



Review

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The ecology of insect–yeast relationships and its relevance to human industry

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Many species of yeast are integral to human society. They produce many of our foods, beverages and industrial chemicals, challenge us as pathogens, and provide models for the study of our own biology. However, few species are regularly studied and much of their ecology remains unclear, hindering the development of knowledge that is needed to improve the relationships between humans and yeasts. There is increasing evidence that insects are an essential component of ascomycetous yeast ecology. We propose a ‘dispersal–encounter hypothesis’ whereby yeasts are dispersed by insects between ephemeral, spatially disparate sugar resources, and insects, in turn, obtain the benefits of an honest signal from yeasts for the sugar resources. We review the relationship between yeasts and insects through three main examples: social wasps, social bees and beetles, with some additional examples from fruit flies. Ultimately, we suggest that over the next decades, consideration of these ecological and evolutionary relationships between insects and yeasts will allow prediction of where new yeast diversity is most likely to be discovered, particularly yeasts with traits of interest to human industry.

1. Introduction

Yeasts, particularly ascomycetous yeasts, include some of the most economically important organisms. In addition to their key roles in the production of foods [1], drinks [1] and biofuels [2], they include some of the most serious human pathogens and the primary model organisms for studies of eukaryotic cell biology [3]. Yeasts have long been central to civilization [4]. It is surprising, in this context, that key aspects of yeast ecology remain poorly resolved and scattered across diverse bodies of literature. Here, we review yeast ecology, with a focus on the relationships with insects. We do this in three steps. First, we suggest a ‘dispersal–encounter’ hypothesis to describe yeast–insect relationships. Second, we use this hypothesis to explain the yeasts’ interactions with wasps, bees, beetles and fruit flies. Finally, we revisit these examples in light of the benefits and potential benefits of insect-associated yeasts to humans.

2. The dispersal–encounter hypothesis

The dispersal–encounter hypothesis is as follows. Many yeasts depend on sources of sugar (carbohydrates) [5]. So too do many insect species [6–9].

The challenge for insects that consume sugar is finding sugar, which tends to occur in small, ephemeral patches (e.g. rotten fruit, floral or extra-floral nectar, weeping tree sap or the hind-end of a mealybug). While flowers often advertise their presence to insects using both visual and odour signals [10], other sources of sugar rarely do. Similarly, key challenges for dispersal-limited yeasts include getting to these patches as well as leaving them for other new patches [11]. In this light, we hypothesize that a mutualism has evolved, or rather a set of diffuse mutualisms [12,13], between insects and yeasts. Early in their evolution, yeasts evolved biochemical pathways to extract energy from sugars, producing as by-products volatile compounds (e.g. ethanol, ethyl acetate, isoamyl acetate, ethyl phenyl acetate, 3-methyl-1-butanol, 2-phenylethyl alcohol [13–15]). These volatiles, which also signal the presence of sugar (or are energy sources themselves in the case of alcohols [16]), attract insects which transport the yeasts (or their descendants) to another patch of sugar. Insects, in turn, evolved the ability to detect the compounds produced by metabolizing yeasts and use them to find sugar sources [17]. The yeasts benefit from getting a free ride (phoresy), the insects from a free and honest signal of an available resource.

3. The classic systems

Although many relationships between insects and yeasts have been described (e.g. in ants [18], Neuroptera [19], Lepidoptera [20,21], Isoptera [21], Hemiptera [22]), those between yeasts and social wasps (Vespidae) [21,23–32], bees (Apidae) [33–37], beetles (Coleoptera) [21,38] and fruit flies (Drosophilidae) [21,39–42] have received the most intensive study. In each of these systems, the insects forage on abundant sugars and are host, or dispersal agent, for diverse yeast genera. The fly–yeast mutualism has been well described elsewhere [14,40,43] and relative to other relationships between insects and yeasts is somewhat unusual in that the flies require yeast for nutrition. We do not discuss it further, except where work on particular fly species is illuminating in a general way.

4. Yeasts as signals of sugar

Despite the varied and diverse relationships between yeasts and insects, we hypothesize that a key value provided by yeasts to wasps, bees, sugar-feeding beetles and flies is via the honest indication of the presence of sugar resources generated by the yeasts' metabolism [44].

In the case of wasps, these insects rely on sight and smell for searching out prey, but also use olfactory signals to find sugar [45]. Many of these sugar signals are produced by yeasts, rather than by the sugars themselves. Traps baited with microbial fermentation products such as fruity esters and alcohols catch far more wasps than do those baited exclusively with sugar [46–48]. The volatile chemicals produced by yeasts are by-products of active sugar fermentation and thus, as hypothesized by others [47,49], probably honest indicators of plentiful sugar, as well as indicating the presence of yeast itself. The presence of fermentative yeasts also indicates the presence of alcohols such as ethanol, carbon-based energy sources consumed by flies [16], honeybees [50] and probably other insects that feed on fermenting fruit and other sugar-

rich environments [44]. We hypothesize a scenario in which some initial transport of yeasts to sugar sources occurs by signals other than the odours produced by yeasts, but those first events occur enough that subsequent insect visitors find the sugar source more rapidly. Such initial dispersal of yeasts could be by non-insect pollinators [51], soil [52] or by insects using visual or plant-derived signals [53].

The floral resources sought out by bees and other pollinators are more visually apparent than are sugar resources in fruits; however, like wasps, bees may prefer flowers with yeasts if yeasts provide pollinators a honest signal to the presence of nectar—and the sugar and alcohols therein. While no studies have provided a definitive test of this hypothesis, Herrera *et al.* [54] and Schaeffer *et al.* [55] found a greater proportion of visits to yeast-inhabited flowers by naive bumblebee foragers, even those never exposed to yeast-treated flowers. In addition, Good *et al.* [56] found that honeybees consume less nectar if the nectar is colonized by bacteria, whereas their nectar consumption was not affected by yeast colonization. These results suggest that yeasts provide a signal to their presence, even before bees taste the solution, similar to the case with wasps and non-floral sugar sources. Assuming the signal yeasts provide to pollinators is scent [57], the presence of a scent could also enhance pollinator discrimination as a function of other floral traits (e.g. multi-modal signalling) or improve memory [53]. Yeasts, in this context, could increase the rate of visitation to flowers by pollinators, though this possibility clearly deserves additional research.

For beetles, use of yeast-generated volatiles as attractants to food patches has been demonstrated in sap beetles (Nitidulidae), which are common visitors to high-sugar foods such as sap or overripe fruit. For example, fruit baits inoculated with the yeast *Saccharomyces cerevisiae* attract twice the number of *Carpophilus hemipterus* (Nitidulidae) beetles as uninoculated controls [58]. Many other nitidulid species, such as *Carpophilus humeralis* and *Aethina tumida*, similarly show a strong preference for yeast-derived volatiles in baits [59,60]. Volatiles from fermentation are also known to promote feeding aggregations in members of various plant-feeding beetle groups such as Chrysomelidae, Scarabaeidae and Scolytinae (Curculionidae) [61–63]. A wide range of wood-associated Coleoptera also responds to yeast-generated signals. Ethanol is a well-known attractant (either alone or in synergy with plant-based compounds) for many wood-feeding members of the Cerambycidae, Cleridae, Curculionidae, Staphylinidae and various other families [62,64–67]. However, the specific compounds to which different beetles are attracted differ.

In each of these insect–yeast systems there is evidence that yeast volatiles are attractive to foraging insects because they indicate sugar resources. This suggests the yeast-laden resources are always beneficial to insects; however, under certain contexts insects may incur costs to visiting fruits with abundant yeasts. Alcohols like ethanol are energy sources, but provide less energy than do sugars. Furthermore, high concentrations of ethanol can have negative effects on insect physiology and behaviour [68]. These negative interactions between yeasts and insects are probably rare though, as the concentrations of ethanol found in most fruits [69] and nectar is uniquely well tolerated by those sugar-feeding insects that have been investigated (e.g. honeybees and various species of fruit flies) [68,70]. This greater tolerance

Table 1. Potential costs and benefits to yeasts and insects of the dispersal–encounter diffuse mutualism hypothesis.

	yeasts	insects
benefit	dispersal to new habitats	increased accuracy in detecting ephemeral sugars
	access to outbreeding opportunities	increased accuracy in detecting sugars with lower bacterial abundance
costs	some propagules may be killed by feeding insects	access to alcohols for energy or self-medication
	metabolic cost to producing certain volatiles/	access to nutritional yeast (in the case of flies)
	dispersal-aiding morphologies	locations with abundant yeasts may have decreased sugar qualities
		locations with abundant yeasts may have high alcohol concentrations, which may have toxic effects on physiology

even affords fruit flies the ability to ‘self-medicate’ with ethanol [71]. For the proposed relationship between yeasts and insects to be a mutualism rather than parasitism of the insects by yeasts, it will be important to determine the fitness effects of ecologically relevant ethanol concentrations on sugar-feeding insects (table 1).

5. Dispersal of yeasts

In each of the high-sugar environments we have mentioned, yeasts often compete with bacteria to metabolize sugar. Because bacteria can monopolize sugar sources faster than can yeasts, yeasts would benefit from arriving at new sugar sources first [72] and then from producing, once present, compounds such as ethanol that kill any newly arriving bacteria. Yeasts may be dispersed to sugar resource patches in a manner similar to other transport mutualisms such as seed dispersal. Evidence exists in each of the insect–yeast systems for successful dispersal of yeasts to sugar patches via insects.

In wasps, feeding on yeast-laden fruit, nectar or sap leads to some portion of the yeast population surviving in the intestines and on cuticles [24]. As wasps forage on various sugar sources throughout territories ranging hundreds of metres from the nest, they probably disperse yeast propagules into new sugar-rich habitats. Wasps have strong mandibles that they use to break open fruit tissue when feeding [73], providing newly accessible sugar resources to any yeasts dispersed during such foraging.

Similar to the case of wasps and fruits, nectar yeasts are vectored among plants by bee pollinators [74]. For example, flowers that are exposed to bee pollinators are more likely to harbour yeasts than flowers that remain bagged to exclude pollinator visits [51,75–77]. Moreover, Herrera *et al.* [34] found a positive correlation between nectar yeast frequency and abundance and the proportion of floral visits by bumblebees.

At larger scales, work on beetles by Lachance *et al.* [78] found evidence that vectoring by nitidulid beetles may be responsible for large-scale biogeographic patterns of yeasts in ephemeral flowers. Furthermore, many yeast species found in association with beetles have also been recovered from diverse plant substrates such as floral nectar and decayed wood [79–81], suggesting that beetles may have the opportunity to vector yeasts among diverse habitats.

Insects may also allow yeasts to disperse through time. Unlike more ephemeral hosts such as short-lived fruit flies, future foundress wasps in temperate zones hibernate during the winter before starting a new nest in the spring.

Similarly, most species of social bees overwinter. Work on vineyards has shown that yeasts can survive in foundress wasps throughout the winter [24], presumably to be dispersed anew among sugar patches (nectar or fruits) when the wasps again forage in the spring. Indeed, hibernating wasps are one of the only known locations to reliably find these yeasts in the winter when sugar sources are nonexistent, and environments are hostile to cell growth. Yeasts can overwinter in some flowers and mummified fruits [82], but particularly in temperate regions this is likely to be the rare exception. Several species of nectar yeasts have been found to be abundant on bees [31] and in bee nests [37,83], and we speculate that beehives, like wasp foundresses, are important sites for the overwintering of yeasts.

In each one of these cases, dispersal of yeasts by insects not only allows those yeasts to find new patches of sugar at various geographical scales, it also has the potential to increase outbreeding. While yeasts typically reproduce asexually, the gut environment of both wasps and fruit flies stimulates yeast outbreeding [84,85]. In fruit flies, the harsh conditions of the gut break up *S. cerevisiae* spore tetrads, allowing for 10× greater hybridization rates than those that were not ingested by flies. This spore tetrad structure is shared by all yeast; thus, insects such as wasps and flies—and potentially beetles and bees—might also be facilitating adaptive outbreeding among diverse yeasts.

To date, the presence of adaptations for phoresy in yeasts has not been studied in any systematic way across insect and yeast species. The anecdotes, however, are noteworthy. The morphology of some nectar yeasts appears conducive to attaching to insects [86]. For example, *Metschnikowia gruessii* produces a clump of spores by subpolar budding in the shape of an airplane. This aeroplane shape, as Brysch-Herzberg [37] notes, might potentially allow the yeast to ‘stick more easily and in greater numbers to the fine hairs of the glossa than other yeast cells’. In addition, in comparison to wind-dispersed fungi, spores of Saccharomycetales yeasts have additional layers of protection to the environment composed of chitosan and a dityrosine-containing polymer. These extra layers allow yeast spores to withstand stressors to a greater degree than do the vegetative or actively growing cells. This might be an adaptation for dispersal on insects as well as for the survival of the yeasts through the guts of insects [87]. Similarly, some nectar yeasts (e.g. *Metschnikowia reukauffii*) readily produce chlamydo spores in addition to vegetative cells [88]. The adaptive significance of chlamydo spores remains unknown, but one possibility may be that it helps extreme osmotic pressure [89], which the yeasts may need to tolerate during insect-assisted dispersal.

Finally, recent research has begun to document the evolution of genes in yeasts that appear to serve no function other than the production of compounds that attract insects. For example, a gene has been discovered in *S. cerevisiae* that is associated with the attraction of *Drosophila*. The upregulation of the gene triggers the production of volatile compounds [90] which in turn attract the flies. Similar genes might exist in other yeasts, and slight differences in these genes might lead to the attraction of very different insect dispersers. One might predict that such genes are lost in examples where yeasts abandon dispersal by insects (such as during domestication). The yeasts in some wasp guts, while as metabolically diverse as those found outside of guts, tend to be enriched for yeast strains that are able to produce organic acid and ethyl acetate, both thought to be attractive to wasps [91]. Such aroma-producing gene pathways are both difficult traits to select for in yeasts [92] and traits of particular interest to the food, beverage and perfume industries [93].

One twist to our general model is the observation that, in addition to yeasts, insects and other flower-visiting animals facilitate dispersal of bacteria among flowers [94,95]. It might, therefore, be suggested that we could expand our dispersal–encounter hypothesis to bacteria as well as yeast. However, four inter-related pieces of evidence suggest that insects have a more mutualistic relationship with yeasts than with bacteria. First, some sugar-foraging insects produce salivary compounds that inhibit the growth of bacteria but not yeasts [96]. Second, compared to yeasts, bacteria seem to rely less on insects and can disperse by other means (e.g. wind) more frequently than do yeasts [51]. Third, perhaps because of this more independent dispersal, bacteria seem to have evolved to reduce sugars in nectar to a greater extent than yeasts do [95]. Bacteria may therefore be more likely to have a competitive rather than mutualistic relationship with insects, for which sugar is often the primary reward that the plants provide them. Fourth, bacteria and yeasts engage in strong priority effects, such that whichever one happens to arrive at nectar first or in higher initial abundance strongly suppresses the other [72,97]. Although it remains unclear how these priority effects work, the most likely mechanism may be that bacteria reduce nectar pH to a level too low for yeast colonization, whereas yeasts reduce amino acids in nectar to a level too low for bacterial colonization [72,95]. We hypothesize that suppression of sugar-consuming bacteria by yeasts is an added benefit to insects, further strengthening insect–yeast mutualism and weakening insect–bacterium mutualism [35,98].

6. Yeasts as food sources

Yeasts are diverse and ancient so it should be no surprise that in certain contexts yeasts provide more to their insect partners than an honest signal of sugar, including a food resource. To date, the main model system in which yeasts have come to be understood as food sources is that of fruit flies, a system that might be highly derived. For *D. melanogaster*, the failure to find and eat yeasts means an early death [39], as these insects use the protein in yeasts for proper immunity and development [99,100].

The absence of yeasts in some adult wasps and the ability of wasps to be reared in the absence of yeast supplementation

suggest yeasts are not critical to social wasp survival [101,102]. Yeasts could provide additional protein for bee colonies that are pollen limited, and similarly could provide nitrogen or vitamins to wasps when arthropod prey are less available. However, experiments with bumblebee colonies at ecologically relevant yeast concentrations have found no benefit to colony productivity with the addition of yeasts. Schaeffer *et al.* [55] manipulated yeast presence and metabolic activity in microcolonies of queenless *Bombus impatiens* workers and found no effect of yeast on bumblebee microcolony reproduction. Moreover, the addition of yeast could not rescue bumblebee reproduction when pollen quantity was limited.

In beetles, symbiotic yeasts have been shown to supply nutritional resources such as nitrogen, amino acids and vitamins [103]. The presence of xylose- and cellobiose-fermenting yeasts in the gut or specialized mycangia of some wood-ingesting beetles (e.g. Cerambycidae, Lucanidae, Passalidae) has been taken as evidence that beetles may receive a nutritional benefit from yeast symbionts that aid in the digestion of cellulose in the insect gut [104–107].

Further study may yield more examples in which insects benefit nutritionally from the yeasts they carry and consume. However, we suspect that in the ancestral (and more common) scenario, insects are in a diffuse mutualism with yeasts in which the benefit the yeasts provide to insects is primarily a signal of the presence of sugar and not food from the yeasts themselves, though clearly more empirical tests are needed.

7. Yeast species specificity

An unresolved mystery in yeast–insect relationships is the apparent specificity of some of these relationships. This specificity will probably have repercussions for the fitness relationships between any given yeast and insect species. In some cases, this specificity appears geographical. Some species of large-spored *Metschnikowia* species, for instance, occur only in the regions in which the beetles with which they are associated occur [108]. In other cases, it is not only geographical but appears to entail a close pairing between one yeast species and one insect species. *Drosophila mojavensis*, for instance, is almost always associated with the same relatively few yeast species, which in turn appear to be found almost exclusively on *D. mojavensis* [109]. Different bee species also appear to often carry different yeasts, even when those bee species are exposed to relatively many species of yeasts in sugar sources [78].

In some cases, specificity appears to be due to selectivity on behalf of the insects. For example, the reason why *D. mojavensis* is associated with only a few yeasts may be because it selectively forages on those yeast species [110]. Such cases might be in the minority, however. In other cases, the yeasts may attract certain insect species more than others. One can imagine a scenario in which yeasts attract the insects most likely to vector them to the sugar or other food resources on which they best grow.

There also may be some specificity, or at least filtering, in which a subset of yeasts carried by insects survive in a given sugar source after having been introduced [34]. The yeasts picked up by mushroom-feeding *Drosophila* species, for example, are distinct from those found on *Drosophila* species

that visit fruits. In the case of nectar, different yeast species have different growth rates. Herrera *et al.* [111] speculate that this difference, which can result in species filtering, may be caused by high osmotic pressure and potential fungicidal compounds in nectar. In some cases, however, reductions in yeasts' growth may not be strong enough for this filtering to contribute to specificity [112].

8. Consequences for humans

In the early days of agriculture, humans became as good as or better than insects at dispersing yeasts among patches of abundant sugar, while offering the additional advantage to yeasts of actually producing those sugar sources. The partnership with yeasts triggered modest selection on the yeasts, but it triggered large selection on humans, favouring particular versions of the alcohol dehydrogenase gene [113]. Humans came to rely on yeasts for food storage, purification of unclean water (by turning it into beer) and nutritional needs, but probably depended on different yeast strains or species in different regions (and when producing different food products).

However, the industrialization of yeasts in the 1900s focused on fewer strains and species, nearly all of which appear to have been part of insect–yeast systems we have already referenced. Since the 1890s, a handful of domesticated yeast species, including *S. cerevisiae* and *S. pastorianus*, have been the sources for many of our foods, industrial processes and even genetic models. We now carry these yeasts among sugar sources because we are attracted to their volatiles (the aroma of bread, for instance), and metabolites (the alcohol in beer and wine, or the fungicidal activity of hydrogen sulfide and acetic acid). However, our choice of these yeasts from the thousands of possible yeasts with which we might partner was probably not a conscious one. We are a species of yeast disperser that has inadvertently become too specialized [114]. There is a need, for example, for stress-tolerant yeast species [92] able to use diverse substrates (such as pentoses, hexoses and lignocellulosic feedstocks [115]), modify food and beverage flavours [116,117], generate perfumes [93], and produce antibiotics, probiotics [118] and plant fungicides [119]. Insects present a source of diverse

stress-tolerant yeasts [105,120] and those with specific traits for industrial applications (e.g. [2,16,45]). We suggest that a better understanding of the ecology of yeast–insect relationships will facilitate bioprospecting. More specifically, we close with the hypothesis that a better understanding of the volatiles used by different insect species to find sugar will lead to the ability to identify the insects most likely to host yeasts with particular attributes of use to industry.

9. Conclusion

Our 'dispersal–encounter' model hypothesizes that insects are in a set of diffuse mutualisms with yeasts. The yeasts provide foraging insects an honest signal of sugar via metabolic by-products. In return, these dispersal-limited yeasts are transported by insects among sugar resources through space and time. While fruit flies have garnered the most research of the classic insect–yeast systems (i.e. social wasps, social bees and beetles), we believe this nutritional reliance on yeasts may be the exception rather than the rule for other insects. Regardless of whether the yeasts are consumed, or cling to the outside of foraging insects, many yeasts survive this transport. This survival appears due in part to specific morphological or physiological adaptations. Questions remain as to the nature and mechanisms of the specificity of relationships between certain insects and yeasts; however, we believe that by investigating insects and yeasts in light of their respective ecologies we can better understand, and even predict these relationships. This can help us overcome our currently limited ability to take advantage of yeast biodiversity for use in industrial processes. We envision a future in which a much better understanding of the biology of sugar-feeding insects allows us to detect novel, useful yeasts from those insects, predictably and in the service of industry and society.

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