337–53.
14. Sánchez C. Lignocellulosic residues: biodegradation and bioconversion by fungi. Biotechnol Adv. 2009;27(2):185–94.
15. Basso LC, De Amorim HV, De Oliveira AJ, Lopes ML. Yeast selection for fuel ethanol production in Brazil. FEMS Yeast Res. 2008;8(7):1155–63.
16. Zaldivar J, Nielsen J, Olsson L. Fuel ethanol production from lignocellulose: a challenge for metabolic engineering and process integration. Appl Microbiol Biotechnol. 2001;56(1–2):17–34.
17. Branco RH, Serafim LS, Xavier AM. Second generation bioethanol production: On the use of pulp and paper industry wastes as feedstock. Fermentation. 2019;5(1):4.
18. Sarkar N, Ghosh SK, Bannerjee S, Aikat K. Bioethanol production from agricultural wastes: an overview. Renew Energy. 2012;37(1):19–27.
19. Vohra M, Manwar J, Manmode R, Padgilwar S, Patil S. Bioethanol production: feedstock and current technologies. J Environ Chem Eng. 2014;2(1):573–84.
20. Jönsson LJ, Alriksson B, Nilvebrant N-O. Bioconversion of lignocellulose: inhibitors and detoxification. Biotechnol Biofuels. 2013;6(1):16.
21. Rosillo-Calle F. Food versus fuel: toward a new paradigm—the need for a holistic approach. ISRN Renew Energy. 2012. https://doi.org/10.5402/2012/954180.
22. Rosegrant MW, Msangi S. Consensus and contention in the food-versus-fuel debate. Annu Rev Environ Resour. 2014;39:271–94.
23. Elobeid A, Hart C. Ethanol expansion in the food versus fuel debate: how will developing countries fare? J Agric Food Indust Organizat. 2007;5(2):6.
24. Ruyters S, Mukherjee V, Verstrepen KJ, Thevelein JM, Willems KA, Lievens B. Assessing the potential of wild yeasts for bioethanol production. J Ind Microbiol Biotechnol. 2015;42(1):39–48.
25. Halder P, Azad K, Shah S, Sarker E: Prospects and technological advancement of cellulosic bioethanol ecofuel production. In: Advances in eco-fuels for a sustainable environment. Elsevier; 2019: 211–236.
26. Zabed H, Faruq G, Sahu JN, Azirun MS, Hashim R, Nasrulhaq Boyce A. Bioethanol production from fermentable sugar juice. Sci World J. 2014;2014:193.
27. Devarapalli M, Atiyeh HK. A review of conversion processes for bioethanol production with a focus on syngas fermentation. Biofuel Res J. 2015;2(3):268–80.
28. Robak K, Balcerek M. Review of second generation bioethanol production from residual biomass. Food Technol Biotechnol. 2018;56(2):174–87.
29. Buruiana C-T, Garrote G, Vizireanu C. Bioethanol production from residual lignocellulosic materials: a review-Part 1. Annals of the University Dunarea de Jos of Galati Fascicle VI--Food Technol. 2013;37(1):9–24.
30. Dimos K, Paschos T, Louloudi A, Kalogiannis KG, Lappas AA, Papayannakos N, Kekos D, Mamma D. Effect of various pretreatment methods on bioethanol production from cotton stalks. Fermentation. 2019;5(1):5.
31. Harun R, Liu B, Danquah MK: Analysis of process configurations for bioethanol production from microalgal biomass. Progress in Biomass and Bioenergy Pro-duction InTech 2011:395–409.
32. Azhar SHM, Abdulla R, Jambo SA, Marbawi H, Gansau JA, Faik AAM, Rodrigues KF. Yeasts in sustainable bioethanol production: a review. Biochem Biophys Rep. 2017;10:52–61.
33. Sims RE, Mabee W, Saddler JN, Taylor M. An overview of second generation biofuel technologies. Biores Technol. 2010;101(6):1570–80.
34. Amin FR, Khalid H, Zhang H, u Rahman S, Zhang R, Liu G, Chen C. Pretreatment methods of lignocellulosic biomass for anaerobic digestion. AMB Express. 2017;7(1):72.
35. Balan V. Current challenges in commercially producing biofuels from lignocellulosic biomass. Int Scholar Res Notices. 2014;2014:463074.
36. Bušić A, Marđetko N, Kundas S, Morzak G, Belskaya H, Šantek MI, Komes D, Novak S, Šantek B. Bioethanol production from renewable raw materials and its separation and purification: a review. Food Technol Biotechnol. 2018;56(3):289.
37. Amin FR, Khalid H, Zhang H, Rahman SU, Zhang R, Liu G, Chen C. Pretreatment methods of lignocellulosic biomass for anaerobic digestion. AMB Express. 2017;7(1):72.
38. Jönsson LJ, Martín C. Pretreatment of lignocellulose: formation of inhibitory by-products and strategies for minimizing their effects. Biores Technol. 2016;199:103–12.

39. Moysés DN, Reis VCB, Almeida JR, Moraes LM, Torres FA. Xylose fermentation by *Saccharomyces cerevisiae*: challenges and prospects. Int J Mol Sci. 2016;17(3):207.
40. Steensels J, Snoek T, Meersman E, Nicolino MP, Voordeckers K, Verstrepen KJ. Improving industrial yeast strains: exploiting natural and artificial diversity. FEMS Microbiol Rev. 2014;38(5):947–95.
41. Rao R, Bhadra B, Shivaji S. Isolation and characterization of ethanol-producing yeasts from fruits and tree barks. Lett Appl Microbiol. 2008;47(1):19–24.
42. Dashtban M, Schraft H, Qin W. Fungal bioconversion of lignocellulosic residues; opportunities & perspectives. Int J Biol Sci. 2009;5(6):578.
43. Deparis Q, Claes A, Foulquié-Moreno MR, Thevelein JM. Engineering tolerance to industrially relevant stress factors in yeast cell factories. FEMS Yeast Res. 2017;17(4):fox036.
44. Haq F, Ali H, Shuaib M, Badshah M, Hassan SW, Munis MFH, Chaudhary HJ. Recent progress in bioethanol production from lignocellulosic materials: a review. Int J Green Energy. 2016;13(14):1413–41.
45. Lane MM, Morrissey JP. Kluyveromyces marxianus: a yeast emerging from its sister's shadow. Fungal Biol Rev. 2010;24(1–2):17–26.
46. Arora R, Behera S, Sharma NK, Kumar S. A new search for thermotolerant yeasts, its characterization and optimization using response surface methodology for ethanol production. Front Microbiol. 2015;6:889.
47. Mabhegedhe M. Cellulolytic activities of the dung beetle, Euoniticellus intermedius, larva gut micro-flora. Open Biotechnol J. 2017;11(1):105–13.
48. Mabhegedhe M, Rumbold K, Ntwasa M. Cellulose degradation capabilities of dung beetle, Euoniticellus intermedius, larva gut consortia. Afr J Biotech. 2016;15(9):315–9.
49. Thiyonila B, Reneeta N, Kannan M, Shantkriti S, Krishnan M. Dung beetle gut microbes: diversity, metabolic and immunity related roles in host system. Int J Sci Innovat. 2018;1(2):84–91.
50. Holter P. Herbivore dung as food for dung beetles: elementary coprology for entomologists. Ecol Entomol. 2016;41(4):367–77.
51. Estes AM, Hearn DJ, Snell-Rood EC, Feindler M, Feeser K, Abebe T, Hotopp JCD, Moczek AP. Brood ball-mediated transmission of microbiome members in the dung beetle, Onthophagus taurus (Coleoptera: Scarabaeidae). PLoS ONE. 2013;8(11):e79061.
52. Suh SO, Marshall CJ, Mchugh JV, Blackwell M. Wood ingestion by passalid beetles in the presence of xylose-fermenting gut yeasts. Mol Ecol. 2003;12(11):3137–45.
53. Madden AA, Epps MJ, Fukami T, Irwin RE, Sheppard J, Sorger DM, Dunn RR. The ecology of insect–yeast relationships and its relevance to human industry. Proceed Royal Soc B Biol Sci. 1875;2018(285):20172733.
54. Stefanini I. Yeast-insect associations: It takes guts. Yeast. 2018;35(4):315–30.
55. Starmer WT, Lachance M-A. Yeast ecology. In: The yeasts. Elsevier; 2011: 65–83.
56. Becher PG, Hagman A, Verschut V, Chakraborty A, Rozpędowska E, Lebreton S, Bengtsson M, Flick G, Witzgall P, Piškur J. Chemical signaling and insect attraction is a conserved trait in yeasts. Ecol Evol. 2018;8(5):2962–74.
57. Douglas AE. The microbial dimension in insect nutritional ecology. Funct Ecol. 2009;23(1):38–47.
58. Vega FE, Dowd PF. The role of yeasts as insect endosymbionts. New York: Insect-Fungal Associations: Ecology and Evolution Oxford University Press; 2005. p. 211–43.
59. Ganter PF. Yeast and invertebrate associations. In: Biodiversity and ecophysiology of yeasts. Springer; 2006: 303–370.
60. Brune A. Symbionts aiding digestion. In: Encyclopedia of Insects (Second Edition). Elsevier; 2009: 978–983.
61. Andreadis SS, Witzgall P, Becher PG. Survey of arthropod assemblages responding to live yeasts in an organic apple orchard. Front Ecol Evol. 2015;3:121.
62. Palanca L, Gaskett AC, Günther CS, Newcomb RD, Goddard MR. Quantifying variation in the ability of yeasts to attract Drosophila melanogaster. PLoS ONE. 2013;8(9):e75332.
63. Ali SS, Wu J, Xie R, Zhou F, Sun J, Huang M. Screening and characterizing of xylanolytic and xylose-fermenting yeasts isolated from the wood-feeding termite, Reticulitermes chinensis. PLoS ONE. 2017;12(7):e0181141.
64. Barriga EJC, Libkind D, Briones AI, Iranzo J, Portero P, Roberts I, James S, Morais PB, Rosa CA. Yeasts biodiversity and its significance: case studies in natural and human-related environments, ex situ preservation, applications and challenges. Changing Diversity in Changing Environment 2011:55–86.
65. Sung-Oui S, McHUGH JV, Pollock DD, Blackwell M. The beetle gut: a hyperdiverse source of novel yeasts. Mycol Res. 2005;109(3):261–5.
66. Kunthiphun S, Endoh R, Takashima M, Ohkuma M, Tanasupawat S, Akaracharanya A. Trichosporon heliocopridis sp nov, a urease-negative basidiomycetous yeast associated with dung beetles (Heliocopris bucephalus Fabricius). Int J Syst Evolut Microbiol. 2016;66(3):1180–6.
67. Moremi ME, Van Rensburg EL, La Grange DC. The improvement of bioethanol production by pentose-fermenting yeasts isolated from herbal preparations, the gut of dung beetles, and marula wine. Int J Microbiol. 2020;2020:13.
68. Moreno AD, Carbone A, Pavone R, Olsson L, Geijer C. Evolutionary engineered Candida intermedia exhibits improved xylose utilization and robustness to lignocellulose-derived inhibitors and ethanol. Appl Microbiol Biotechnol. 2019;103(3):1405–16.
69. Dashko S, Zhou N, Compagno C, Piškur J. Why, when, and how did yeast evolve alcoholic fermentation? FEMS Yeast Res. 2014;14(6):826–32.
70. Kang A, Lee TS. Converting sugars to biofuels: ethanol and beyond. Bioengineering. 2015;2(4):184–203.
71. Berłowska J, Pielech-Przybylska K, Balcerek M, Dziekońska-Kubczak U, Patelski P, Dziugan P, Kręgiel D. Simultaneous saccharification and fermentation of sugar beet pulp for efficient bioethanol production. BioMed Res Int. 2016;2016:188–96.
72. Chandel AK, Singh OV, Chandrasekhar G, Rao LV, Narasu ML. Key drivers influencing the commercialization of ethanol-based biorefineries. J Commer Biotechnol. 2010;16(3):239–57.
73. Karagöz P, Özkan M. Ethanol production from wheat straw by *Saccharomyces cerevisiae* and *Scheffersomyces stipitis* co-culture in batch and continuous system. Bioresour Technol. 2014;158:286.
74. Long TM, Su Y-K, Headman J, Higbee A, Willis LB, Jeffries TW. Cofermentation of glucose, xylose, and cellobiose by the beetle-associated yeast Spathaspora passalidarum. Appl Environ Microbiol. 2012;78(16):5492–500.
75. Ho NW, Chen Z, Brainard AP, Sedlak M. Successful design and development of genetically engineered Saccharomyces yeasts for effective cofermentation of glucose and xylose from cellulosic biomass to fuel ethanol. In: Recent Progress in Bioconversion of Lignocellulosics. Springer; 1999: 163–192.
76. Demeke MM, Dietz H, Li Y, Foulquié-Moreno MR, Mutturi S, Deprez S, Den Abt T, Bonini BM, Liden G, Dumortier F. Development of a D-xylose fermenting and inhibitor tolerant industrial *Saccharomyces cerevisiae* strain with high performance in lignocellulose hydrolysates using metabolic and evolutionary engineering. Biotechnol Biofuels. 2013;6(1):89.
77. Jansen ML, Bracher JM, Papapetridis I, Verhoeven MD, de Bruijn H, de Waal PP, van Maris AJ, Klaassen P, Pronk JT. *Saccharomyces cerevisiae* strains for second-generation ethanol production: from academic exploration to industrial implementation. FEMS Yeast Res. 2017;17(5):fox044.
78. Selim KA, El-Ghwas DE, Easa SM, Hassan A, Mohamed I. Bioethanol a microbial biofuel metabolite; new insights of yeasts metabolic engineering. Fermentation. 2018;4(1):16.
79. Lugani Y, Rai R, Prabhu AA, Maan P, Hans M, Kumar V, Kumar S, Chandel AK, Sengar RS. Recent advances in bioethanol production from lignocelluloses: a comprehensive review with a focus on enzyme engineering and designer biocatalysts. 2020.
80. Amaya-Delgado L, Flores-Cosío G, Sandoval-Nuñez D, Arellano-Plaza M, Arrizon J, Gschaedler A. Comparative of Lignocellulosic Ethanol Production by Kluyveromyces marxianus and *Saccharomyces cerevisiae*. In: Special Topics in Renewable Energy Systems. IntechOpen; 2018.
81. Zafar S, Owais M. Ethanol production from crude whey by Kluyveromyces marxianus. Biochem Eng J. 2006;27(3):295–8.
82. Goshima T, Tsuji M, Inoue H, Yano S, Hoshino T, Matsushika A. Bioethanol production from lignocellulosic biomass by a novel Kluyveromyces marxianus strain. Biosci Biotechnol Biochem. 2013;77:130173.
83. Codato CB, Martini C, Ceccato-Antonini SR, Bastos RG. Ethanol production from *Dekkera bruxellensis* in synthetic media with pentose. Braz J Chem Eng. 2018;35(1):11–7.

84. Galafassi S, Merico A, Pizza F, Hellborg L, Molinari F, Piškur J, Compagno C. Dekkera/Brettanomyces yeasts for ethanol production from renewable sources under oxygen-limited and low-pH conditions. J Ind Microbiol Biotechnol. 2011;38(8):1079–88.
85. de Barros PW, Teles GH, Peña-Moreno IC, da Silva JM, Ribeiro KC, de Morais Junior MA. The biotechnological potential of the yeast *Dekkera bruxellensis*. World J Microbiol Biotechnol. 2019;35(7):103.
86. Mukherjee V, Radecka D, Aerts G, Verstrepen KJ, Lievens B, Thevelein JM. Phenotypic landscape of non-conventional yeast species for different stress tolerance traits desirable in bioethanol fermentation. Biotechnol Biofuels. 2017;10(1):216.
87. Lehnen M, Ebert BE, Blank LM. Elevated temperatures do not trigger a conserved metabolic network response among thermotolerant yeasts. BMC Microbiol. 2019;19(1):100.
88. Buzzini P, Turchetti B, Yurkov A. Extremophilic yeasts: the toughest yeasts around? Yeast. 2018;35(8):487–97.
89. Ryabova OB, Chmil OM, Sibirny AA. Xylose and cellobiose fermentation to ethanol by the thermotolerant methylotrophic yeast *Hansenula polymorpha*. FEMS Yeast Res. 2003;4(2):157–64.
90. Kurylenko OO, Ruchala J, Hryniv OB, Abbas CA, Dmytruk KV, Sibirny AA. Metabolic engineering and classical selection of the methylotrophic thermotolerant yeast *Hansenula polymorpha* for improvement of high-temperature xylose alcoholic fermentation. Microb Cell Fact. 2014;13(1):122.
91. Radecka D, Foulquié-Moreno MR, Stojiljkovic M, Mateo RQ, Thevelein JM, Mukherjee V. Looking beyond Saccharomyces: the potential of non-conventional yeast species for desirable traits in bioethanol fermentation. FEMS Yeast Res. 2015;15(6):053.
92. Kumar A, Singh L, Ghosh S. Bioconversion of lignocellulosic fraction of water-hyacinth (Eichhornia crassipes) hemicellulose acid hydrolysate to ethanol by Pichia stipitis. Bioresour Technol. 2009;100(13):3293–7.
93. Aditiya H, Mahlia TMI, Chong W, Nur H, Sebayang A. Second generation bioethanol production: a critical review. Renew Sustain Energy Rev. 2016;66:631–53.
94. Selim KA, Easa SM, El-Diwany AI. The xylose metabolizing yeast Spathaspora passalidarum is a promising genetic treasure for improving bioethanol production. Fermentation. 2020;6(1):33.
95. Hou X. Anaerobic xylose fermentation by Spathaspora passalidarum. Appl Microbiol Biotechnol. 2012;94(1):205–14.
96. Cadete RM, Alejandro M, Sandström AG, Ferreira C, Gírio F, Gorwa-Grauslund M-F, Rosa CA, Fonseca C. Exploring xylose metabolism in Spathaspora species: XYL1. 2 from Spathaspora passalidarum as the key for efficient anaerobic xylose fermentation in metabolic engineered *Saccharomyces cerevisiae*. Biotechnol Biofuels. 2016;9(1):167.
97. Lopes MR, Morais CG, Kominek J, Cadete RM, Soares MA, Uetanabaro APT, Fonseca C, Lachance M-A, Hittinger CT, Rosa CA. Genomic analysis and D-xylose fermentation of three novel Spathaspora species: Spathaspora girioi sp. nov., Spathaspora hagerdaliae fa, sp. nov. and Spathaspora gorwiae fa, sp. nov. FEMS Yeast Res. 2016;16(4):044.
98. Benjaphokee S, Hasegawa D, Yokota D, Asvarak T, Auesukaree C, Sugiyama M, Kaneko Y, Boonchird C, Harashima S. Highly efficient bioethanol production by a *Saccharomyces cerevisiae* strain with multiple stress tolerance to high temperature, acid and ethanol. New Biotechnol. 2012;29(3):379–86.
99. Blomqvist J, Passoth V. *Dekkera bruxellensis*—spoilage yeast with biotechnological potential, and a model for yeast evolution, physiology and competitiveness. FEMS Yeast Res. 2015;15(4):fov21.
100. Passoth V, Sandgren M. Biofuel production from straw hydrolysates: current achievements and perspectives. Appl Microbiol Biotechnol. 2019;103(13):5105–16.
101. Fonseca GG, Heinzle E, Wittmann C, Gombert AK. The yeast Kluyveromyces marxianus and its biotechnological potential. Appl Microbiol Biotechnol. 2008;79(3):339–54.
102. Limtong S, Sringiew C, Yongmanitchai W. Production of fuel ethanol at high temperature from sugar cane juice by a newly isolated Kluyveromyces marxianus. Biores Technol. 2007;98(17):3367–74.
103. Hahn-Hägerdal B, Jeppsson H, Skoog K, Prior B. Biochemistry and physiology of xylose fermentation by yeasts. Enzyme Microb Technol. 1994;16(11):933–43.
104. Tomás-Pejó E, Oliva J, González A, Ballesteros I, Ballesteros M. Bioethanol production from wheat straw by the thermotolerant yeast Kluyveromyces marxianus CECT 10875 in a simultaneous saccharification and fermentation fed-batch process. Fuel. 2009;88(11):2142–7.
105. Lachance M-A: Kluyveromyces van der Walt (1971). In: The Yeasts. Elsevier; 2011: 471–481.
106. Fröhlich-Wyder MT, Arias-Roth E, Jakob E. Cheese yeasts. Yeast. 2019;36(3):129–41.
107. Talukder AA, Easmin F, Mahmud SA, Yamada M. Thermotolerant yeasts capable of producing bioethanol: isolation from natural fermented sources, identification and characterization. Biotechnol Biotechnol Equip. 2016;30(6):1106–14.
108. Kosaka T, Lertwattanasakul N, Rodrussamee N, Nurcholis M, Dung NTP, Keo-Oudone C, Murata M, Götz P, Theodoropoulos C, Maligan JM. Potential of Thermotolerant Ethanologenic Yeasts Isolated from ASEAN Countries and Their Application in High-Temperature Fermentation. In: Fuel Ethanol Production from Sugarcane. IntechOpen; 2018.
109. Makhuvele R, Ncube I, van Rensburg ELJ, La Grange DC. Isolation of fungi from dung of wild herbivores for application in bioethanol production. Brazilian J Microbiol. 2017;48(4):648–55.
110. Dhaliwal SS, Oberoi HS, Sandhu SK, Nanda D, Kumar D, Uppal SK. Enhanced ethanol production from sugarcane juice by galactose adaptation of a newly isolated thermotolerant strain of *Pichia kudriavzevii*. Bioresour Technol. 2011;102(10):5968–75.
111. Isono N, Hayakawa H, Usami A, Mishima T, Hisamatsu M. A comparative study of ethanol production by *Issatchenkia orientalis* strains under stress conditions. J Biosci Bioeng. 2012;113(1):76–8.
112. Oberoi HS, Babbar N, Sandhu SK, Dhaliwal SS, Kaur U, Chadha B, Bhargav VK. Ethanol production from alkali-treated rice straw via simultaneous saccharification and fermentation using newly isolated thermotolerant *Pichia kudriavzevii* HOP-1. J Ind Microbiol Biotechnol. 2012;39(4):557–66.
113. Chamnipa N, Thanonkeo S, Klanrit P. Thanonkeo PJbjom: The potential of the newly isolated thermotolerant yeast *Pichia kudriavzevii* RZ8–1 for high-temperature ethanol production. Brazilian J Microbiol. 2018;49(2):378–91.
114. Martorell P, Stratford M, Steels H, Fernández-Espinar MT, Querol A. Physiological characterization of spoilage strains of *Zygosaccharomyces bailii* and *Zygosaccharomyces rouxii* isolated from high sugar environments. Int J Food Microbiol. 2007;114(2):234–42.
115. Fleet GH: Yeast spoilage of foods and beverages. In: The yeasts. Elsevier; 2011: 53–63.
116. Michel M, Meier-Dörnberg T, Jacob F, Methner FJ, Wagner RS, Hutzler M. Pure non-Saccharomyces starter cultures for beer fermentation with a focus on secondary metabolites and practical applications. J Inst Brew. 2016;122(4):569–87.
117. Breuer U, Harms H. *Debaryomyces hansenii*—an extremophilic yeast with biotechnological potential. Yeast. 2006;23(6):415–37.
118. Vigentini I, Brambilla L, Branduardi P, Merico A, Porro D, Compagno C. Heterologous protein production in *Zygosaccharomyces bailii*: physiological effects and fermentative strategies. FEMS Yeast Res. 2005;5(6–7):647–52.
119. Sipiczki M. Overwintering of vineyard yeasts: survival of interacting yeast communities in grapes mummified on vines. Front Microbiol. 2016;7:212.
120. Johnson EA, Echavarri-Erasun C: Yeast biotechnology. In: The yeasts. Elsevier; 2011: 21–44.
121. Ruchala J, Kurylenko OO, Dmytruk KV, Sibirny AA. Construction of advanced producers of first-and second-generation ethanol in *Saccharomyces cerevisiae* and selected species of non-conventional yeasts (*Scheffersomyces stipitis*, *Ogataea polymorpha*). J Ind Microbiol Biotechnol. 2020;47(1):109–32.
122. Schifferdecker AJ, Dashko S, Ishchuk OP, Piškur J. The wine and beer yeast *Dekkera bruxellensis*. Yeast. 2014;31(9):323–32.
123. Benito Á, Calderón F, Benito S. The influence of non-saccharomyces species on wine fermentation quality parameters. Fermentation. 2019;5(3):54.
124. Kwon Y-J, Ma A-Z, Li Q, Wang F, Zhuang G-Q, Liu C-Z. Effect of lignocellulosic inhibitory compounds on growth and ethanol fermentation of newly-isolated thermotolerant *Issatchenkia orientalis*. Biores Technol. 2011;102(17):8099–104.

125. Matsushika A, Negi K, Suzuki T, Goshima T, Hoshino T. Identification and characterization of a novel *Issatchenkia orientalis* GPI-Anchored protein, IoGas1, required for resistance to low pH and salt stress. PLoS ONE. 2016;11(9):e0161888.
126. Martorell P, Fernández-Espinar MT, Querol A. Molecular monitoring of spoilage yeasts during the production of candied fruit nougats to determine food contamination sources. Int J Food Microbiol. 2005;101(3):293–302.
127. Passoth V, Blomqvist J, Schnürer J. *Dekkera bruxellensis* and *Lactobacillus vini* form a stable ethanol-producing consortium in a commercial alcohol production process. Appl Environ Microbiol. 2007;73(13):4354–6.
128. Díaz C, Molina AM, Nähring J, Fischer R. Characterization and dynamic behavior of wild yeast during spontaneous wine fermentation in steel tanks and amphorae. BioMed Res Int. 2013;2013:540465.
129. Çelik ZD, Erten H, Darici M, Cabaroğlu T: Molecular characterization and technological properties of wine yeasts isolated during spontaneous fermentation of *Vitis vinifera L*. cv. Narince grape must grown in ancient wine making area Tokat, Anatolia. In: BIO Web of Conferences: 2017. EDP Sciences: 02017.
130. Tikka C, Osuru HP, Atluri N. Raghavulu PCVJB: Isolation and characterization of ethanol tolerant yeast strains. Bioinformation. 2013;9(8):421.
131. Suh S-O, Nguyen NH, Blackwell M. Yeasts isolated from plant-associated beetles and other insects: seven novel Candida species near Candida albicans. FEMS Yeast Res. 2008;8(1):88–102.
132. Sandhu DK, Waraich MK. Yeasts associated with pollinating bees and flower nectar. Microb Ecol. 1985;11(1):51–8.
133. Urubschurov V, Janczyk P. Biodiversity of yeasts in the gastrointestinal ecosystem with emphasis on its importance for the host. The dynamical processes of biodiversity-Case studies of evolution and spatial distribution. 2011:277–302.
134. Tauber JP, Nguyen V, Lopez D, Evans JD. Effects of a resident yeast from the honeybee gut on immunity, microbiota, and nosema disease. Insects. 2019;10(9):296.
135. Lachance M-A: Metschnikowia Kamienski (1899). In: The Yeasts. Elsevier; 2011: 575–620.
136. Vadkertiová R, Molnárová J, Vránová D, Sláviková E. Yeasts and yeast-like organisms associated with fruits and blossoms of different fruit trees. Can J Microbiol. 2012;58(12):1344–52.
137. Tolieng V, Kunthiphun S, Savarajara A, Tanasupawat S. Diversity of yeasts and their ethanol production at high temperature. J Appl Pharm Sci. 2018;8:136–42.
138. Daniel H-M, Vrancken G, Takrama JF, Camu N, De Vos P, De Vuyst L. Yeast diversity of Ghanaian cocoa bean heap fermentations. FEMS Yeast Res. 2009;9(5):774–83.
139. Sarbu I, Csutak O: The Microbiology of Cocoa Fermentation. In: Caffeinated and Cocoa Based Beverages. Elsevier; 2019: 423–446.
140. Batista NN, Ramos CL, Ribeiro DD, Pinheiro ACM, Schwan RF. Dynamic behavior of *Saccharomyces cerevisiae*, *Pichia kluyveri* and Hanseniaspora uvarum during spontaneous and inoculated cocoa fermentations and their effect on sensory characteristics of chocolate. LWT-Food Sci Technol. 2015;63(1):221–7.
141. Prillinger H, Molnár O, Eliskases-Lechner F, Lopandic K. Phenotypic and genotypic identification of yeasts from cheese. Antonie Van Leeuwenhoek. 1999;75(4):267–83.
142. Fadda ME, Cosentino S, Deplano M, Palmas F. Yeast populations in Sardinian feta cheese. Int J Food Microbiol. 2001;69(1–2):153–6.
143. Górz A, Boroń P. The yeast fungus Trichosporon lactis found as an epizoic colonizer of dung beetle exoskeletons. Microb Ecol. 2016;71(2):422–7.
144. Suh S-O, Blackwell M. Three new beetle-associated yeast species in the *Pichia guilliermondii* clade. FEMS Yeast Res. 2004;5(1):87–95.
145. Suh S-O, McHugh JV, Blackwell M, Microbiology E. Expansion of the Candida tanzawaensis yeast clade: 16 novel Candida species from basidiocarp-feeding beetles. Int J Systemat Evolut Microbiol. 2004;54(6):2409–29.
146. Ebert KM, Arnold WG, Ebert PR, Merritt DJ. Hindgut microbiota reflects different digestive strategies in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Appl Environ Microbiol. 2021;87(5):e02100-e2120.
147. Kurtzman CP, Fell JW, Boekhout T, Robert V: Methods for isolation, phenotypic characterization and maintenance of yeasts. In: The yeasts. Elsevier; 2011: 87–110.

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