

SPECIAL FEATURE

Community and Evolutionary Ecology of Nectar¹

Pollination is an integral part of reproduction of most flowering plants. Worldwide, 90% of some 250 000 angiosperm species rely on pollination for successful reproduction, and nectar is the primary resource provided by plants to attract mutualist visitors. Despite the ubiquity of nectar as an ecosystem resource, our understanding of the importance of nectar has primarily been confined to nectar as a food reward for pollinators. However, recent findings suggest that nectar may mediate interactions with a wide variety of plant visitors other than pollinators. Nectar is frequently consumed by organisms ranging from insect predators and parasitoids to lizards, and can confer increased plant resistance or susceptibility to antagonistic plant visitors. The composition of nectar may be important in structuring insect communities, multi-trophic interactions, and ultimately plant communities via direct and indirect interactions. The physiology and costs of nectar production, and the heritability of nectar traits, may limit the extent to which selection by pollinators or other agents can shape the evolution of nectar traits. On the other hand, the ability of floral visitors to find nectar may limit the extent to which animals can specialize on this resource.

The focus of this Special Feature is to highlight the community and evolutionary ecology of interactions that revolve around nectar as a resource. The last in-depth review of nectar was published in 1983, (*The Biology of Nectaries*, B. Bentley and T. Elias, Editors. Columbia University Press, New York, New York, USA). That volume summarized advances in the understanding of both the physiological mechanisms of nectar secretion and the ecological role of nectar in plant-animal interactions. In the subsequent two decades, great strides have been made in these topics, and summarizing this literature is beyond the scope of this feature. Our goal is to highlight the areas that represent the most exciting recent ecological and evolutionary advances, and to draw attention to questions that are still largely unexplored in an effort to inspire future research.

Traditionally, nectar has been thought of as a relatively simple food resource; however, recent chemical advances combined with field ecological investigation have shown the importance of nectar composition to community ecology. The feature opens with strong demonstrations of the importance of nectar composition, with three papers focusing on insect community structure (Blüthgen and Fiedler), animal foraging and nectar scent (Raguso), and plant evolution in a geographic context (Rudgers and Gardener).

In the next section, we highlight the mechanistic role that nectar plays in nonpollinating interactions. A considerable fraction of floral visitors do not act as pollinators, but rather consume nectar without providing pollination service. Because nectar attracts both pollinators and nectar robbers, plants face a dilemma or possible trade-off in defending against nonpollinating floral visitors without deterring pollinators. Irwin, Adler, and Brody offer conceptual and empirical insight into how plants cope with attack by nectar robbers through nectar and floral traits. With the defensive function of nectar in mind, Wäckers and Bonifay continue this line of reasoning by demonstrating that foliar and bracteal nectar respond in different ways to herbivory, following predictions of the Optimal Defense Theory. Bracteal nectar may serve a role in pollination as well as an indirect defensive function in attracting predators and parasitoids of herbivores. However, the function of foliar nectar is more likely strictly defensive. On the flip side, Adler and Bronstein show that floral nectar may increase plant susceptibility to herbivore attack, especially in cases where pollinators act as herbivores in different life history stages. Through these inter-

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actions, nonpollinating floral visitors may impose strong selection on plants that could reinforce or conflict with selection by pollinators.

Despite the almost dogmatic view that nectar traits have evolved in response to selection by pollinators and other floral visitors, surprisingly little is known about the magnitude of additive genetic variation for nectar traits. The feature closes with a synopsis of our current understanding of the heritability of nectar traits and constraints on their response to selection, highlighting both the methodological advances and pitfalls to measuring heritability of nectar (Mitchell). Understanding the degree to which nectar traits are heritable is critical to argue that the ecological effects of nectar on community-level interactions, described above, can have evolutionary consequences.

Although this work is focused on the community and evolutionary ecology of nectar, the diversity of approaches highlighted in this Special Feature can be applied profitably to the study of many other phenotypic traits and interactions. For example, geographic approaches to the study of coevolution (see Rudgers and Gardener) have been successfully applied to understand how chemical traits mediate predator–prey interactions. Similarly, nectar traits that mediate community structure of ants (see Blüthgen and Fiedler) are functionally similar to chemical traits in plants that affect the community structure of grazers in terrestrial and aquatic ecosystems. The diversity of approaches and systems addressed in this feature demonstrate the fundamental importance of nectar in mediating a wide variety of multispecies interactions. We hope this feature will inspire a future generation of biologists to integrate nectar into the conceptual framework of community and evolutionary ecology.

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