Plant biology: Nectar bacteria grow by germinating and bursting pollen

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Microbial residents of floral nectar must survive in a carbohydrate-rich yet seemingly nitrogen-poor environment. A new study shows that *Acinetobacter* spp., common nectar-inhabiting bacteria, differentially induce the pollen commonly found in nectar to germinate and burst, releasing nutrients for microbial growth.

Microbes are ubiquitous residents of flowering plants and active participants in plant–pollinator mutualisms[1,2]. While bacteria and fungi are the most common microscopic epiphytes on flowers and can significantly affect plant and pollinator health, fitness and communication[3–6], how these microbes gain access to nutrients from flowers is still poorly understood. Bacteria and yeasts are particularly common and abundant in floral nectar, an ephemeral and harsh microenvironment with high osmolarity and abundant carbohydrates but a particularly low concentration of biochemically available nitrogen. While nectar alone is thus a poor growth medium for floral microbes, pollen is commonly found in nectar[6,7]. Pollen is high in amino acids, coenzymes and lipids and thus complements nectar carbohydrates, facilitating microbial growth[7]. Yet, these nutrients are enclosed within pollen's incredibly durable outer layer or exine, which is composed primarily of sporopollenin — one of the most biologically inert polymers[7]. Until now, it was unknown how nectar microbes accessed pollen nutrients. In this issue of *Current Biology*, Christensen, Munkres and Vannette[8] demonstrate the ability of nectar-residing *Acinetobacter* species to induce germination and bursting of pollen and thereby gain access to its nutrient-dense protoplasm to grow (Figure 1).

Acinetobacter and *Metschnikowia* are the most common bacteria and yeasts found in floral nectar, respectively[9]. These taxa coexist in natural nectar metacommunities more frequently than expected by chance[10], suggesting a history of living together in a specialized niche. Previous research has also demonstrated that pollen, when present in nectar, can be a key resource enhancing the growth of both *Acinetobacter* and *Metschnikowia* species. For instance, *Metschnikowia* species grow faster when artificial nectar medium is supplemented with pollen, with the effects on microbial growth depending on the amount and species of pollen[11]. Similarly, growth varies among *Acinetobacter* species and depends on the type of nitrogen source, including amino acids commonly found in pollen[12].

In this new study, Christensen *et al.*[8] corroborate and significantly extend our understanding of how these two commonly co-occurring microbial taxa survive and grow in nectar by exploiting pollen nutrients. Conventionally, the high osmolarity of nectar (due to its high sugar concentration) and the presence of antimicrobial compounds have been considered the primary 'filters' limiting the kinds of microbes that can live in nectar[13,14]. The new work demonstrates that another key filter could be the ability of microbes to effectively and quickly access nutrients from pollen present in nectar. Christensen *et al.*[8] show that pollen in nectar can be essential to the growth of certain nectar specialists, *Acinetobacter* and *Metschnikowia* (Figure 1), as none of the tested strains of either clade could grow in artificial nectar without the presence of California poppy pollen (*Eschoscholzia californica*). Importantly, the authors suggest that the capacity to acquire pollen nutrients is likely a key trait accounting for the prevalence of these microbial taxa in nectar.

Given that certain nectar microbes rely on pollen nutrients enclosed seemingly securely beneath the pollen exine, how do *Acinetobacter* and *Metschnikowia* access pollen nutrients? To answer this question, Christensen *et al.*[8] ingeniously tested whether *Acinetobacter* and *Metschnikowia* strains influence pollen germination and bursting within nectar, thereby exposing the nutrient-rich protoplasm. The authors find that inoculation with *Acinetobacter* strains resulted in much higher levels of pollen germination and bursting (Figure 1) compared with those seen with *M. reukaufii*, with the non-nectar-specialist bacterium *Pectobacterium carotovorum*, or in the uninoculated control. Yet, while *Metschnikowia* did not germinate pollen, it still grew better in the presence of pollen. Accordingly, Christensen *et al.*[8] provided ungerminable (microwaved) pollen to *Acinetobacter* and *Metschnikowia*, elegantly demonstrating that pollen germination is necessary for *Acinetobacter* growth but not *Metschnikowia* growth. In fact, *Metschnikowia* grew equally well when provided with germinable or ungerminable pollen. Excitingly, this study thus shows that the mechanisms to acquire pollen nutrients differ substantially between these two prevalent and commonly co-occurring microbial taxa[8]. Given prior research showing that *M. reukaufii* reduces pollen germination[15] and this new work showing that *Acinetobacter* cannot use ungerminable pollen[8], future research that examines the potential interference among co-occurring *Acinetobacter* and *Metschnikowia* in terms of acquisition of pollen nutrients will likely be exceptionally valuable in

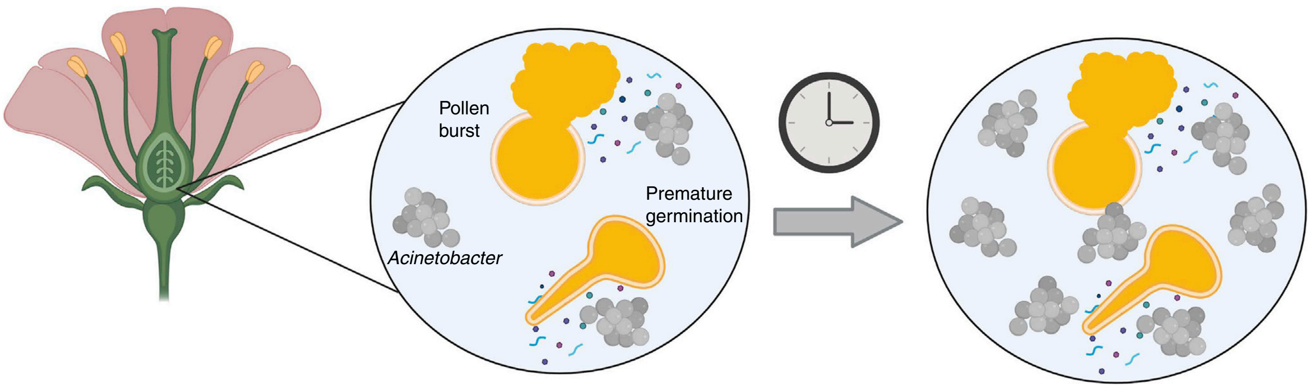

Figure 1. Nectar bacteria burst and germinate pollen to access nutrients.
Some *Acinetobacter* species differentially promote bursting and premature germination of pollen present in nectar, releasing nutrients (depicted by blue/purple dots and lines) and resulting in increased microbial growth in an otherwise carbohydrate-rich but nitrogen-poor environment. (Created with BioRender.com.)

modeling nectar metacommunity structure.

Additionally, this new study establishes that the capacity to germinate pollen varies among *Acinetobacter* strains[8]. For example, pollen inoculated with *A. pollinis* and *A. boissieri* resulted in the highest pollen germination and bursting over the shortest amount of time. In contrast, *A. nectaris*, although a close relative of *A. pollinis*[16], did not induce changes to pollen physiology[8]. Christensen *et al.*[8] thus provide tantalizing evidence that this mechanism to access pollen nutrients may be under strong selection among *Acinetobacter* strains and species. The authors also point out that variation in the capacity to germinate pollen may depend on the plant species and the degree to which the microbe is specialized. Questions for future work will be whether nectar-specialist microbes are unique in having evolved mechanisms to access nutrients from pollen and how widespread are these mechanisms of induced germination and bursting.

The accessibility of nutrients released from germinated and burst pollen could potentially have a strong effect on nectar community dynamics. Christensen *et al.*[8] show that germinable pollen exposed to *Acinetobacter* releases nearly twice as much protein into artificial nectar solution as ungerminable pollen. In contrast, previous research has observed aggregates of *Metschnikowia* around pollen[11], suggesting that pollen degraded by *Metschnikowia* may release its nutrients more selectively. Taken together, these studies suggest that *Acinetobacter* may be ‘ecosystem engineers’, releasing protein (and presumably other nutrients; Figure 1) into an environment previously low in biochemically available nitrogen and thereby facilitating growth and competition with other floral microbes.

Of particular importance to the ecology of nectar microbes, Christensen *et al.*[8] also characterize the ontogeny of pollen germination induced by *Acinetobacter*. Flowers and floral nectar are ephemeral environments for microbes; flowers typically bloom and senesce within hours or days and floral nectar is periodically depleted by foraging animals. As a result, microbes living in nectar must grow rapidly to survive and be dispersed to other flowers. The present study demonstrates that germination and bursting of pollen by *Acinetobacter* occurs remarkably quickly. For example, within just 15 minutes, two of the *Acinetobacter* strains induced germination of three times the amount of pollen in artificial nectar as that seen in uninoculated artificial nectar, and within 45 minutes these strains had burst 45–75 times the amount of pollen[8]. As a result, this work provides strong evidence that pollen germination induced by *Acinetobacter* is adaptive on time scales that are ecologically relevant.

Finally, Christensen *et al.*[8] point out that the implications of the effects of microbes on pollen in nectar are potentially significant and widespread across pollination ecology. Changes to nectar composition mediated by nectar microbes are well understood to affect pollinator foraging, as well as pollination[17]. For instance, pollinators learn or avoid scent cues associated with floral yeast and bacteria[6], and pollen nutrients in sucrose solution can even enhance learned preferences[18], which in turn can result in changes to pollination, visitation, and seed set[1,19]. Furthermore, while yeast–bacterial interactions in nectar have barely been explored, the present work offers a tantalizing explanation for why some nectar yeast and bacteria have been found to have contrasting effects on the composition and abundance of nutrients within nectar[20]. A necessary and fascinating next step will be to determine how patterns of nutrient release from pollen differ among phylogenetically diverse nectar microbes and the consequences of these patterns for microbe–plant–pollinator interactions.

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Animal behavior: Innovation in the city

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Behavioral innovations may help animals cope with new environments, but how such behaviors start is hard to capture. A new study reports the innovation and transmission of a new foraging culture in an urban parrot.

British tits opening milk bottles[1], dolphins foraging from prawn trawlers[2] or crows making use of vehicles to crack walnuts[3] — these are just a few examples of the many behavioral innovations that animals use to profit from human civilization. Innovation — that is a new or modified learned behavior not previously known in a population[4] — allows animals to exploit new resources and to cope with environmental change[4]. Such new behaviors can spread through a population by social transmission from informed individuals to uninformed individuals via social learning[5] and potentially lead to adaptive cultures[6]. In recent decades, studies of animal social learning, information spread and arising culture have increased rapidly, spanning a great variety of behavioral domains and species[7,8]. Nevertheless, the identification of cultures in wild populations remains difficult. This is because behavioral innovations often arise unpredictably, are usually difficult to track across space and time and alternative explanations for local variation in the novel behavior, such as genetic or ecological factors, can be difficult to eliminate[8,9]. In a new study[6], Barbara Klump, Lucy Aplin and colleagues report in detail the development of a novel cultural adaptation to an anthropogenic resource by Sulphur-crested cockatoos (*Cacatua galerita*).

Sulphur-crested cockatoos are long-lived and highly social parrots, native to eastern Australia. These curious and intelligent birds increasingly inhabit urban environments and adapt well to city life. Klump and colleagues[6] document the social spread of a new foraging behavior of these parrots in Sydney, Australia: the opening of household-waste bins (Figure 1). The new study maps the