

Special Issue: Specificity of plant–enemy interactions

Synthesizing specificity: multiple approaches to understanding the attack and defense of plants

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The concept of specificity in plant–herbivore and plant–pathogen interactions excites plant pathologists, molecular biologists and animal ecologists alike. This excitement grows out of the notion that individual plant and enemy species (or populations) are reciprocally interacting in a way that shapes their traits and evolution [1,2]. Why is it that most herbivores and pathogens attack a minute fraction of the plants or even plant organs available to them? How do plants manage to defend against diverse enemies? Why are plant enemies specialized at all, given that specialization seems to simply limit the number of available hosts? Are most current plant–enemy interactions the result of a coevolutionary history, and can these be manipulated to protect agricultural crops from pest insects and disease, and ecosystems from invasive species? These are the questions central to this Special Issue of *Trends in Plant Science*. Here, we combine perspectives of the plant with that of its enemies in order to focus on the traits that allow for successful plant defense versus successful exploitation of plant tissues. Although the topic is often approached from different research traditions (ecology, genetics, physiology, etc.), scientists studying herbivores and plant pathogens have occasionally joined forces and should continue to do so, because there is much to be learned by crossing traditional academic boundaries [3–5]. In addition, we now realize that co-infection, multiple attack, and interactions between herbivores and pathogens are themselves commonplace [6,7].

At the core of issues relating to specificity are two contrasting views, one from the perspective of the plant and one from the perspective of the enemy. First, from a plant's perspective, there are myriad primary protective barriers, and some of these will be effective against many, if not most attackers [8]. For example, the plant cuticle represents the first barrier encountered by most herbivores and pathogens. Even once this is breached, general strategies, such as the production of hydrogen peroxide, are used to strengthen cell walls. Phenolics occur in most plants, and many of these compounds likely serve some protective role. Even more common, perhaps ubiquitous, are defensive proteins, which are frequently induced upon attack and, depending on their specific structure, can protect plants from pathogens and/or herbivores. Other fairly general forms of defense include the production of hydrogen cyanide and latex, each found in nearly 10%

of all flowering plants, and both activated upon tissue damage [9].

Despite these general barriers against enemies, the diversity of enemies that are likely to attack any given plant begs two important questions: (i) Do some traits that protect the plant against one attacker make the plant more susceptible to attack from others?; and (ii) Given the limited resources available, even if the first question does not apply, could a plant simultaneously defend against all attackers? This leads to further questions on the strategies of the attackers. What are the central traits of enemies enabling them to overcome these multiple defensive strategies? Are enemies that are particularly efficient at exploiting one specific host necessarily suffering from a lower performance on others, and what are the causal mechanisms that underlie this 'jack of all traits – master of none' principle?

The good news is that we know some of the answers. It is reasonably certain that some plant traits that are expressed in a defensive context are a double-edged sword from the plant's perspective [10,11], and there is no way to simultaneously deploy even a fraction of the total plant defensive traits in a plant genome. As a result, phenotypically plastic means of defense are the norm in plants. Two articles in this Special Issue by Matthias Erb and colleagues, and Noah Whiteman and colleagues are devoted to understanding the mechanisms and evolution of attacker specific responses and how they may be coordinated. From a more ecological perspective, the extent to which plant traits (driven by genotypic variation) impact single enemies, guilds of attackers and entire communities, is addressed by Thomas G. Whitham and colleagues. The extent to which we expect specific plant responses to specific enemies will depend on the extent of natural selection imposed by each enemy and this, in turn, may be driven by the extent to which enemies are specialized on particular plants (Figure 1).

The issue of specificity, from the perspective of the enemy, is tied up in the potential benefits of being able to make a living on a plant resource that is perhaps less available to more generalized enemies or more predictable in its chemical composition [12]. For generalists, in the extreme form, some microbes can infect both plant and animal hosts. In a provocative opinion piece in this issue, Adam Schikora and Heribert Hirt explores the specifics of growth and propagation by *Salmonella* in plant and animal hosts. Although there are a few super-generalist insect

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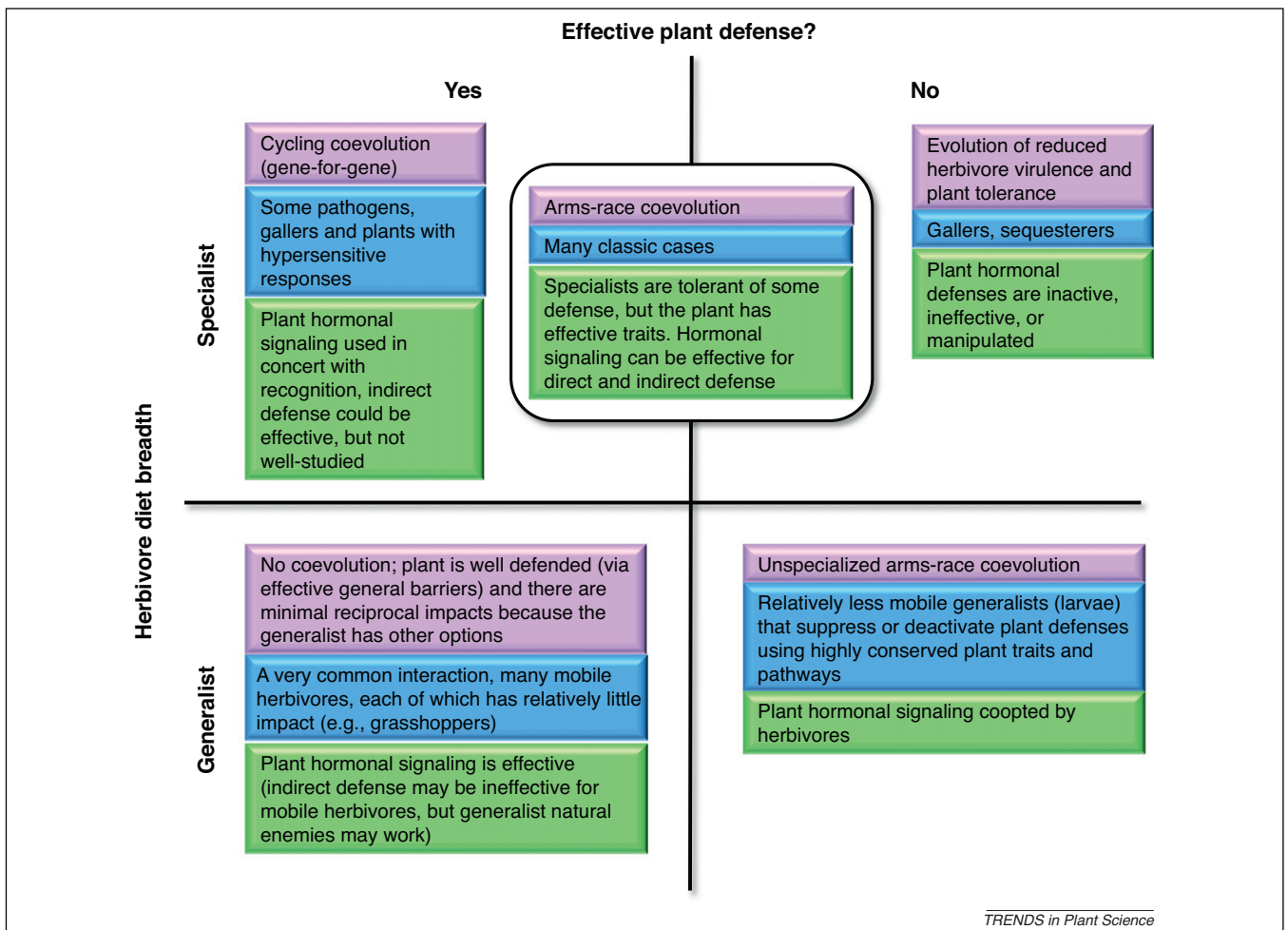


Figure 1. A preliminary scheme for conceptualizing specificity in multitrophic interactions. For specialist and generalist herbivores, we outline the predicted evolutionary interaction (purple), types of species involved (blue), and mechanisms and roles of plant defense signaling in mediating such interactions (green). Arms-race coevolution sits in the middle because herbivores are adapted to plant defense, but selection continually favors more effective defenses (including indirect defense).

herbivores (typically some of the worst agricultural pests), most herbivores specialize to species in one plant family, and often one or a few genera, and generalists are typically limited to utilizing defined plant organs [13]. Some of the classic predictions in plant–enemy interactions revolve around not only why organisms specialize, but also how specialists differentially interact with their host plants compared with generalists. This is the subject of the papers by Luke G. Barrett and Martin Heil, and Jared G. Ali and Anurag A. Agrawal.

At the extreme, some specialist herbivores use plant defenses for host finding or even to sequester secondary compounds that are then used as defenses against their own enemies [10,11]. Although it has been rarely considered in the past, a sequestering versus non-sequestering specialist herbivore is predicted to have different relations with plants, both in terms of the attacker’s tolerance of plant defenses and the most adaptive defense strategy by plants. Indeed, the paradigms about specialists are changing, and it is now well documented that at least some generalist herbivores and pathogens are highly manipulative of their host plants [14]. The papers in this Special Issue elaborate on these issues, and demonstrate why such interactions may make sense in the evolutionary context, despite a muddled interpretation in past literature.

Novel approaches that span phylogenetic to transgenic methods will greatly aid in our progress of understanding specificity in the interactions of different species. Many modern theories of plant–enemy interactions typically invoke three trophic levels, with the potential for several specific linkages between any of the potential pairings (plant–enemy, enemy–predator and plant–predator) [15]. Jonathan Gershenzon and colleagues focus on the issue of indirect defense (i.e. plant–predator signaling), and whether natural selection could well have resulted in specific adaptations across trophic levels. Demonstration of such specificity has long been a holy grail and we still have remarkably few examples of adaptive specificity in plant defense against herbivores. Nonetheless, most researchers believe that there is the potential for such adaptive defense tailoring by plants, as it is commonly seen in effector-mediated and highly specialized interactions between plants and pathogens. Similarly, we don’t yet understand why specialist herbivores specialize, and what the consequences may be for interactions with plants or predators. However, all is not lost. Technological advances, such as those outlined by Marcel Dicke and colleagues and, perhaps more importantly, conceptual advances, some of which are outlined in this Special Issue, provide a roadmap for how to proceed.

An evolutionary framework

Among all the papers in this Special Issue, there is an underlying evolutionary framework. To solidify this here, we offer a novel conceptualization for plant–enemy interactions (Figure 1). Although ‘arms race coevolution’ has been the dominant paradigm in plant–enemy interactions for decades, we posit that such interactions only occupy a small space of the conceptual landscape (Figure 1). In particular, arms race coevolution is only expected when plants interact with specialist parasites, where plant traits can directly impact the fitness of the parasite, and when the parasite is virulent and abundant enough to impose fitness losses to the plant. As suggested by several papers in this Special Issue, specialist enemies may be somewhat tolerant of certain plant defenses, but plants nonetheless can defend against them, often using hormonal signaling to upregulate direct and indirect defenses. By contrast, when specialists have truly broken the code of plant defense, most of the secondary compounds that have evolved as induced defenses may be ineffective, and plant parasites typically evolve low virulence (and plants evolve tolerance).

The view of coevolution in plant–pathogen interactions is dominated by the gene-for-gene concept [4]; in this alternative to arms race coevolution, virulence and avirulence genes in a population may show stable cycles due to frequency-dependent selection (Figure 1). In particular, plant and pathogen phenotypes do not ‘escalate’ here, but instead persistent attack results in the evolution of a novel plant resistance (typically alleles that are unrecognized or impervious to particular alleles in pathogens). Ultimately, a matching allele evolves in the pathogen and sweeps through the population, conferring virulence against the plant. This interaction cycles via frequency dependence, because the critical phenotypes have to do with allele matching, rather than increasingly virulent parasites and increasingly defended host plants. Although such cycling is a hallmark of coevolutionary interactions between plants and pathogens, relatively little is known about such interactions of plants with herbivores.

The evolutionary landscape for generalist plant enemies is often different to that of specialists [11]. Yes, occasionally generalists attack large parts of local host populations, leaving them with reduced fitness to the point where selection favors defense. However, such defenses are likely only maintained by natural selection in the cases where generalized defenses will be effective against several, taxonomically unrelated enemies. Thus, the reciprocal impact of plant traits on generalists is often composed of general barriers (Figure 1). In other words, we argue that the main lines of general defense of plants may well be effective against generalist herbivores, but these are likely to be well conserved among plant species. Hormonally regulated defense expression may indeed be effective against generalists (in an attempt to send these herbivores away), but these same means, because they are highly conserved, may be subject to manipulation and suppression by some generalist enemies [16]. As some of the articles in this Special Issue discuss, it is still too early to know whether such suppression is most common among generalist enemies.

However, perhaps the key point to emphasize is that the outcome of plant–enemy interactions depends not

only on the strategy of the enemy, but also of the plant’s ability to recognize that enemy and defend appropriately. Too often we take a single perspective, that of the enemy or the plant, and assume the other party is static. The way it appears however, and this should not surprise anyone, is that coevolution proceeds as a reciprocal evolutionary interaction. Such coevolutionary interactions play out in ecological time as a back-and-forth, as envisioned in Dangl and Jones’ zig-zag model [17]. Plants and their enemies each produce substances involved in recognition and signaling of plant defense [18,19]. Similarly, both plants and their enemies can respond in a highly phenotypically plastic manner to interactions with specific partners, adding a further level of complexity to studies that aim at understanding the reasons of specificity in plant–enemy interactions or its consequences for future evolution [20]. Thus, there will be surprises! In addition, there is a strong need for solid predictions and rigorous analyses that integrate research at the molecular, physiological and ecological level to span the measure of plant traits, resistance to enemies and fitness impacts. We hope that this Special Issue contributes to this needed new synthesis.

The Guest Editors

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