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Microbiome: Insect Herbivory Drives Plant Phyllosphere Dysbiosis

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A well-known trade-off exists between plant defenses against herbivores and defenses against pathogens, but few studies incorporate the plant microbiome. A new study by Humphrey and Whiteman shows that herbivory reshapes the leaf microbiome and increases susceptibility to potential bacterial pathogens.

There is longstanding interest in describing trade-offs among defense strategies. The vast majority of organisms are under simultaneous selection by multiple natural enemies, and yet responding to one selection pressure often comes at the cost of responding to another. This is clearly demonstrated by the mutually antagonistic relationship between jasmonic acid- and salicylic acid-signaling responses in plants; which of these responses dominates will determine whether plant defenses focus on countering herbivorous insects and necrotrophic pathogens or on opposing biotrophic pathogens, respectively [1]. However, work on the above–below ground interactions between beneficial rhizosphere Pseudomonas species and the herbivorous cabbage looper showed that, in some cases, treatment with a bacterial symbiont can actually increase both jasmonic acid- and salicylic acid-mediated defenses [2]. The emerging role of the microbiome in shaping host fitness and defenses against antagonists (including parasites, predators, and herbivores) [3] emphasizes the need to integrate the role of the microbiome in plant-defense studies. For example, plants under insect herbivore attack are able to recruit protective microorganisms to their rhizosphere microbiome [4]. However, until recently, the effect of insect herbivores on the structure of the leaf microbiome, which is very different from that found in the rhizosphere, remained unclear. A new study by Humphrey and Whiteman [5] elegantly demonstrates that insect herbivory in bittercress changes the leaf microbiome drastically, contributing new insights into the interactions between insect herbivore, plant microbiome, and host plant.

The plant microbiome, like the gut microbiome, is not only shaped by host defense mechanisms but also itself impacts those defenses in turn. Increasing evidence suggests that microbiome homeostasis is maintained through a constant tug of war between a host and its microbes. In a microbially rich environment, a healthy plant tends to establish a specific yet diverse microbiome [6], which we could classify as being 'healthy'. The concept of a healthy microbiome recently gained popularity in the context of the human microbiome, despite the many challenges associated with actually defining microbiome health (discussed by Bäckhed and colleagues [7]). Overall, a healthy microbiome should be associated with a healthy host and should display a certain degree of community stability, whereby both sufficient species richness and species evenness are important community characteristics [7]. The healthy microbiome not only modulates host defense, but its ecological stability resists microbial intruders, hence the host is doubly protected from pathogens. In contrast, microbiome 'dysbiosis' describes a shift in the microbiome that is

associated with host disease; a situation in which microbiome homeostasis collapses and the plant becomes more vulnerable to potentially harmful microbial intruders. Although it is often unclear and case-dependent whether dysbiosis is a cause or consequence of disease [7], understanding dysbiosis may be useful when trying to revert a microbial community so as to mitigate the damage to the host plant.

In their recent paper, Humphrey and Whiteman [5] explore the impact of herbivory by the common leaf-mining fly, *Scaptomyza nigrita*, on the microbiome of bittercress leaves. They found that bittercress under herbivory by *S. nigrita* had overall higher bacterial densities than undamaged leaves, mainly due to the increased abundance of common leaf bacteria [5]. The most spectacular rise in numbers was achieved by a particular species of *Pseudomonas*, where three to six doublings were observed [5]. As the authors [5] point out, the increase in microbial numbers in the damaged leaf tissue is likely caused by both an increase in released nutrients and the plant response. This is further supported by the fact that many pseudomonads are pathogenic (this study did not have the resolution required to distinguish pathogenic from non-pathogenic *Pseudomonas*), and that damaged leaf tissue may provide nutrients that are particularly favored by plant pathogens. The increase of jasmonic acid in the plant is known to be a common plant response to insect herbivory and, in an additional experiment using previously described *Pseudomonas syringae* strains, the authors found a positive effect of jasmonic-acid increase on the abundance of some, but not all, strains in the host plant [5]. One untested possibility is that the insects themselves could have delivered the *Pseudomonas* to the leaves by oral secretion, as was shown for *Leptinotarsa decemlineata* larvae, which secrete *Pseudomonas* sp. to downregulate the jasmonic-acid response and suppress the plant's anti-herbivore response [8]. Hence, three potential causes contribute to the increase of the total bacterial numbers observed by Humphrey and Whiteman [5]: nutrient increase by plant cell death, jasmonic-acid increase, and bacterial inoculation by insect secretions.

The shift of several community characteristics seems to be typical of dysbiosis. The spectacular increase of *Pseudomonas* and several other taxa is reflected in the decrease of evenness of the community, a change that has been proposed before to be an unhealthy shift from the original healthy microbiome [7]. Furthermore, the microbiomes associated with damaged leaves were more dissimilar to each other than those of undamaged leaves. This supports previous findings that, in a healthy state, the host plant maintains a strong selection towards its microbiome [6]. This selectivity can no longer be preserved by a compromised host; hence, the microbiome becomes unstable and can change in many different ways, as random effects become a relatively larger contributor to the community composition than selection. Interestingly, the effect of herbivores on the leaf microbiome (where tissue damage is happening) therefore seems very different than that on the rhizosphere microbiome, where protective microbes are recruited [4]. Whether this dysbiosis-like shift in the leaf microbiome indeed has a negative impact on the host plant and its interaction with both insect herbivores and plant pathogens remains a topic of speculation and an interesting question for future research.

Humphrey and Whiteman [5] suspect that the herbivory likely caused the increase in potential pathogens, but the possibility that the herbivores are attracted to microbially compromised locations on the leaf tissue cannot be excluded. Despite the lack of knowledge on the direction of causation, the co-occurrence of potential plant pathogens and insect herbivores is related to a decreased fruit set of the victim plant, indicating decreased fitness [5]. Humphrey and Whiteman [5] concluded that, besides being bad for the plant, the co-occurrence of insect herbivory and increased numbers of potential plant pathogens is likely to be common. However, the implications of their findings strongly depend on whether the *Pseudomonas* strains found in this study indeed have plant pathogenic potential, since the *Pseudomonas* genus covers a variety of organisms including even biocontrol agents (for example [9]). Nevertheless, as microorganisms in a genus may share many similarities, the findings of Humphrey and Whiteman [5] could be generalizable to other members of the *Pseudomonas* genus, which includes several common plant pathogens.

Humphrey and Whiteman [5] argue that it is possible that their results may be generalizable to other plant–microbe–insect herbivore combinations as well. Hence their findings may have major implications for agricultural practices and plant-microbiome studies. Firstly, the estimated damage to crops as a consequence of insect herbivory will be higher when taking into account the increased chances of co-occurring plant disease. This encourages agricultural management to tackle insect pests sooner and more thoroughly. Additionally, when insect herbivory is observed in an agricultural setting, we may anticipate the co-occurrence of potential plant pathogens. In that case, preventive measures against these pathogens can be taken before disease symptoms even occur. However, to implement this strategy successfully, more research to determine common plant–insect–pathogen combinations is needed. Secondly, the leaf microbiome — often referred to as the phyllosphere — is being increasingly studied for both its application potential and its utility for ecological studies. Recognizing dysbiosis of the leaf microbiome may be very useful in developing applications that could revert dysbiosis and decrease plant damage or even bring the host plant back to a healthy state. Phyllosphere researchers will need to distinguish between healthy microbiomes and dysbiosis, as these states may respond differently to an experimental treatment. Regarding research on biocontrol agents in the phyllosphere, there seems to be an urgent need to address whether addition of biocontrol agents could attract insect herbivores before making these agents more widely available. Moreover, if reverting dysbiosis is indeed beneficial to the host plant, the development of biocontrol agents that restore a healthy microbiome may help to limit damage to a compromised host plant.

Importantly, if Humphrey and Whiteman [5] had only studied the communities on a compositional level

(which is true of most microbiome studies to date), they would not have been able to determine whether the bacterial taxa decreased or increased in absolute abundance. The increase of Pseudomonads under herbivory they observed was found to be associated with decreased relative abundances of all other taxa in the same sample. Normalization using host DNA allowed them to observe that several taxa, as well as the total bacteria, increased in absolute abundance [5]. This demonstrates how adding a quantitative analysis to the marker-gene sequencing data can move us towards better estimates of bacterial densities within hosts, and it was essential in reaching biologically relevant conclusions. This practice is increasingly advised for microbial community studies in general, and the authors [5] provide a straightforward method that can readily

be applied in future plant-microbiome studies.

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Brain Mapping: Understanding the Ins and Outs of Brain Regions

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A recent study in which primary motor cortex activity was imaged with sub-laminar resolution has found that, while overt motor actions led to activity in both superficial and deep cortical layers, motor imagery engaged only superficial layers.

The goal of cognitive neuroscience is to explain behavior in neural terms. In the service of that goal, the past several decades have seen new tools and analytic techniques support ever more detailed maps of human brain structure and function. One of the most widely used techniques, blood-oxygen-level-dependent (BOLD) functional magnetic resonance imaging (fMRI), has relatively high spatial resolution in the setting of whole brain coverage, but is notoriously limited by low temporal resolution. On the other hand, methods that measure extra-

cranial electrical potentials — magnetoencephalography (MEG) and electroencephalography (EEG) — have millisecond temporal resolution but, because of their limited spatial resolution, cannot resolve functional activity associated with temporally overlapping inputs and outputs in a brain region. As they report in this issue of *Current Biology*, Persichetti et al. [1] have broken the impasse by using a functional MRI method with the sensitivity to distinguish superficial laminar activity, associated with afferent inputs, from deep laminar

activity, associated with efferent outputs [2]. This technique, vascular space occupancy (VASO), is based on measuring cerebral blood volume, and has higher contrast-to-noise at high spatial resolution than conventional BOLD fMRI [1,2].

Persichetti et al. [1] scanned healthy adult subjects who performed either an overt hand action with their left hand (finger tapping) or imagined doing so. Functional imaging focused on the primary motor representation of the left hand. The authors report two core