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REVIEW

The invisible communities of nectar: How yeast and bacteria alter nectar characteristics

Anthony Schmitt

Abstract

Plant - pollinator relationships are based off a binary reward system. Plants present pollinators with nectar as an energetic reward, while pollinators transfer genetic material to help plants achieve full reproductive success. The constituents of nectar play a crucial role in facilitating this mutual relationship. A new area of research is emerging that may change the way biologists view this binary system; it may no longer be a two-way interaction. Microorganisms - yeasts and bacteria - have been found to inhabit nectars across a wide geographic range and across a large range of plant species. These microorganisms change the characteristics of nectar in such a way to can alter pollinator behavior. For example, yeasts and bacteria can modify the sugar composition and concentration of nectar. Sugars in nectar are a chief reward for pollinator visitation. This review examines the new field of research presented by these microbes by breaking down changes in nectar as a result of microbial communities. The implications presented by these findings may significantly change the way biologists view plant-pollinator interactions as research continues to develop.

*Biology Department, University of Minnesota Duluth
*Writing Studies Department, University of Minnesota Duluth

Introduction

Understanding the interactions of species within a community is important in expanding our ecological and evolutionary knowledge, especially when two species rely on each other for reproductive success. Many plants rely on the mutual relationship between themselves and their pollinators in order to produce a maximum seed set. There are many ways that plant species attract the pollinators that help plants achieve reproductive success. A few examples include flower morphology, flower placement, flower color and scent. Perhaps the most important attractant is the production and enticement of nectar within flowers. Nectar is a major energetic reward plants present to their pollinators in order to help facilitate this desired interaction. The specificity of this system can be important in facilitating co-evolution (Cronk and Ojeda 2008). It was long believed that the plant-pollinator system was a binary relationship. However, new studies are finding a new factor in this relationship.

The chemistry of nectar is understood to have an important role in the plant-pollinator binary system. Constituents attract and deter specific organisms to help facilitate pollination in a way that will maximize fecundity (Adler 2000; Heil 2011). Although some constituents, such as H_2O_2, is thought to sterilize nectar by killing off microbes (Adler 2000; Carter et al. 2007; Carter and Thornburg 2004), but some microbes are still present in nectar.

It has long been known that microorganisms, such as yeasts, inhabit floral nectars (Sandhu and Waraich 1985), but their role was never closely examined. However, new research indicates that

Corresponding Author:
Anthony Schmitt
schm2692@d.umn.edu

microorganisms are emerging as a source of variation in the characteristics of nectar and therefore may have a significant role in the plant-pollinator relationship. Microbial community structure and ecology, in general, is a field that is largely unexplored and research in this area may be beneficial to understanding the ecology of nature on a wide spectrum (Furhman 2009).

This review aims to present the current knowledge of how yeasts and bacteria shift nectar characteristics. Additionally, the review will briefly discuss the potential impact microorganisms may have on plant – pollinator interactions. The purpose of this paper is to bring awareness to this emerging ecological niche within nectars that may hold larger implications in the important role pollinators have with plant fecundity.

Nectar chemical composition is important for plant-pollinator facilitation

The chemistry of nectar and its relation to pollinators has been extensively reviewed (for instance see reviews by Gonzalez-Teuber and Heil 2009; Heil 2011). To fully understand all the components regarding the function of nectar, some background information on nectar chemistry may be useful. It is well established that nectar is mainly a solution of water and sugars (Baker and Baker, 1983), although other constituents including amino acids, proteins, lipids, alkaloids and several other compounds have also been found in nectars (Baker and Baker 1983; Gonzalez-Teuber and Heil 2009). Some nectar compounds are thought to attract beneficial species (Brandenburg et al. 2009), while some, such as alkaloids, are thought to deter harmful species, such as **nectar robbers**. The concentration and abundance of certain components that make up a flower's nectar chemistry is believed to be strongly correlated to plant – pollinator mutualism.

Nectar robber
Organisms who consume a flowers nectar generally by drilling a hole in the corolla. Nectar robbers generally do not provide any benefit to the plant.

Sugars and free amino acids are understood to be important for the attraction of pollinators. In his review, Heil (2011) wrote that nectars rich in sucrose generally attract hummingbirds, butterflies, moths, long-tongued bees, and ants whereas nectars rich in hexose (glucose and fructose) attract short – tongued bees and flies. Amino acids have been reported to be more attractive to insects rather than bird pollinators since birds may be able to gain essential nutrients from other sources (Gonzalez-Teuber and Heil 2009; Heil 2011). Some components are thought to be specifically for defending against microbial infection and some are thought to be toxic to organisms that may harm the plant (Adler 2000; Carter et al. 2007; Carter and Thornburg 2004). All the different components within nectar provide some type of function, which leads to the central purpose of this review. Microbes, such as yeasts, use nectar as a habitat and are interacting with the varying characteristics that allow nectar to provide its ecological role in plant reproduction.

Yeasts in Nectar

The approach to studying yeasts, and other microbiota, in nectar has resulted in two core fields of research. Recent studies support the assertion that yeasts are present in flower nectars across a wide range of plants species in separate plant communities. These studies provide evidence that nectar-living yeasts are geographically wide spread. Additionally, other recently published studies support the notion that yeasts have the ability to modify nectar chemistry.

Yeasts are common in nectar

In order to establish the importance of yeasts in nectar, recent studies examined whether or not there was support for the postulate that yeasts are found throughout a wide variety of plant nectars. Herrera et al. (2009) performed a quantitative survey across two continents that helped establish the wide-ranging occurrence of yeasts in the nectar of insect-pollinated plants.

Yeast communities were frequently

established throughout floral nectars in the species and flowers surveyed reaching high densities within these nectars (Herrera et al. 2009). The study examined plant communities from two separate continents and three different locations with different habitat variations (see study for further explanation)– Donana (south-western Spain), Cazorla (south-eastern Spain) and Yucatan (eastern Mexico). Overall, nectar from 44 plant families and 130 plant species were examined. In Donana 31.8% of flowers contained yeasts, 42.3% of Cazorla flowers contained yeasts, and 54.4% of flowers in Yucatan contained yeasts (Herrera et al. 2009). Herrera et al. (2009) also found that yeast cell densities of 10^4 cells mm^{-3} were quite common. It should be noted that other studies have found that yeasts can reach higher densities within nectar (de Vega et al. 2009), but generally densities were close to what was found in this survey (Brysch-Herzberg, 2004; Herrera et al. 2009; de Vega et al. 2009 and Belisle et al. 2011).

Since yeasts are found in rather high densities in nectar, researchers began to explore how community structures developed in within nectar habitats. One key finding was that generally there was low species richness of yeasts. Pozo et al. (2011) explored the richness of yeast species within the nectars of different Spanish plants. The main assertion from the study was that yeasts were present in all the nectar droplets but there was low species richness among the nectar samples with 1.2 yeast species per nectar sample on average. Pozo et al. (2011) identified two species of yeasts, ***Metschnikowia reukaufii*** (73.4% nectar drops) and *Metschnikowia gruessii* (29.7% nectar drops) together having a frequency of 84.7% among the 216 yeast isolates – there were 12 total yeast species isolated. The yeast species *M. reukaufii* has been found as a chief inhabitant of nectar.

Low species richness could be an indication that the habitat of nectar may play a selective role by filtering out yeast species (Herrera et al. 2010). This may be due to the nature of nectar as a rather hostile environment to yeasts (Adler 2000; Carter and Thornburg 2004). The hostile environment may allow yeast species with osmotolerance and resistance to secondary compounds found in nectar to have an advantage over other yeast species (Herrera et al. 2010).

Pozo et al. (2011) tested the osmophilic tolerance of nectar-living yeast species by testing their growth response (positive or negative response) in solutions of 50% glucose in order to classify them as osmophilic species versus non – osmophilic species. There was a higher frequency of osmophilic yeast species (35.5% of plant species surveyed) when compared to non – osmophilic yeast species (4.8% of the plant species surveyed).

As mentioned earlier, *M. reukaufii* has been found in high densities across all the studies reviewed and may be a species with specialized traits to allow it to thrive in nectar. Once source of this nectar niche-filling characteristic of *M. reukaufii* seems to be due to **DNA methylation** polymorphisms that occur in nectar dwelling communities (Herrera et al. 2012). In short, *M. reuakufii* undergoes **epigenetic** changes within its genome as a result of variation in sugar concentration and composition (sucrose, glucose or fructose ratios in nectars). Both sugar concentration and composition vary both intra- and interspecifically among plants. This genotypic plasticity, through an alteration of DNA methylation, was positively correlated with *M. reukaufii's* ability to survive in these varying nectars. When the methylation inhibitor 5-azacytidine was introduced to yeasts, their ability to cope with variations in nectar concentration and composition decreased (Herrera et al. 2012). This plasticity in *M. reukaufii* is most likely critical in their adaptability to inhabit and utilize nectars, especially since yeast species generally are introduced to their nectar habitats through

Metschnikowia reukaufii
A nectar living yeast species that is found in the nectar of almost all plant species that have been surveyed so far. It is a fungus part of the Ascomycota phylum and the Metschnikowiaceae family.

DNA methylation
The process of adding a methyl group to the cytosine or adenine in DNA nucleotides. Methylation can alter the expression of specific genes.

Epigenetics
Changes in gene expression that are caused by something other than DNA sequence, i.e. DNA methylation.

modes of transportation that are out of their control.

How yeasts arrive to the nectars they inhabit is also an emerging field of research. One hypothesis that has received support in several studies is that the pollinators are the vectors that transfer the yeasts to the nectar. Belisle et al. (2011), Brysch-Herzberg (2004), and de Vega and Herrera (2012) examined hummingbirds, bees and ants as potential vectors and all found evidence that these pollinators may be the source for nectar dwelling yeasts. Unsurprisingly, these studies exemplify once again that the mutual relationship between plants and pollinators is more complicated than a simple two-way system. Pollinators are introducing yeasts into nectar. Once yeasts are established in nectar they begin going to work in changing their habitats characteristics, potentially altering the nectar in a way that may compete with the interests of the pollinators that acted as the yeasts vector.

For further information about nectar yeast community features and community distribution, the following studies may be of interest: Belisle et al. (2011), Herrera et al. (2010), Peay et al. (2011), and Pozo and Herrera (2012).

Yeasts in nectar alter its characteristics

Yeasts alter the characteristics of nectar in a variety of ways. Research is finding that yeasts can alter the concentrations of sugars in nectar, as well as the temperature of nectar. Both of these components have important implications in facilitating pollinator behavior.

Herrera et al. (2008) performed a study involving nectar samples from three species of bee-pollinated plants in southern Spain: *Helleborus foetidus, Aquilegia vulgaris and Aquilegia pyrenacia cazorlensis* (family: Ranunculaceae). Flowers of each plant were allowed to open before they were collected to allow natural pollinator visits. The study found that sugar concentration was significantly altered among yeast-inhabited flowers (Herrera et al. 2008). Yeast cell density increased steadily as flowers progressed through their floral stages, and as the density of cells changed, so did nectar chemistry. All combinations of sucrose:fructose concentrations (glucose always had low concentrations) were found among the plant species including pure-sucrose nectars and pure-fructose nectars. As cell density increased the level of sucrose decreased while, in contrast, fructose increased. The average density found among all late stage nectaries was about $10^4 – 10^5$ cells/mm^{-3}, which was common among most studies. A pattern in sugar concentration also emerged between “clean” nectars with no yeasts and nectars that supported yeast communities. Clean nectars had higher concentrations of sugar overall and were generally sucrose dominated, while nectars supporting dense yeast communities had lower overall concentrations of sugar and were either completely fructose (*H. foetidus*) or fructose dominated (*Aquilegia*). In summary, the researchers found a significant alteration of nectar sugar components that was correlated to the presence of increasing yeast cell density.

The trend of sugar concentration varying inversely with yeast cell density was also found in a study done on 40 South African plant species (de Vega et al. 2009) providing further support that there is a correlation between the presence of nectar-living yeasts and alteration of chemical composition in flower nectars. South African plants were lacking a quantitative study establishing the presence of yeasts in South African plant species, so de Vega and colleagues surveyed 40 plant species (19 families) across several locations that differed by geography and habitat type. They were able to confirm that yeasts were prevalent in the flowers they surveyed. Of the plants examined, 51.3% individual plants had yeasts and 43.2% of the flowers had yeasts. In order to explore changes in nectar composition, the researchers further investigated the nectar of the bird-pollinated species *Watsonia pillansii* (family: Iridaceae). Once again there was a significant inverse correlation between yeast cell density and both sugar concentration (%) as well as sugar content (mg/ul); as yeast cell density increased sugar concentration and content decreased.

In a third study in southern Spain researchers studied the plant species *Cytinus hypocistis,* a parasitic plant pollinated by ants, which emerged as another example of yeast-altered nectar chemistry. Nectar samples were taken from flowers that were allowed to be visited by pollinators, and these samples were evaluated for yeast frequency. As expected there was a high incidence of yeasts in both plants (94%) and flowers (77%) (de Vega and Herrera 2012). Again there was a significant correlation between increased yeast cell density and a drop in sugar concentration. The relationship between increased cell density and drop in nectar sugar concentration was only significant in the presence of *M. reukaufii* ($p = 0.01$) perhaps again showing the specialization this species may have for nectar microhabitats (de Vega and Herrera 2012).

These studies together reveal a significant shift in sugar composition, content and concentration in response to yeasts (Herrera et al. 2008; de Vega et al. 2009; de Vega and Herrera 2012). The energetic reward provided by nectar sugars is fundamental to the mutual relationship between a plant and its pollinator. Both birds and bees prefer nectars with higher sugar concentrations (Cnaani et al. 2006 and Roberts 1996). Once yeasts are introduced into nectar they seemingly begin to degrade the sugar reward provided by nectar that drives this mutual relationship. Curiously though, the pollinators themselves are the vectors for some yeast species and perhaps are introducing competitors into their precious source of energy (Brysch-Herzberg 2004; de Vega and Herrera 2012).

Nectar chemistry is not the only aspect found to be altered by yeast inhabitants. Temperature change in nectar may also be a consequence of nectar-living yeasts. This was found in another examination of the winter-blooming *H. foetidus.* Instead of looking at nectar chemistry, this time nectar temperature was investigated as a varying factor consequential of yeast inhabitance. Herrera and Pozo (2010) found that yeast presence partly contributed to internal floral temperature (other factors such as the plants own metabolic functions were taken into account). There was an observable change in interior floral temperature between yeast-inhabited nectar versus “clean” nectars that did not have any yeasts. The change in temperature was also correlated with yeast cell density. As cell density increased so did temperature, proportionally. Yeast cell densities of 10^5 cells mm^{-3} resulted in an increase of 5-6º C (change in nectar temperature was measured as $T_{nect} - T_{air}$) (Herrera and Pozo 2010). These few studies clearly indicate that yeast cells, at high densities, are significantly altering the characteristics of nectar and could have substantial effects on pollinator visitation and behavior, although to what extent these changes have on plant-pollinator ecology still remains rather elusive.

The evidence of yeasts altering nectar temperature may have implications for shifting pollinator behavior. Studies have found that bees tend to prefer warmer nectars (Dyer et al. 2006 and Norgate et al. 2010). In addition to temperature, sugar concentration may influence bee behavior independent of nectar temperature. Whitney et al. (2008) found that regardless of warmer nectar, bees preferred nectars with higher concentrations of sucrose. Bumble bees, *Bombus terrstris*, sense the temperature and sugar concentration independently and would more often select for higher sugar concentration over a higher temperature of nectar. Nectar concentration and temperature are believed to both provide metabolic rewards for the bumble bee. The trio of interactions between yeasts, plants and pollinators needs to be further explored in order to better understand all the ecological implications of these findings. The degradation of overall nectar quality could potentially be significantly influencing pollinator foraging behavior.

Bacteria in Nectar

Perhaps an even less explored niche in the microbiota of nectar is the effect of bacteria on nectar. Five proteins, known as Nectarins I-V, have been found in nectar (Carter and Thornburg 2004). Nectarins are involved in the production of compounds, such as H_2O_2, that may play a pivotal role in nectar to prevent bacterial invasion within nectar (Carter et al. 2007; Carter and Thornburg 2004). The presence of these constituents implies that nectar may be a rather hostile environment for bacteria to inhabit. However, recent studies are finding contradicting evidence.

Bacteria are evident in nectar much like yeasts

Two studies published in 2012 surveyed the prevalence of bacteria in nectar (Alvarez-Perez et al., 2012 and Fridman et al., 2012). There were five key findings: (i) bacteria were found among most plants surveyed with low species richness in nectar (Alvarez-Perez et al., 2012 and Fridman et al., 2012), (ii) different plant species have unique bacterial communities (Fridman et al., 2012), (iii) novel bacterial species were identified in nectar (Alvarez-Perez et al. 2013 and Fridman et al., 2012), (iv) key physiological adaptations may be evident in nectar inhabiting bacteria (Alvarez-Perez et al. 2012) and (v) bacteria of the *Gammaproteobacteria* class were the most prevalent in nectar.

Alvarez-Perez et al. (2012) conducted a study that tested and found support that bacteria, much like yeasts, are widespread in nectars across different plant species. The study surveyed 27 South African plant species (the same plant community that were examined for yeasts in de Vega et al. 2009) for bacterial establishment. Twenty-one of the 27 plant species harbored bacterial communities (77.8%). Although many plants contained bacterial communities, there was low species richness, similar to species richness patterns among nectar dwelling yeasts. Perhaps this is a trend that will continue to emerge among microbial communities in nectar. Only three different bacterial phyla were identified: *Proteobacteria, Actinobacteria,* and *Firmicutes* (Alvarez-Perez et al. 2012). Within these phyla, *Gammaproteobacteria* seemed to be the most dominant.

These results were paralleled in Fridman et al.*'s* (2012) study. Fridman and colleagues examined three plant species: *Amygdalus communis, Citrus paradisi,* and *Nicotiana glauca*. *Gammaproteobacteria* were the dominant species in these nectars making up 59% of the isolates in *A. communis*, 82% of the isolates in *C. paradisi,* and 45% of isolates in *N. glauca*. Another noteworthy finding that emerged from work by Fridman et al. (2012) was the discovery of novel bacteria species in each of the three plant species studied. The presence of novel bacteria species may be indicative of nectar playing a selective role in filtering out bacteria unsuited for the habitat within nectar as well as leading to newly developed species or genera that are better adapted for the specific characteristics in nectar.

The bacteria isolated from nectar had key physiological characteristics. Species were able to grow in the presence of 3% H_2O_2 indicating **catalase** production in these bacterial isolates. Additionally the isolates were able to grow at low levels of oxygen (microbaerobiosis) and could generally tolerate sucrose levels of 10%-30% (Alvarez-Perez et al. 2012). All of these tested variables are characteristics of nectar that were previously thought to serve

Catalase
A common enzyme found in many species that breaks down H_2O_2 into water and oxygen. Catalase activity may allow some microbes to survive the presence of H_2O_2 in nectar.

an anti-microbial function. In the study done by Fridman et al. (2012), the plant species were specifically chosen for their secondary metabolites. *N. glauca* contains nicotine and anabasine, *A. communis* contains amygdalin and *C. paradisi* contains caffeine. These secondary metabolites were thought to potentially serve as a potential antimicrobial, but Fridman et al. (2012) found that there were no negative effects when these secondary metabolites were introduced to agar plates containing isolated bacteria. More research is required to better understand the physiological characteristics of bacterial nectar and their phylogenetic relationships.

Yeasts and bacteria both alter nectar and effect pollinator behavior

Yeasts and bacteria have been found to coexist in the same nectar environment (Alvarez-Perez and Herrera 2012). Each species alters nectar characteristics, but how these alterations affect plant fecundity and pollinator still requires further investigation. To address these relationships a rather interesting study examined the hummingbird pollinated plant species, *Mimulus aurantiacus* (Phrymaceae), and the difference in pollinator behavior and pollination success when nectars were inoculated with either *Gluconobacter spp.* (bacteria) or *M. reukaufii* (yeast) (Vannette et al. 2012). Both species of microbes altered nectar chemistry. Each species similarly reduced H_2O_2 concentration by about 80% perhaps making the nectar a more inhabitable environment though the yeasts and bacteria differed in altering other characteristics. *Gluconobacter* had a greater impact on both pH (reduced by 5 units) and sucrose (reduced by 35%) where as *M. reukaufii* had smaller reduction impacts (2 pH units and 17%). *Gluconobacter* also increased fructose concentrations and reduced glucose concentrations where *M. reukaufii* was not found to have any effect. Anna's hummingbird (*Calypte anna)* is recognized as the most frequent pollinator for *M. aurantiacus.* The researchers explored what impact bacteria and yeasts may have on Anna's hummingbird foraging behavior and *M. aurantiacus* reproduction success. *Gluconobacter* reduced the proportion of closed stigma, which is a reproductive indicator for effective pollination in *M. aurantiacus* on average by 23% on average when compared to control nectar and yeast inoculated flowers. *Gluconobacter* reduced the number of seeds produced by an average of 18% (*M. reukaufii* had no significant reduction). Further, in *Gluconobacter* inoculated flowers on average 27% less nectar was removed, indicating less visitation by pollinators.

The authors (Vannette et al. 2012) theorized that several factors may impact pollinator foraging behavior and pollination success as the result of *Gluconobacter* in nectar. First, hummingbirds are fond of higher sucrose concentrations and tend to avoid nectars with higher fructose concentrations. Hummingbirds also tend to respond more so to compounds within nectar rather than attractant signals produced flower nectars. Thus, the pollinating hummingbird may need to taste the nectar before it is deterred. This may be why less nectar was taken from *Gluconobacter* inoculated nectar and flowers had decreased pollination success. Hummingbirds may have foraged on those flowers less, reducing pollen distribution.

In addition to studying hummingbird foraging, the behavior of bumble bee foraging has also received recent attention to better understand nectar dwelling microbes and their implications for plant reproductive ecology. Studies found differences in foraging behavior that were correlated with nectar microbial communities. Good et al. (2014) tested how bacteria and yeasts modify feeding preference in *Apis millifera,* a honey bee species. Three bacterial species were studied: *Asaia astilbes, Erwinia tasmaniensis* and *Lactobaccillus kunkeei*. Each of these bacterial species were selected because they are known to be *A. milifera* symbiotic gut microflora and can survive in nectar as well as alter its characteristics. The researchers examined the yeast species *M. reukaufii* since it is a central nectar inhabiting yeast species, and this yeast species is also found in the bee gut. It should be noted that the researchers used artificial flowers and nectar, but the flowers and nectar were very similar to what is found in the field. Nectar removal was less (3 – 32%) in nectars inoculated with bacteria versus the control (no microbes) and nectars inoculated with *M. reukaufii*. All species of microbes studied were able to alter nectar chemistry, although the researchers only examined *A. astilbes* (bacteria), *M. reukaufii* (yeast) and a different *Erwinia* (bacteria) species than listed above. They no longer had access to their bacterial species *E. tasmaniensis* and *L. kunkeei*. In summary, all microbes reduced pH, while H_2O_2 and sucrose remained unchanged. A difference was observed in the glucose and fructose levels of *A. astilbes* inoculated nectar. There were significantly higher concentrations of glucose and fructose than in the control, *M. reukaufii* inoculated flowers and *Erwinia* sp. inoculated nectars. The authors suggest that this alteration of sugar concentration may be the driving force behind the preference of the bee pollinators to remove less nectar from bacteria inoculated nectars. It's the difference in nectar chemistry rather than just the presence of bacteria that is altering bee behavior (Good et al. 2014).

M. reukaufii did not deter bees from removing nectar of the flowers they inhabited. This is supported in another study as well. Herrera et al. (2013) found that the bee species *B. terrestris* preferred nectars inhabited by yeasts than nectars without yeasts when they examined the plant species *H. feotidus*. The statistical significance of nectar consumed was in nectars inoculated with *M. reukaufii* and not *M. gruessi*. The authors were unsure as to the direct source of attraction that was produced by the presence of *M. reukaufii* in nectar or how bees sense the presence of yeasts, but they speculated that it might be due to the way yeasts are altering characteristics. Some sources of attraction Herrera and colleagues suggested include a shift in nectar temperature, yeast metabolites, sugar or amino acid profiles, taste alterations and volatile emissions (Herrera et al. 2013).

Although plants with nectars containing yeasts had more nectar removed and more visits from foraging bees, they had lower reproductive success. *H. feotidus* plants with nectar inhabiting yeasts reduced the number of pollen tubes, fruit set, seed set and seed size, which are all indicators of plant reproduction (Herrera et al. 2013). Herrera et al. (2013) considered longer pollinator visitation as a potential source of reduced plant fecundity when bees removed more nectar. The authors mentioned another study found that when *H. feotidus* is self-pollinated they produce fewer and smaller seed sets; longer visits by pollinators would facilitate more self-pollinations.

The new data emerging from the studies discussed in this section are just beginning to break down the ecological role microbes may play in plant reproduction. Researchers are continuing to find support that yeasts and bacteria play a significant part in facilitating the foraging behavior of pollinators. More follow up studies are needed to continue to test the different roles nectar-living microbes, pollinators, and plants have in this intertwined system.

Conclusion

The perception of plant-pollinator relationships as being a binary system, when a plant essentially attracts a specific pollinator, is changing with emerging evidence of microbial organisms altering nectar characteristics - a major energetic reward for pollinators provided by flowers in exchange for reproductive services to increase fecundity. This review analyzed studies that present growing evidence of microbes inhabiting nectars across a wide geographic range as well as evidence that these microbial communities are altering the characteristics of nectar. In some cases, microbes can degrade the nectar reward produced by a plant by reducing sucrose concentrations. On the other hand, in bumble bee pollinated plants, microbe activity may be beneficial by warming the nectar. This field of research is still in its infancy and there is still much to be learned about the implications of microbial communities in nectar. There is a need for continued studies on a wider, global scale that evaluate microbial communities and their ecological implications in flowers throughout the world. Closer examination as to how microbial communities develop and directly impact pollinator interactions is needed. Additionally, research should focus on how plant reproductive success is influenced by microbial nectar alteration. The complexity and lack of knowledge involved with microbial ecology opens the door for further experimentation to better understand this rather elusive biological system.

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Author Biography

Anthony Schmitt is a senior at the University of Minnesota Duluth. He will be graduating with B.A. in both Biology and Writing Studies. He currently works as an undergraduate research assistant for Dr. Clay Carter. Dr. Carter studies genes and other molecular processes that underly the production of nectar in plants, specifically in the Brassicaceae family. After graduating he plans to attend graduate school and pursue a PhD in a field of biology, although he is currently undecided. Anthony studied abroad in New Zealand his sophomore year and loves to travel. He also loves hunting, fishing and anything that gets him outdoors.

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