Research Advances on Nectar Microorganisms and Their Ecological Functions: Postprint

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Abstract

Nectar represents the most effective reward provided by entomophilous plants to pollinators, and investigations into plant-pollinator mutualisms mediated by nectar characteristics have emerged as one of the most active domains within contemporary pollination biology. The original nectar secreted by flowering plants is sterile; however, microorganisms can colonize nectar through airborne transmission or (and) via contact with pollinators' proboscises, subsequently exploiting nectar nutrients for rapid proliferation. The hyperosmotic environment of nectar constrains microbial species diversity, resulting in relatively low richness of microorganisms (yeasts, bacteria). Furthermore, both biotic factors (pollinator assemblage composition, inter-microbial competition) and abiotic factors (osmotic pressure, sugar composition, secondary metabolites, antimicrobial compounds, available nitrogen sources, temperature, pH) shape the assembly of nectar microbial communities. Microbial metabolic activities within nectar modify its physical (temperature, viscosity) and chemical (pH, H_2O_2 content, sugar composition and concentration, amino acid profile and concentration, and odor) properties, consequently influencing pollinator foraging behavior and plant reproductive fitness. Accordingly, research on nectar microorganisms and their ecological functions has garnered substantial attention among pollination biologists in recent years. Building upon a synthesis of existing literature, we propose that future investigations should integrate molecular biological and chemical analytical techniques to further uncover the mechanistic underpinnings of factors governing nectar microbial communities, while providing more comprehensive elucidation of how nectar microorganisms alter nectar physicochemical properties and plant-pollinator interactions, and particularly advancing our understanding of the ecological functions that nectar microorganisms fulfill within ecosystems.

Full Text

Preamble

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Nectar-dwelling microorganisms and their ecological functions

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Abstract

Floral nectar, a sweet, aqueous secretion consisting mainly of sugars and to a lesser extent amino acids, is an effective reward that entomophilous plants provide for their pollinators. Plant-pollinator relationships mediated by nectar characteristics have become one of the most active research areas in pollination biology. Although initially sterile, floral nectar can harbor yeasts and bacterial species that are dispersed via air or by flower-visiting insects such as pollinators, which then utilize nectar nutrients for rapid proliferation. The high osmotic pressure environment of nectar results in relatively low microbial species diversity. Pollinator composition, microbial competition, and abiotic factors also influence nectar microbial community formation. Microbial metabolic activities can alter nectar' s physical properties, sugar composition and concentration, and amino acid profiles, thereby affecting pollinator foraging behavior and plant reproductive fitness. Research on nectar microorganisms and their ecological functions has attracted considerable attention from pollination biologists. Based on a synthesis of published studies, future research should combine molecular biology and chemical analysis techniques to further elucidate the mechanisms underlying potential factors affecting nectar microbial communities, provide more detailed explanations of how nectar microorganisms alter nectar physicochemical characteristics and plant-pollinator interactions, and particularly advance our understanding of the ecological functions of nectar microorganisms in ecosystems.

Keywords: nectar-dwelling microorganisms; nectar characteristics; pollinator behavior; reproductive fitness

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1. Main Microorganisms in Nectar

1.1 Yeasts in Nectar

Microbiologists have long recognized that microorganisms are ubiquitous in floral nectar, with studies dating back to the late 19th century. However, it was only with deeper pollination biology research that nectar microorganisms began attracting attention from pollination biologists. While freshly secreted nectar is initially sterile, certain microorganisms—primarily yeasts and bacteria—can colonize nectar through air dispersal or contact with pollinator mouthparts, subsequently utilizing nectar nutrients for rapid proliferation.

Published studies indicate that yeasts occur at relatively high frequencies in plant nectar. Jimbo found yeast occurrence rates of 67.8% in nectar samples from Japan, with individual plant species showing rates between 0%-100% and an average of 54.4%. Sandhu and Waraich reported yeast occurrence rates of 39.5%-92.1% in nectar from cultivated plants in northwestern India, with an average of 51.3%. De Vega et al. documented a 43.2% yeast occurrence rate in South African forest and grassland plants. Herrera et al. surveyed 316 plant species in southwestern Spain and 635 species in Mexico' s Yucatan Peninsula, finding yeast occurrence rates of 37.4% and 39.8%, respectively. Mittelbach et al. reported that 32% of 740 nectar samples from bird-pollinated plants in the Canary Islands contained culturable yeasts. Overall, yeast occurrence rates in floral nectar across different regions range from 30% to 70%.

Yeast densities in nectar are typically high, though species diversity remains low, with most nectar samples containing only 1–2 yeast species. The most commonly isolated yeasts belong to the family Metschnikowiaceae within the phylum Ascomycota, particularly the osmotolerant species *Metschnikowia reukaufii* and *M. gruessii*. Basidiomycetous yeasts are rare and may result from contamination from other plant parts. Recent work suggests that ascomycetous yeasts dominate sucrose-rich nectars, while hexose-dominated nectars favor basidiomycetous yeasts. Other genera such as *Candida* (Ascomycota) and *Rhodotorula*, *Cryptococcus*, and *Sporobolomyces* (Basidiomycota) also occur, albeit at lower frequencies. Most yeast species found in nectar are not nectar specialists and likely invade through contact with floral corollas or visiting insects.

Spatial and temporal distribution patterns of nectar yeasts have become a recent focus. Studies reveal significant variation in yeast occurrence, density, and diversity across different spatial scales: among geographic regions, populations, individual plants, flowers on the same plant, and even among nectaries within the same flower. Temporal variation also exists across years, flowering periods, and sexual phases. For example, in *Helleborus foetidus*, yeast occurrence and density varied among populations and flowering stages, with higher rates during early flowering (100%) compared to female-phase flowers (4%). These patterns appear driven primarily by pollinator composition and activity.

1.2 Bacteria in Nectar

Bacteria are also common nectar inhabitants. Surveys in Mediterranean and South African plants show bacterial occurrence rates of 20%-80%, with densities reaching up to 10^3 CFUs/mm^3. Bacterial diversity is similarly low, with most nectar samples containing only 1-2 species. Nectar bacteria primarily belong to Proteobacteria, Actinobacteria, and Firmicutes, with novel species such as *Acinetobacter nectaris*, *A. boissieri*, and *Rosenbergiella* spp. identified. Bacteria often co-occur with yeasts, possibly through complementary nutrient utilization.

Nectar bacteria exhibit specialized physiological traits, including tolerance to high sucrose concentrations (10%-30%), low oxygen conditions, and the presence of H_2O_2. These adaptations enable survival in nectar' s harsh environment.

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2. Factors Influencing Nectar Microbial Communities

Nectar microbial communities typically consist of phylogenetically clustered, low-diversity assemblages whose occurrence, density, and composition show significant spatiotemporal variation. These patterns likely result from interactions between biotic and abiotic factors.

2.1 Biotic Factors

Microbes colonize nectar primarily through pollinator vectors, making pollinator composition and activity crucial determinants of microbial community structure. Flower density, nectar characteristics, and flowering phenology influence pollinator visitation patterns, thereby indirectly affecting microbial dispersal. For instance, in *Mimulus aurantiacus*, fungal occurrence correlated positively with flower density. In *Helleborus foetidus*, pollinator composition explained spatial and temporal variation in yeast communities.

Microbial interactions also shape community assembly. Early colonizers can reduce nectar sugar concentration and osmotic pressure, facilitating establishment of non-osmotolerant species. Competition among yeasts for resources can exclude inferior competitors, particularly among closely related species. The metabolic activities of established microbes further modify nectar chemistry, influencing subsequent colonization.

2.2 Abiotic Factors

Nectar' s high sugar content and low water activity create a selective environment that filters microbial colonists. The "nectar filtering hypothesis" proposes that high osmotic pressure, secondary metabolites, and antimicrobial proteins limit microbial diversity, favoring only the most adapted strains. While some secondary compounds like alkaloids and glycosides show limited antimicrobial effects, high sugar concentrations strongly inhibit non-osmotolerant microbes, explaining why most nectar yeasts belong to osmotolerant Ascomycota.

Carbon-to-nitrogen ratios also influence community composition. Nectar is typically carbon-rich but nitrogen-poor, making nitrogen a limiting resource. Pollen grains in nectar may provide essential nitrogen through amino acid release. Environmental factors such as relative humidity, rainfall, and temperature affect nectar secretion, sugar concentration, and pollinator behavior, thereby indirectly shaping microbial communities. Temperature directly impacts microbial growth rates, with nectar yeasts showing broad thermal tolerance (8–30°C).

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3. Effects of Nectar Microorganisms on Nectar Physicochemical Characteristics

Nectar microorganisms can alter physical properties (temperature, viscosity), chemical composition (sugars, amino acids, H_2O_2), and scent. Yeast metabolism generates heat, raising nectar temperature and reducing viscosity, which benefits cold-weather foragers. In *Helleborus foetidus*, temperature increase correlated positively with yeast density.

Microbial fermentation significantly modifies sugar profiles. Inoculation experiments with *Mimulus aurantiacus* showed that both bacteria and yeasts reduced total sugar and sucrose concentrations, with bacteria causing greater reductions. Field surveys revealed species-specific relationships between yeast density and sugar composition. Yeasts also decreased concentrations of specific amino acids (proline, valine, tyrosine), suggesting they utilize amino acids as nitrogen sources.

Microbial activity alters nectar scent. While plants produce some volatile organic compounds (VOCs), yeasts like *Metschnikowia* spp. produce ethanol and other volatile alcohols that contribute to nectar' s fermented odor. In *Silene caroliniana*, nectar with microorganisms contained more aromatic compounds than sterile nectar, with yeasts producing the volatile alcohols responsible for the floral wine-like scent.

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4. Effects on Pollinator Behavior and Plant Fitness

Nectar microorganisms influence pollinator foraging and plant reproductive success by modifying nectar quality. Early studies showed mixed results: bees could not always distinguish yeast-inoculated nectar, while some yeasts producing high ethanol concentrations deterred wasps. More recent work demonstrates that bumblebees prefer yeast-inoculated *Delphinium barbeyi* nectar, possibly because yeasts provide proteins and amino acids or produce attractive volatiles.

Microbial effects on plant fitness are context-dependent. In *Helleborus foetidus*, *Metschnikowia reukaufii* increased bumblebee visitation but reduced female fitness by decreasing pollen tube growth and seed set. In *Delphinium nuttallianum*, high yeast densities enhanced male fitness by increasing pollen export without affecting female fitness. In *Mimulus aurantiacus*, nectar bacteria (but not yeasts) reduced female fitness by decreasing seed production per fruit.

These effects depend on floral morphology, breeding system, and pollen limitation. Microbial fermentation produces ethanol and other volatiles that can alter pollinator behavior, while spatial variation in microbial communities within plant species may create "risky" flowers that deter pollinators, potentially reducing pollination services.

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5. Future Directions

Despite progress, several knowledge gaps remain:

1. **Phenotypic and genotypic diversity**: Nectar microbes likely possess broad ecological niches and high phenotypic plasticity. Molecular studies of genotype diversity in nectar yeasts and bacteria are needed to understand population structure and adaptation.
2. **Broader ecological interactions**: Research has focused on pollinators, but effects on nectar robbers, herbivores, and other flower visitors remain unexplored. Nectar microbes may influence biological control systems by affecting predators and parasitoids that feed on nectar.
3. **Microbe-pollinator coevolution**: Pollinators may derive nutritional benefits from nectar microbes, and microbes may aid in nectar digestion. Understanding these mutualisms could reveal tripartite plant-pollinator-microbe interactions.
4. **Plant defense mechanisms**: Plants likely evolved antimicrobial defenses to protect nectar quality. Identifying antimicrobial proteins and secondary compounds in nectar and testing their efficacy will clarify mechanisms controlling microbial diversity.
5. **Chemical ecology**: Microbial volatiles influence pollinator attraction. Comparative analysis of nectar scent profiles before and after microbial inoculation will elucidate how microbes mediate plant-pollinator communication.

Nectar microorganisms represent a dynamic component of plant-pollinator systems, possessing unique adaptations to thrive in harsh nectar environments and exerting important ecological functions that warrant continued investigation.

References

[1] Werner EE, Peacor SD. A review of trait-mediated indirect interactions in ecological communities. Ecology, 2003, 84(5): 1083-1100.
[2] Abrams PA. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. The American Naturalist, 1995, 146(1): 112-134.
[3] Wootton JT. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. The American Naturalist, 1993, 141(1): 71-89.
[4] Strauss SY, Irwin RE. Ecological and evolutionary consequences of multispecies plant-animal interactions. Annual Review of Ecology, Evolution and Systematics, 2004, 35(1): 435-566.
[5] Strauss SY, Conner JK, Rush SL. Foliar herbivory affects floral characters and plant attractiveness to pollinators: implication for male and female plant fitness. The American Naturalist, 1996, 147(6): 1098-1107.
[6] McCall AC, Irwin RE. Florivory: the intersection of pollination and herbivory. Ecology Letters, 2006, 9(12): 1351-1365.
[7] Irwin RE, Bronstein JL, Manson JS, Richardson L. Nectar robbing: ecological and evolutionary perspectives. Annual Review of Ecology, Evolution and Systematics, 2010, 41(1): 271-292.
[8] Cresswell JE, Hagen C, Woolnough JM. Attributes of individual flowers of Brassica napus L. are affected by defoliation but not by intraspecific competition. Annals of Botany, 2001, 88(1): 111-117.
[9] Theis N, Kesler K, Adler LS. Leaf herbivory increase floral fragrance in male but not female flowers. American Journal of Botany, 2009, 96(5): 897-903.
[10] Lehtilä K, Strauss SY. Effects of foliar herbivory on male and female reproductive traits of wild radish, Raphanus raphanistrum. Ecology, 1999, 80(1): 116-124.
[11] Cozzolino S, FineSChi S, Litto M, Scopece G, Trunschke J, Schiestl FP. Herbivory increases fruit set in Silene latifolia: a consequence of induced pollinator-attracting floral volatiles? Journal of Chemical Ecology, 2015, 41(7): 622-630.
[12] Baker HG, Baker I. Studies of nectar-constitution and pollinator-plant coevolution. In: Gilbert LE, Raven PH, eds. Coevolution of animals and plants. Austin, TX: University of Texas Press, 1975: 100-104.
[13] Adler LS, Bronstein JL. Attracting antagonists: does floral nectar increase leaf herbivory. Ecology, 2004, 85(6): 1519-1526.
[14] Herrera CM, García IM, Pérez R. Invisible floral larcenies: microbial communities degrade floral nectar of bumble bee-pollinated plant. Ecology, 2008, 89(9): 2369-2376.
[15] Betts AD. Nectar yeasts. The Bee World, 1920, 1: 252-253.
[16] Jimbo T. Yeasts isolated from flower nectar. Science Reports of the Tohoku Imperial University, 1926, 2: 161-187.
[17] Lund A. Studies on the ecology of yeasts. Haislund N, Trans. Copenhagen: Tubory Breweries, 1954.

[18] Brysch-Herzberg M. Ecology of yeasts in plant-bumblebee mutualism in Central Europe. FEMS Microbiology Ecology, 2004, 50(2): 87-100.
[19] Álvarez-Pérez S, Lievens B, Jacquemyn H, Herrera CM. Acinetobacter nectaris sp. nov. and Acinetobacter boissieri sp. nov., two novel bacterial species isolated from floral nectar of wild Mediterranean insect-pollinated plants. International Journal of Systematic and Evolutionary Microbiology, 2013, 63(4): 1532-1539.
[20] Álvarez-Pérez S, Herrera CM, de Vega C. Zooming-in floral nectar: a first exploration of nectar-associated bacteria in wild plant communities. FEMS Microbiology Ecology, 2012, 80(3): 591-602.
[21] Fridman S, Izhaki I, Gershman Y, Halpern M. Bacterial communities in floral nectar. Environmental Microbiology Reports, 2012, 4(1): 97-104.
[22] Golonaka AM, Vilgalys R. Nectar inhabiting yeasts in Virginian populations of Silene latifolia (Caryophyllaceae) and coflowering species. The American Midland Naturalist, 2013, 169(2): 235-258.
[23] Herrera CM, de Vega C, Canto A, Pozo MI. Yeasts in floral nectar: a quantitative survey. Annals of Botany, 2009, 103(9): 1415-1423.
[24] Peay KG, Belisle M, Fukami T. Phylogenetic relatedness predicts priority effects in nectar yeast communities. Proceeding of the Royal Society B, 2012, 279(1729): 749-758.
[25] Pozo MJ, de Vega C, Canto A, Herrera CM. Presence of yeasts in floral nectar is consistent with the hypothesis of microbial-mediated signaling in plant-pollinator interactions. Plant Signal & Behavior, 2009, 4(11): 1102-1104.
[26] de Vega C, Herrera CM. Microorganisms transported by ants induce changes in floral nectar composition of an ant-pollinated plant. American Journal of Botany, 2013, 100(4): 729-800.
[27] Vannette RL, Gauthier MPL, Fukami T. Nectar bacteria, but not yeast, weaken a plant-pollinator mutualism. Proceeding of the Royal Society B, 2013, 280(1752): 20122601.
[28] Good AP, Gauthier MPL, Vannette RL, Fukami T. Honey bees avoid nectar colonized by three bacterial species, but not by a yeast species, isolated from the bee gut. Plos One, 2014, 9(1): e86494.
[29] Lenaerts M, Álvarez-Pérez S, de Vega C, van Aschchea A, Johnsond SD, Willemsa KA, Herrerac CM, Jacquemyn H, Lievensa B. Rosenbergiella australoborealis Rosenbergiella collisarenozi Rosenbergiella epipactidis sp. nov., sp. nov. and sp. nov., three novel bacterial species isolated from floral nectar. Systematic and Applied Microbiology, 2014, 37(6): 402-511.
[30] [Title not provided] Comparative study on antimicrobial activity and culturable microbial diversity in nectar of Datura arborea [D]. Yunnan Normal University, 2014: 15-21.
[31] Pozo MI, Lievens B, Jacquemyn H. Impact of microorganisms on nectar chemistry, pollinator attraction and plant fitness. In: Peck RL, ed. Nectar: Production, Chemical Composition and Benefits to Animals and Plants. New York: Nova Science Publishers, Inc., 2014.
[32] Boutroux L. Sur la Conservation des ferments alcooliques dans la nature. Annales des Sciences Naturelles, Série IV, Botanique, 1884, 17: 145-209.

[33] Kevan PG, Eisikowitch D, Fowle S, Thomas K. Yeast-contaminated nectar and its effects on bee foraging. Journal of Apicultural Research, 1988, 27(1): 26-19.
[34] Eisikowitch D, Kevan PG, Lachance MA. The nectar-inhabiting yeasts and their effect on pollen germination in common milkweed, Asclepias syriaca L. Israel Journal of Botany, 1990, 39(1/2): 217-225.
[35] Álvarez-Pérez S, Herrera CM. Composition, richness and nonrandom assembly of culturable bacterial-microfungal communities in floral nectar of Mediterranean plants. FEMS Microbiology Ecology, 2013, 83(3): 685-699.
[36] Schaeffer RN, Phillips CR, Duryea MC, Andicoechaea J, Irwin RE. Nectar yeasts in the tall larkspur Delphinium barbeyi (Ranunculaceae) and effects on components of pollinator foraging behavior. Plos One, 2014, 9(10): e108214.
[37] Canto A, Herrera CM, Medrano M, Pérez R, García IM. Pollinator foraging modifies nectar sugar composition in Helleborus foetidus (Ranunculaceae): An experimental test. American Journal of Botany, 2008, 95(3): 315-320.
[38] de Vega C, Herrera CM, Johnson SD. Yeasts in floral nectar of some South African plants: quantification and associations with pollinator type and sugar concentration. South African Journal of Botany, 2009, 75(4): 798-806.
[39] Pozo MI, Herrera CM, Bazaga P. Species richness of yeast communities in floral nectar of southern Spanish plants. Microbial Ecology, 2011, 61(1): 82-91.
[40] Pozo MI, Lachance MA, Herrera CM. Nectar yeasts of two southern Spanish plants: the roles of immigration and physiological traits in community assembly. FEMS Microbiology Ecology, 2012, 80(2): 281-293.
[41] Aizenberg-Gershtein Y, Izhaki I, Halpern M. Do honeybees shape the bacterial community composition in floral nectar? Plos One, 2013, 8(7): e67556.
[42] Manson JS, Lachance MA, Thomson JD. Candida gelsemii sp. nov., a yeast of the Metschnikowiaceae clade isolated from nectar of the poisonous Carolina Jessamine. Antonie van Leeuwenhoek, 2007, 92(1): 37-52.
[43] Babjeva IP, Gorin S. About the spore formation and the life cycle of Metschnikowia pulcherrima and M. reukaufii in the nature. Bulletin of Moscow University, 1973, 5: 82-85.
[44] Sandhu DK, Waraich MK. Yeasts associated with pollinating bees and flower nectar. Microbial Ecology, 1985, 11(1): 51-58.
[45] Pozo MI. Yeasts in floral nectar: community ecology and interactions with insect pollinators and host plants [D]. Seville, Spain: University of Seville, 2012.
[46] Mittelbach M, Yurkov AM, Nocentini D, Nepi M, Weigend M, Begerow D. Nectar sugars and bird visitation define a floral niche for basidiomycetous yeast on the Canary Island. BMC Ecology, 2015, 15(1): 2.
[47] Jacquemyn H, Lenaerts M, Tyteca D, Lievens B. Microbial diversity in the floral nectar of seven Epipactis (Orchidaceae) species. Microbiology Open, 2013, 2(4): 644-658.
[48] Mushtaq M, Jamal A, Nahar S. Biodiversity of yeast mycoflora in nectar of Hibiscus rosa-sinensis Ixora coccinea flowers. Pakistan Journal of Botany, 2007, 39(4): 1367-1376.

[49] Belisle M, Peay KG, Fukami T. Flowers as islands: spatial distribution of nectar-inhabiting microfungi among plants of hummingbird-polloinated shrub. Microbial Ecology, 2012, 63(4): 711-718.
[50] Jacquemyn H, Lenaerts M, Brys R, Willems K, Honnay O, Lievens B. Among-population variation in microbial community structure in the floral nectar of the bee-pollinated forest herb Pulmonaria officinalis L. Plos One, 2013, 8(3): e56917.
[51] Pozo MI, Herrera CM, Alonso C. Spatial and temporal distribution patterns of nectar-inhabiting yeasts: how different floral microenvironments arise in winter-blooming Helleborus foetidus. Fungal Ecology, 2014, 11: 173-180.
[52] Schmitt A. The invisible communities of nectar: how yeast and bacteria alter nectar characteristics. The Duluth Journal of Undergraduate Biology, 2014, 1: 19-29.
[53] Samuni-Blank M, Izhaki I, Laviad S, Bar-Massada A, Gerschman Y, Halpern M. The role of abiotic environmental conditions and herbivory in shaping bacterial community composition in floral nectar. Plos One, 2014, 9(6): e99107.
[54] Halpern M, Fridman S, Atamna-Ismaeel N, Izhaki I. Rosenbergiella nectararea gen. nov. sp. nov. in the family Enterobacteriaceae, isolated from floral nectar. International Journal of Systematic and Evolutionary Microbiology, 2013, 63(11): 4259-5265.
[55] Herrera CM, Canto A, Pozo MI, Bazaga P. Inhospitable sweetness: nectar filtering of pollinator-borne inocula leads to impoverished, phylogenetically clustered yeast communities. Proceedings of the Royal Society B, 2010, 277(1682): 747-754.
[56] Pozo MI, Herrera CM, Lachance MA, Verstrepen K, Lievens B, Jacquemyn H. Species coexistence in simple microbial communities: unraveling the phenotypic landscape of co-occurring Metschnikowia species in floral nectar. Environmental Microbiology, 2015, doi: 10.1111/1462-2920.13037.
[57] Nicolson SW, Thornburg RW. Nectar chemistry. In: Nicolson SW, Nepi M, Pacini E, eds. Nectaries and Nectar. Netherlands: Springer, 2007. 215-264.
[58] Adler LS. The ecological significance of toxic nectar. Oikos, 2000, 91(3): 406-520.
[59] Kyung KH, Woo YH, Kim DS, Park HJ, Kim YS. Antimicrobial activity of an edible wild plant, Clematis apiifolia Virgin' s Bower (Clematis apiifolia DC). Food Science and Biotechnology, 2007, 16(6): 1051-1054.
[60] Pozo MI, Herrera CM, Van den Ende W, Verstrepen K, Lievens B, Jacquemyn H. The impact of nectar chemical features on phenotypic variation in two related nectar yeasts. FEMS Microbiology Ecology, 2015, 91(6): fiv055.
[61] Carter C, Healy R, Nicole M, O' Tool NM, Naqvi SM, Ren G, Park S, Beattie GA, Horner HT, Thornburg RW. Tobacco nectaries express a novel NADPH oxidase implicated in the defense of floral reproductive tissues against microorganisms. Plant Physiology, 2007, 143(1): 389-399.
[62] Nicolson SW. Eucalyptus nectar: production, availability, composition and osmotic consequences for the larva of the eucalypt nectar fly, Drosophila flavohirta. South African Journal of Science, 1994, 90(2): 75-79.

[63] Lievens B, Hallsworth JE, Pozo MI, Belgacem ZB, Stevenson A, Willems KA, Jacquemyn H. Microbiology of sugar-rich environments: diversity, ecology and system constraints. Environmental Microbiology, 2015, 17(2): 278-298.
[64] Carter C, Thornburg R. Is the nectar redox cycle a floral defense against microbial attack? Trends in Plant Science, 2004, 9(7): 320-324.
[65] Lachance MA. Yeast biodiversity: how many and how much? In: Péter G, Rosa C, eds. Biodiversity and Ecophysiology of Yeasts. Berlin Heidelberg: Springer, 2006: 1-9.
[66] Corbet SA, Unwin DM, Pry^s-Jones OE. Humidity, nectar and insect visits to flowers, with special reference to Crataegus Tilia and Echium. Ecological Entomology, 1979, 4(1): 9-22.
[67] Herrera CM. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. Ecology, 1995, 76(5): 1516-1524.
[68] Freeman CE, Head KC. Temperature and sucrose composition of floral nectars in Ipomopsis longiflora under field conditions. The Southwestern Naturalist, 1990, 35(4): 423-526.
[69] Sánchez-Lafuente AM, Guitián J, Medrano M, Herrera CM, Rey PJ, Cerdá X. Plant traits, environmental factors, and pollinator visitation in winter-flowering Helleborus foetidus (Ranunculaceae). Annals of Botany, 2005, 96(5): 845-852.
[70] Deak T. Environmental factors influencing yeasts. In: Péter G, Rosa C, eds. Biodiversity and Ecophysiology of Yeasts. Berlin Heidelberg: Springer, 2006: 155-174.
[71] Wiens F, Zitzmann A, Lachance MA, Yegles M, Pragst F, Wurst FM, von Holst D, Guan SL, Spanagel R. Chronic intake of fermented floral nectar by wild treeshrews. Proceedings of the National Academy of Sciences of the United States of America, 2008, 105(30): 10426-10431.
[72] Raguso RA. A wrapped Bouquet: the untapped potential of floral chemistry. Journal of Chemical Ecology, 2014, 40(5): 412-513.
[73] Herrera CM, Pozo MI. Nectar yeasts warm the flowers of a winter-blooming plant. Proceedings of the Royal Society B, 2010, 277(1689): 1827-1834.
[74] Matiashe I, Mahara P, Marume P. Development of Lemon and lime nectar at Mazoe Citrus Estate, Zimbabwe. IOSR Journal of Engineering, 2014, 4(1): 51-60.
[75] Canto A, Herrera CM. Micro-organisms behind the pollination scenes: microbial imprint on floral nectar sugar variation in a tropical plant community. Annals of Botany, 2012, 110(6): 1173-1183.
[76] Raguso RA. Why are some floral nectars scented? Ecology, 2004, 85(6): 1486-1494.
[77] Goodrich KR, Zjhra ML, Ley CA, Raguso RA. When flowers smell fermented: the chemistry and ontogeny of yeasty floral scent in pawpaw (Asimina triloba: Annonaceae). International Journal of Plant Sciences, 2006, 167(1): 33-56.
[78] Nicolson SW, de Veer L, Köhler A, Pirk CWW. Honeybees prefer warmer nectar and less viscous nectar, regardless of sugar concentration. Proceedings of the Royal Society B, 2013, 280(1767): 20131597.

[79] Raguso RA. Wake up and smell the roses: the ecology and evolution of floral scent. Annual Review of Ecology, Evolution, and Systematics, 2008, 39: 549-569.
[80] Golonka AM, Obi Johnson B, Freeman J, Hinson DW. Impact of nectarivorous yeasts on Silene caroliniana’ s scent. Eastern Biologist, 2014, 3: 1-26.
[81] Canto A, Pérez R, Medrano M, Castellanos MC, Herrera CM. Intraplant variation in nectar sugar composition in two Aquilegia species (Ranunculaceae): contrasting patterns under field and glasshouse conditions. Annals of Botany, 2007, 99(4): 653-660.
[82] Ehlers BK, Olesen JM. The fruit-wasp route to toxic nectar in Epipactis orchids? Flora, 1997, 192(3): 223-229.
[83] Herrera CM, Pozo MI, Medrano M. Yeasts in nectar of an early-blooming herb: sought by bumblebees, detrimental to plant fecundity. Ecology, 2013, 94(2): 273-279.
[84] Schaeffer RN, Irwin RE. Yeasts in nectar enhance male fitness in a montane perennial herb. Ecology, 2014, 95(7): 1792-1798.
[85] Biernaskie JM, Cartar RV, Hurly TA. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? Oikos, 2002, 98(1): 98-104.
[86] Lin Y, Tanaka S. Ethanol fermentation from biomass resources: current state and prospects. Applied Microbiology and Biotechnology, 2006, 69(6): 627-642.
[87] Swiegers JH, Bartowsky EJ, Henschke PA, Pretorius IS. Yeast and bacterial modulation of wine aroma and flavour. Australian Journal of Grape and Wine Research, 2005, 11(2): 139-173.
[88] Roughgarden J. Evolution of niche width. The American Naturalist, 1972, 106(952): 683-718.
[89] Baythavong BS. Linking the spatial scale of environmental variation and the evolution of phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments. The American Naturalist, 2011, 178(1): 75-87.
[90] Herrera CM, Pozo MI, Bazaga P. Nonrandom genotype distribution among floral hosts contributes to local and regional genetic diversity in the nectar living yeast Metschnikowia reukaufii. FEMS Microbiology Ecology, 2014, 87(3): 568-575.
[91] Herrera CM. Population growth of the floricolous yeast Metschnikowia reukaufii: effects of nectar host, yeast genotype and host × genotype interaction. FEMS Microbiology Ecology, 2014, 88(2): 250-257.
[92] Bale JS, Van Lenteren JC, Bigler F. Biological control and sustainable food production. Philosophical Transactions of the Royal Society B, 2008, 363(1492): 761-776.
[93] Zender G, Gurr GM, Kuhne S, Kühne S, Wade MR, Wratten SD, Wyss E. Arthropod pest management in organic crops. Annual Review of Entomology, 2007, 52: 57-80.
[94] Johnson M, Wratten SD, Landis DA, Gurr GM. Recent advances in conservation biological control of arthropods by arthropods. Biological Control, 2008, 45(2): 172-175.

[95] Lee FJ, Rusch DB, Stewart FJ, Mattila HR, Newton ILG. Saccharide breakdown and fermentation by the honey bee gut microbiome. Environmental Microbiology, 2015, 17(3): 796-815.
[96] Somerville D. Fat bees skinny bees: a manual on honey bee nutrition for beekeepers. Goulburn: NSW Department of Primary Industries, 2005.
[97] Nepi M. Beyond nectar sweetness: the hidden ecological role of non-protein amino acids in nectar. Journal of Ecology, 2014, 102(1): 108-115.
[98] González-Teuber M, Heil M. Nectar chemistry is tailored for both attraction of mutualists and protection from exploiters. Plant Signaling & Behavior, 2009, 4(9): 809-813.

Note: Figure translations are in progress. See original paper for figures.