Review

Special Issue: Specificity of plant–enemy interactions

Specialist versus generalist insect herbivores and plant defense

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There has been a long-standing hypothesis that specialist and generalist insects interact with plants in distinct ways. Although many tests exist, they typically compare only one species of each, they sometimes confound specialization and feeding guild, and often do not link chemical or transcriptional measures of the plant to actual resistance. In this review, we synthesize current data on whether specialists and generalists actually differ, with special attention to comparisons of their differential elicitation of plant responses. Although we find few consistencies in plant induction by specialists versus generalists, feeding guilds are predictive of differential plant responses. We outline a novel set of predictions based on current coevolutionary hypotheses and make methodological suggestions for improved comparisons of specialists and generalists.

Why might specialist and generalist herbivores have distinct interactions with plants?

'Jack of all trades is master of none'. Here lies the theoretical basis for why ecologists and plant scientists have long argued that specialist insect herbivores, as compared with generalists, will have distinct and predictable interactions with their host plants (Box 1). With specialization, it was proposed that alongside the loss of ability to use many host plants, herbivores would gain the ability to tolerate plant defenses, manipulate hosts to their benefit and evolve ways to reduce predation and parasitism [1,2]. This powerful and seductive hypothesis has been a mainstay of coevolutionary studies for over 40 years, and yet little resolution has been reached on certain predictions. In particular, we argue below that ecologists and plant scientists have been too quick to position the specialist–generalist dichotomy as a paradigm, and often uncritically. Below we evaluate the current evidence and provide a roadmap for future studies.

There have been several specific predictions made about the specialist–generalist paradigm. First, specialists should be less impacted by a given plant defense compared with a generalist [2] (Figure 1). In addition to being less affected by particular defense traits, some specialist herbivores have even evolved the capacity to use these same traits in host finding or protection from predators (sequestration or fecal shields). Second, generalists should have 'general' mechanisms to tolerate an array of plant defenses and also possess mechanisms to manipulate plants via highly conserved plant pathways [1,2]. The notion behind this prediction is that although generalists do not master any one defense, many aspects of plant defense can be overcome because plants possess a common evolutionary history leading to shared physiological features in core signal transduction chains [e.g. jasmonate (JA) signaling] [3]. Third, upon damage, induced plant responses to specialists will be distinct compared with responses to generalists. This general prediction is complicated by coevolution: are observed plant responses adaptive for the plant or manipulated by herbivores? The perspective from which we view the interaction distinctly shapes our predictions (Figure 2).

Although we will touch on the first prediction above, the focus of our review is on the latter two: how and why specialists and generalists might elicit differential plant responses (or manipulate the plants in different ways). Since the origin of the specialist–generalist paradigm, there have been hundreds of studies of insect tolerance and detoxification of plant defense [4]. However, it is only in the past 20 years that plant biologists have realized that induced responses are a crucial component of plant defense, and ideas about how specialists and generalists differ in this regard are continuing to develop. In addition,

Box 1. Who's who on the diet breadth continuum?

Insect herbivores have been conventionally grouped into categories based on their degree of dietary specialization. When limited to only one or a few closely related plant taxa, often a single genus, herbivores are considered monophagous (or highly specialized). Insect herbivores that feed on several plant species, usually within one botanical family, are designated oligophagous. Finally, polyphagous (or highly generalized) species are insects that feed on species in more than one plant family. Although these terms are helpful for generalizing broad groups of herbivores into simpler categories, their basis is drawn on fairly arbitrary observations and may lead to inherit limitations in their use. Nonetheless, some groups of herbivores, such as aphids, leaf hoppers and leaf miners are dominated (>75%) by monophages [71]. Across all herbivorous insects, it is estimated that <10% feed on plants in more than three different plant families [72].

The distribution of feeding on one plant species to a diversity of plants is truly a graded continuum. We also recognize that polyphagous individuals can show preferences over their distribution of hosts, where herbivores may be more limited than we predict. Here we have adopted the terms specialists and generalists to focus on the extremes, usually meaning species that consume a few related species to species in several plant families, respectively. Nonetheless, the comparison is a relative one and the specific contrast of a specialist and generalist should be explained as fully as possible for each case.

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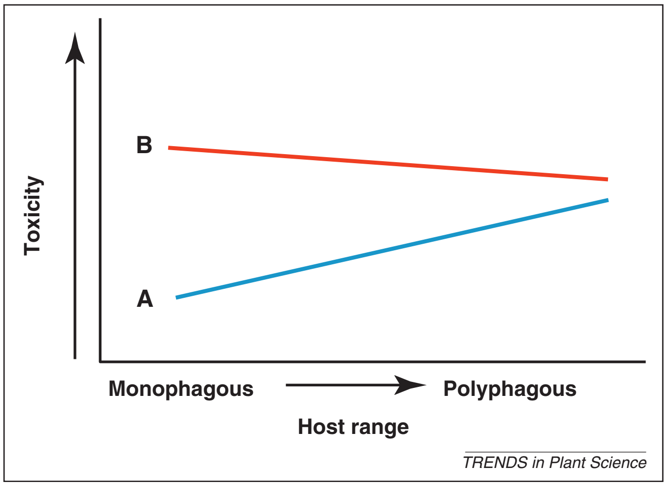

Figure 1. A conceptualization of the impacts of plant defensive compounds on specialist and generalist herbivores, based on a meta-analysis of >290 empirical studies [4]. **A** Compounds within the normal host range: for specialists that normally encounter a particular defense, toxicity is lower compared with the impact on generalists. **B** Novel compounds: for specialists that do not typically encounter a particular defense, toxicity to the specialist is greater than or equal to that compared with the generalist. In other words, it is empirically the case that specialists are less impacted by the toxicity of the plant defenses they typically consume compared with generalists; nonetheless, specialists can be highly susceptible to novel plant secondary compounds.

modern studies that span bioassays of insect preference and performance, plant production of hormonal signals and defensive secondary metabolites, and transcriptional responses have the potential to aid us in making rapid progress in understanding how and why specialists and generalist herbivores differ.

Impacts of plant defense on specialists and generalists

The notion that specialists are immune to the defenses of the host plant is widespread but incorrect. Cases where specialist herbivores are negatively impacted by defense compounds include: parsnip webworms (*Depressaria pastinacella*) eating furanocoumarins [5], buckeye caterpillars (*Junonia coenia*) ingesting iridoid glycosides [6], monarch caterpillars (*Danaus plexippus*) on cardenolide-containing sandhill milkweed (*Asclepias humistrata*) [7], cabbage white caterpillars (*Pieris rapae*) being poisoned by isothiocyanates [8] and tobacco hornworms (*Manduca sexta*) fed artificial diets containing nicotine [9]. In nearly all of these cases, the specialists do have physiological adaptations to cope with the plant defenses, which allow greater tolerance than most generalists. Indeed, on average, specialist herbivores are less negatively impacted by defense compounds than generalists [4] (Figure 1). Our main message is that tolerance of specialist insects to low levels of toxins is to be expected; however, at higher levels of defense, few insects are immune to the deleterious effects of plant toxins.

It is unclear whether certain classes of plant defense are more effective against generalists or specialists. A study 35 years ago suggested that although toxins could be overcome by specialists, digestibility reducers are likely to be effective against all attackers [10]. Others have argued that indirect defense (i.e. attracting enemies of herbivores) is likely to be more difficult to overcome compared with direct defense (e.g. digestibility reducers and toxins) [11]. Although most plants produce all of these classes of defense, both generalists and specialists can overcome some digestibility reducers, although it is unclear how common this is [12–14]. In addition, some generalists possess remarkable abilities to consume highly toxic host plants [15–17]. Thus, based on the literature and the commonly used experimental designs, few conclusions can be reached about the relative impact of different classes of plant defense on specialists and generalists.

Do specialists and generalists elicit different defensive responses?

A hypothesis that grew out of the specialist–generalist paradigm is that specialist herbivores will cause distinct induction of plant defenses compared with those induced by generalists [18–20]. Nonetheless, there have been few explicit predictions in the literature about how and why specialists will differ from generalists with regard to elicitation of induced defenses. Given that generalists are typically more sensitive to plant toxins than specialists, from the perspective of the insect, one prediction is that generalists should suppress induced plant responses, whereas specialists should only minimize the induction of high levels of defense (Figure 2). From the perspective of the plant, the predicted responses are less consistent: induction of direct defenses could be variable against specialists (Figure 2), but induction of indirect defenses [e.g. extrafloral nectar and parasite-attracting volatile organic compounds (VOCs)] should be strong if the specialist is not sequestering. Nonetheless, it is presumably adaptive for plants to respond, as strongly as possible, to most generalists (Figure 2).

Experiments comparing phenotypic or transcriptional responses to both specialist and generalist herbivores often include only one specialist and one generalist species, making rigorous conclusions impossible; in addition, many studies compare specialist and generalist species from different feeding guilds [21–23]. We found 20 studies comparing the phenotypic or transcriptional responses of a plant to both specialist and generalist herbivores using one feeding guild (Table 1). Although we interpret these results in light of the predictions in Figure 2, we recommend caution because nearly every result can be interpreted in an adaptive context, because what is beneficial for the plant and beneficial for the insect herbivore can be different. In addition, we assumed that the authors were careful to match the amount and timing of damage by the two herbivores; we highly recommend that future studies explicitly address this issue (Box 2).

A few generalizations emerged from our review. First, there are few studies linking mechanistic plant response to impacts on herbivores; however, these links are crucial for interpreting specific consequences of plant defenses. For example, some studies in the Brassicaceae found that generalist and specialist elicited a similar plant response [20,24], whereas other studies that only measured impacts on herbivores found differential induction of resistance [19]. Second, of the generalist chewers, 14 out of 16 studies used only noctuid agricultural pests in one of a few genera. All four studies of generalist and specialist aphids used the same two species on Brassicaceae hosts (Table 1). Aside from the potential taxonomic bias in herbivores, there was

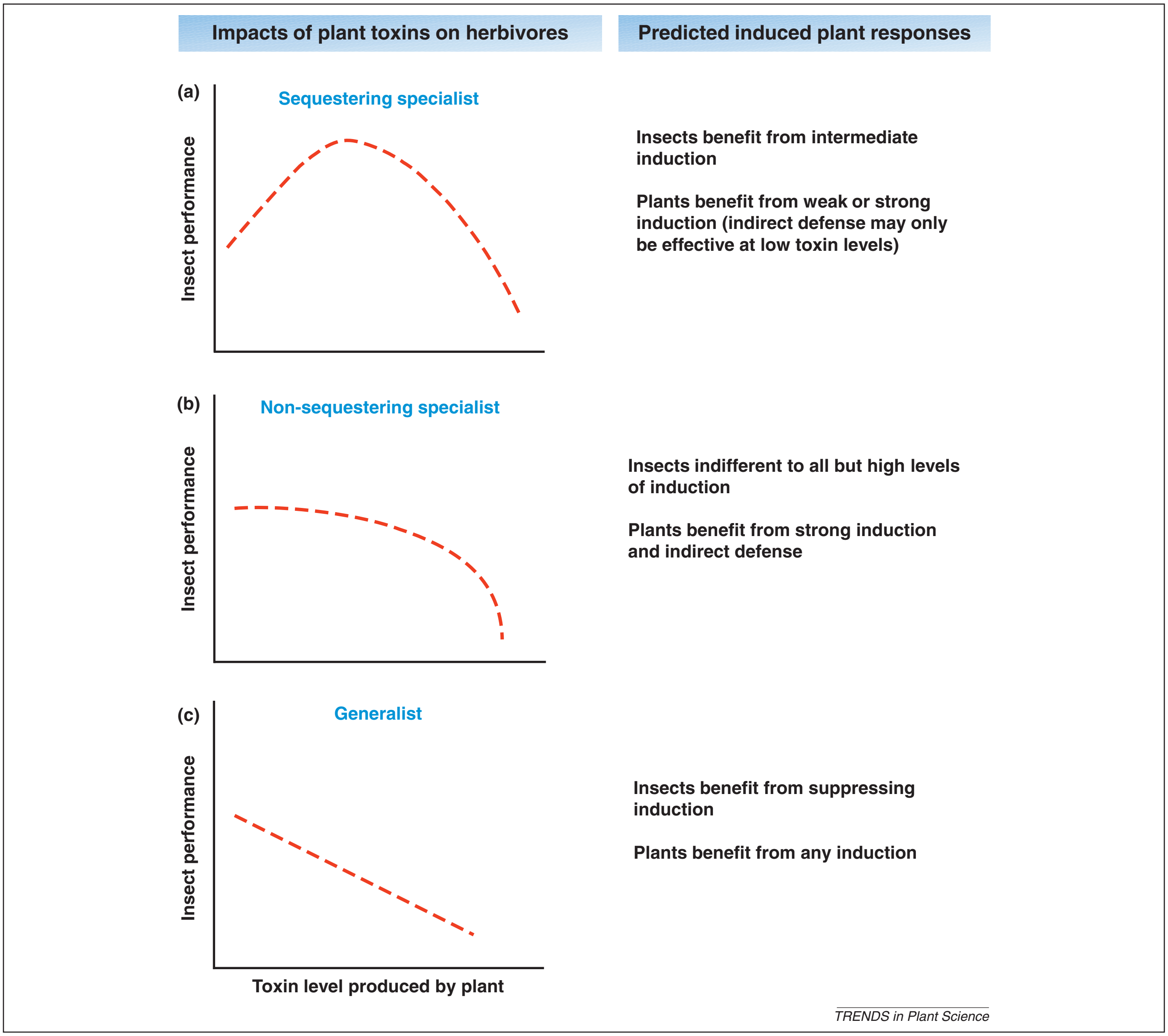

Figure 2. Three herbivore strategies **(a–c)** and their expected relationships with plant toxins. Sequestering specialists benefit from the toxins at intermediate levels (via protection from predation) and nonsequestering specialists are tolerant of toxins at low levels; however, in both cases toxins eventually impose a cost. From the perspective of the insect, induction should maximize their own growth, and across all herbivore strategies induction should be low (either intermediate, minimal or suppressed (a–c), respectively). From the perspective of the plant, maximizing defense, induction responses can be more variable and alternative strategies (i.e. indirect defense via induction of volatile organic compounds) might be the most effective defense against specialists. We note that there are special cases that might not fit this model; for example, some generalists benefit from feeding on toxic plants, even if they do not sequester the toxins [59].

Table 1. Comparison of plant defensive response to at least one specialist and one generalist insect herbivore from the same feeding guild

Plant	Generalist	Specialist	Measure of plant response	Results[a]
(Brassicaceae) *A. thaliana*	(Aphididae) *Myzus persicae*	(Aphididae) *Brevicoryne brassicae*	Transcriptional responses, glucosinolates (GS)	The generalist caused slightly more changes in gene expression than did the specialist (sequesterer). General stress-responsive genes and octadecanoid and indole GS synthesis genes were similarly induced by generalist and specialist [22,32]. The specialist induced a lower GS response than did the generalist [26].
(Brassicaceae) *Brassica oleraceae*	(Aphididae) *M. persicae*	(Aphididae) *B. brassicae*	GS	Induction pattern by the two species depended on water status of the plant [58].

Table 1 (*Continued*)

Plant	Generalist	Specialist	Measure of plant response	Results[a]
(Brassicaceae) *A. thaliana*	(Noctuidae) *Spodoptera exigua*	(Piridae) *Pieris rapae*	Transcriptional response, GS	🟨 Expression of GS genes was similar for generalist and specialist, but GS levels only showed an increase in response to *S. exigua*. Mean aliphatic GS levels were equal. *P. rapae* caused a higher increase in indolyl GS content [22].
(Brassicaceae) *A. thaliana*	(Noctuidae) *S. littoralis*	(Piridae) *P. rapae*	Transcriptional response	🟥 Transcription profiles were indistinguishable [24].
(Brassicaceae) *A. thaliana*	(Noctuidae) *S. exigua*	(Piridae) *P. rapae* (Plutellidae) *P. xylostella*	Parasitoid specificity for herbivore induced plant volatiles (HIPVs)	🟨 Parasitoid attracted to damaged plants over controls for both generalists and specialists. Parasitoids only discriminate between induction by insects in different guilds [21].
(Brassicaceae) *A. thaliana*	(Noctuidae) *T. ni*, *S. exigua*	(Piridae) *P. rapae*, (Plutellidae) *P. xylostella*	Transcriptional responses, GS	🟥 Transcriptional responses and GS were not consistently influenced by degree of insect specialization [26].
(Brassicaceae) *Brassica nigra*	(Noctuidae) *Mamestra brassicae*	(Piridae) *P. rapae*, (Plutellidae) *Plutella xylostella*	GS	🟥 Indole GS was significantly higher after feeding by *P. rapae* and *M. brassicae* than after *P. xylostella* feeding [60].
(Brassicaceae) *B. nigra*	(Noctuidae) *Trichoplusia ni*	(Piridae) *P. rapae*	Foliar trichomes, sinigrin, foliar nitrogen	🟨 Differential induction by specialist versus generalist led to increased trichomes, but the effect reversed on different leaf positions [61].
(Brassicaceae) *Boechera divaricarpa*	(Noctuidae) *T. ni*	(Plutellidae) *P. xylostella*	Transcriptional response	🟩 Specialist induced SA- and ethylene-associated genes, whereas generalist induced JA and ET genes [36]. The specialist might be well adapted, but the plant defends against the generalist.
(Brassicaceae) *Raphanus sativus*	(Noctuidae) *T. ni*, *S. exigua*	(Piridae) *P. rapae*, (Plutellidae) *P. xylostella*	Induced resistance, herbivore performance	🟥 Variation in induction was found, but it was not associated with insect specialization. *P. xylostella* and *S. exigua* induced resistance to all, whereas *P. rapae* only induced resistance to *P. rapae* and *S. exigua*. *T. ni* did not induce resistance [19].
(Brassicaceae) *Sinapis alba*	(Noctuidae) *S. frugiperda*	(Tenthredinidae) *Athalia rosae*	GS, myrosinase (MYR)	🟩 Specialist (sequesterer) and mechanical wounding induced GS and MYR threefold, whereas generalist induced only GS (twofold) [37] – generalist might be adaptively suppressing defense.
(Lauraceae) *Lindera benzoin*	(Noctuidae) *S. exigua*	(Geometridae) *Epimecis hortaria*	Peroxidase activity (POD), C/N ratio, protein content, insect bioassays	🟩 POD activity was more strongly induced by generalist than specialist (no difference in bioassay) [62] – plant might be adaptively defending against generalist.
(Plantaginaceae) *Plantago lanceolata*	(Nymphalidae) *Junonia ceonia*	(Erebidae) *Spilosoma congra*	Iridoid GS (IrGS), protein, foliar nitrogen	🟩 Higher IrGS induced by specialist (sequesterer) compared with generalist [63] – plant might be adaptively defending against generalist.
Poaceae *Zea mays*	(Chrysomelidae) *Diabrotica balteata*	(Chrysomelidae) *Diabrotica virgifera virgifera*	Parasitoid specificity for herbivore induced plant volatiles	🟩 Natural enemies preferred roots attacked by specialist over roots damaged by generalist. The specialist induced significantly more (E)-β-caryophyllene than the generalist.
(Solanacae) *Nicotiana attenuata*	(Noctuidae) *S. exigua*	(Sphingidae) *Manduca sexta*	Phytohormones	🟩 Specialist induced JA/ET burst, generalist induced SA [64] – might be adaptive for generalists to suppress resistance by activating SA.
(Solanacae) *N. attenuata*	(Noctuidae) *Heliothis virescens*, *S. exigua*	(Sphingidae) *M. sexta*	Transcriptional response	🟨 Despite large overlap, the plant response to the generalists was more similar than the response to the specialist. This was correlated to FACs/oral secretions. Both generalists were noctuids and downregulated a large number of similar genes [54].
(Solanacae) *N. attenuata*	(Noctuidae) *T. ni*, *S. littoralis*	(Sphingidae) *M. sexta*	Phytohormones	🟨 *M. sexta* induced a JA and SA response, whereas *S. littoralis* and *T. ni* induced stronger SA responses [33].
(Solanacae) *N. tabacum*	(Noctuidae) *Helicoverpa armigera*	(Noctuidae) *Helicoverpa assulta*	Lipoxygenase (LOX), proteinase inhibitors (PIs), nicotine, peroxidase (POD), polyphenol oxidase (PPO)	🟨 Both herbivores induced a similar defensive response, but response intensity of plants was different: specialist induced a lower PPO response and more intensive nicotine and POD response than generalist (JA, LOX and PIs were not different) [65].

[a] Color-coding reflects consistency with the hypotheses in Figure 2 (green = consistent, but only two species are compared). Yellow indicates no consistent pattern and red indicates that the level of specialization was not predictive of plant responses.

Box 2. Testing for differences in induced plant defense among specialist and generalist herbivores

If the goal is to test the hypothesis that specialists elicit differential plant resistance compared with generalists, we recommend the following experimental design (Figure I). Ideally, a comparison of more than two species is necessary because any two species will differ in a myriad of ways. We suggest a minimum of comparing four species that are all from one feeding guild (e.g. leaf chewers or phloem-suckers) and in two taxonomic pairs. As an example, consider the plant defense response induced by two *Helicoverpa* spp. (one specialist and one generalist) and two sawfly species (Tenthredinidae) (one specialist and one generalist). Note that the two pairs in this case are grouped at differing taxonomic levels (within genus versus within family). Nonetheless, the comparisons are both valid because within each group, a specialist and generalist are compared. A common shortcoming of studies is that both specialists (or both generalists) are from one group (e.g. noctuids), confounding the comparison between specialists and generalists and taxonomic grouping. A benefit of having the four species in two taxonomic groups is that a two-way analysis of variance approach can be used to partition the relative impact of herbivore specialization and taxonomic grouping in the plant response.

To test for the differences in the induction of the defense response, it is crucial to conduct all treatments at the same time and intermixed within the experimental arena, for example, a growth chamber (in our scenario of four species there would be six treatments: a control, mechanical damage and damage by each of the four herbivores). The reason for this approach is that differences between the induced defense responses are often subtle and, thus, it is important to have treatments intermixed. The timing, location, extent of herbivory (and mechanical damage), developmental stage and diet on which the insects are raised must also be highly controlled because differences can arise because of differences in feeding style unrelated to specialization. Finally, we strongly recommend some measure of the plant responses (e.g. chemical and transcriptional) be coupled with some biological effect (i.e. a bioassay). An important benefit of this approach is the connection between complex (often multivariate) response measures being linked to the hypothesized effect on organisms.

We note that although the proposed experimental design appears onerous, there should be possibilities, particularly for crop plants and trees with well-known insect faunas.

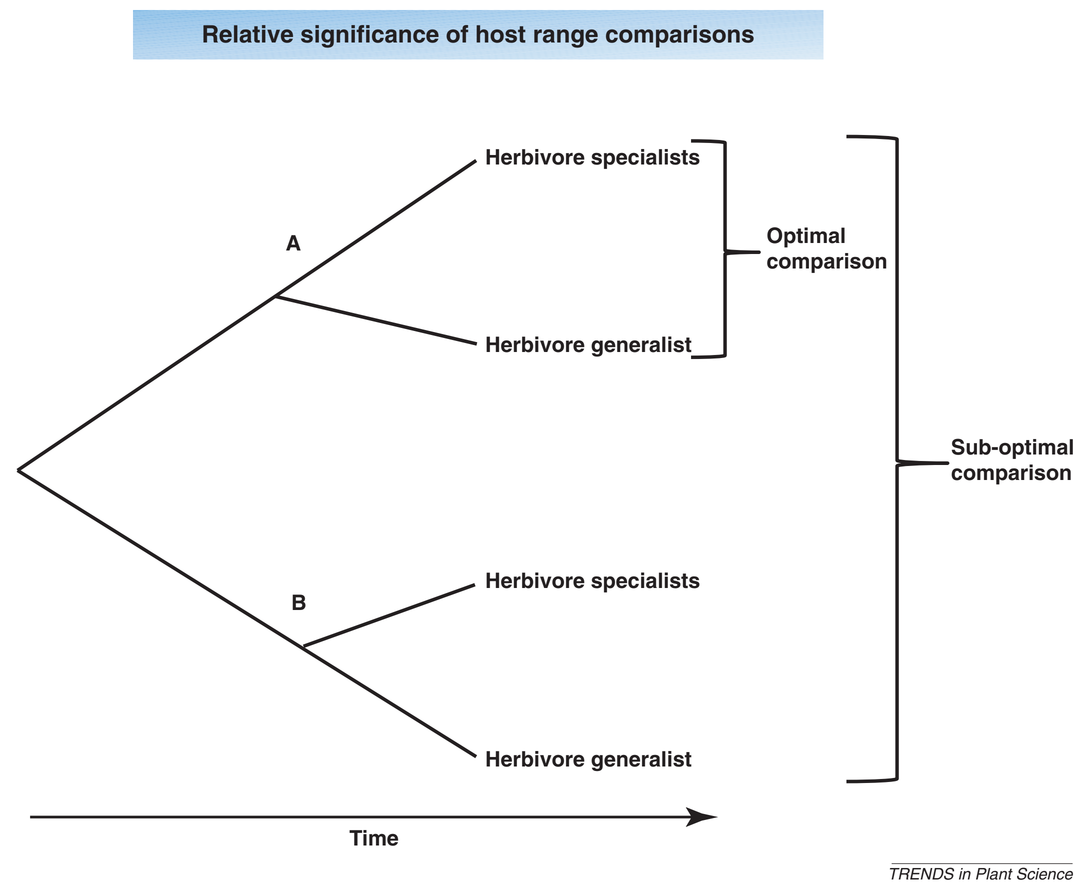

Figure I. A phylogenetic representation for suggested comparisons in studies comparing herbivores with different levels of specialization. In one scenario, **A** represents a chewing herbivore lineage and **B** represents a piercing-sucking lineage; here, the optimal comparison between specialists and generalists is within guild (and also within lineage). In a second scenario, all represented herbivores are chewers, but A are Lepidoptera and B are sawflies; again, the within lineage comparison is superior to the across lineage comparison because it controls for many other differences between the species.

also a very limited range in the plant species, as all species were herbaceous, and most were representatives of the Brassicaceae or Solanaceae. Third, few studies compared induction of indirect defenses [21,25]. This area requires further studies because the adaptive value of indirect defenses, particularly VOCs, can be associated with the ability of a specialist to sequester toxins (Figure 2). The additional trophic level further complicates generalizations of plant–herbivore interactions because the involvement of a natural enemy incorporates dynamics of foraging behavior and signal reliability (see review by Jonathan Gershenzon and colleagues in this special issue). Finally, despite efforts to align appropriate comparisons (i.e. within taxon and guild), we found no consistent pattern of differential elicitation based on the degree of host plant specialization (Table 1). None of the studies that compared more than two herbivores showed consistency with regard to responses associated with insect specialization.

The strongest studies compared at least two herbivores each from both the generalist and specialist categories and within the same feeding guild; only two studies met this criteria, and neither found consistent differential induction by specialists and generalists [19,26]. Although one of the studies [19] found specificity of induction among four caterpillar species [the beet armyworm (*Spodoptera exigua*) and cabbage looper (*Trichoplusia ni*), which are generalists, and the diamondback moth (*Plutella xylostella*) and the cabbage white (*Pieris rapae*), which are specialists] damaging wild radish (*Raphanus sativus*), this was not associated with diet specialization. The other study [26] approached the paradigm with a rigorous analysis of plant response to three specialists [diamondback moth, small cabbage white and the cabbage aphid (*Brevicoryne brassicae*)] and three generalists [cabbage looper, beet armyworm and the green peach aphid (*Myzus persicae*)], taking into consideration the role that feeding-guild might play. This excellent study on *Arabidopsis* (*Arabidopsis thaliana*) was able to partition the relative effects of specialists and generalists and simultaneously compare the induction by two guilds [26]. Nonetheless, an examination of genome-wide transcriptional responses, major defense-related pathways and phenotypic responses in terms of glucosinolate levels revealed that plant responses were not consistently influenced by the degree of specialization. In summary, given the methodological issues with testing the generalist–specialist hypothesis, it is premature to draw any strong conclusions about differential induction based on host plant specialization (Box 2).

To address whether alternative categorizations (irrespective of specialization) of herbivores, namely feeding-guild (e.g. chewers versus phloem-feeders), can have consistent predictive value for differential induction, we reviewed the recent literature (Table 2). Indeed, it has been widely suggested that depending on the feeding mode of a herbivore, different plant responses will be induced, resulting in the activation of different plant defense mechanisms [26,27]. Many studies have suggested the involvement of salicylic acid (SA) in defense against phloem-sucking insects [27,28], whereas chewing larvae (mainly Lepidopterans) are often shown to cause extensive tissue damage and JA and ethylene (ET) induction [29,30]. Of the 13 studies that directly compared chewers and suckers, there was a strong trend for phloem-feeding insects to induce fewer genes associated with the JA pathway, whereas the chewers induced fewer genes associated with the SA pathway. This is consistent with the prediction that phloem-feeding herbivores, such as aphids, leafhoppers and whiteflies, cause only minor tissue damage and induce defense signaling pathways resembling those activated against pathogens (SA regulated) [27,31,32].

A second emerging trend is that phloem-feeders cause a less drastic, more subtle response in the plant. Often they suppress more genes than the chewing herbivores (e.g. [23,29,33]), suggesting that they minimize the activation of plant defenses. Again (Table 1), we found few studies linking observations of plant responses to herbivore performance [34,35]. An exception is a study that compared adult potato aphids (*Macrosiphum euphorbiae*) and beet armyworm caterpillars attacking tomato (*Solanum lycopersicum*) [35], where alongside experiments that compared transcriptional and chemical responses of the plant, bioassays were conducted on the caterpillars. Aphid feeding changed the level of expression of 2.8 times more plant genes than caterpillar feeding, downregulating significantly more genes, and yet increasing the expression of fewer herbivore defense-related genes (and secondary metabolites). Accordingly, caterpillars were heavier and had a lower mortality on aphid-damaged plants compared with controls, but weighed less and had increased mortality on plants previously damaged by caterpillars compared with controls [35]. By linking plant responses to herbivore performance, the authors provided evidence of aphids minimizing the magnitude of induction by reducing the ability of the plant to respond to caterpillar feeding.

Who is in charge: insects or plants?

Interpreting which party is 'in charge' is of crucial importance when attempting to understand the induction of the plant defense response by specialists and generalists. For example, observing a minimal induced response might be adaptive for the plant because a sequestering herbivore benefits from plant toxins (Figure 2). However, this response might be adaptive for a generalist insect that suppresses the potentially harmful defenses of the plant. It is important to consider the respective qualities of the herbivore (e.g. sequestering or stealthy) and the consequences of a given plant response in the context of each herbivore in order to distinguish the roles of a plant response. Moreover, the fitness impact of each herbivore is likely to dictate the extent to which a coevolutionary process is likely between any two herbivores. We suggest that one way to specifically address this problem of the response being interpreted as beneficial to different parties is to include an extra control treatment in induction studies. In particular, treatments that provide a baseline for induction in the absence of herbivore-specific cues allow for greater interpretation of differential induction by different herbivores.

Such controls can involve: (i) mechanical damage, typically realistic maceration of leaves, exactly matching the amount of maceration to that in real herbivory treatments, and with treatments that span the timing of real herbivory; (ii) a JA or other phytohormone treatment; or (iii) insect manipulations that reduce the salivary activity of the herbivore (e.g. ablation of the spinnerets). For example, in a study comparing the transcript profiles after insect herbivory, wounding and response to JA, SA and ET in *Boechera divaricarpa* (Brassicaceae), analyses revealed that responses to the specialist diamondback moth (*P. xylostella*) were determined by effects associated with the ET and SA pathways, whereas responses to the generalist cabbage looper (*T. ni*) were determined by the ET and JA pathways [36]. Mechanical damage induced all three pathways, yet was dominated by a JA effect. Thus, each herbivore appears to elicit a distinct response from mechanical damage. Another study investigated specificity in induction patterns of chemical defenses from plants damaged by a sequestering specialist herbivore (turnip sawfly, *Athalia rosae*), a generalist herbivore (fall armyworm, *Spodoptera frugiperda*) or mechanical wounding (cork borer) in

Table 2. Comparisons of plant defense elicitation by chewing versus phloem-feeding insects[a]

Plant	Herbivores	Measure of plant response	Results[b]
(Brassicaceae) *Arabidopsis thaliana*	*Plutella xylostella*, *Pieris rapae*, *Spodoptera exigua*, *Brevicoryne brassicae*, *Myzus persicae*	Transcriptional responses	🟩 Chewers upregulated defense-related pathways involving JA signaling, sulfate metabolism and aliphatic glucosinolate biosynthesis. Phloem-feeders downregulated the above [26].
(Brassicaceae) *A. thaliana*	*M. persicae*, *B. brassicae*, *S. exigua*, *P. rapae*	Transcriptional responses, glucosinolates (GS)	🟨 Phloem-feeders increased aliphatic GS. Chewers increased indolyl and aliphatic GS (*P. rapae* did not induce aliphatics) [22].
(Brassicaceae) *A. thaliana*	*M. persicae*, *P. rapae*	Phytohormones, transcriptional responses	🟩 Phloem-feeders downregulated genes significantly and did not induce detectable changes in SA, JA and ET, whereas chewers induced JA-dependent responses [29].
(Brassicaceae) *A. thaliana*	*P. xylostella*, *P. rapae*, *S. exigua*, *M. persicae*	Parasitoid specificity for herbivore-induced plant volatiles (HIPVs)	🟩 Parasitoids preferred chewer damaged over phloem-feeder damaged plants [21].
(Brassicaceae) *Brassica nigra*	*P. rapae*, *B. brassicae*	Transcriptional responses	🟩 Caterpillars induced more genes (JA-dependent), repressed fewer genes (SA dependent), whereas phloem-feeder repressed ET-dependent genes [28].
(Fabaceae) *Glycine max*	*Cerotoma trifurcata*, *Spissistilus festinus*	Oxidative enzymes	🟨 Phloem-feeders caused increases in the activities of LOX, POD, ascorbate oxidase and PPO, the chewers induced LOX only [66].
(Malvaceae) *Gossypium hirsutum*	*Bemisia tabaci*, *S. exigua*	HIPVs	🟩 Phloem-feeders did not induce volatile emissions or affect the density of pigment glands, whereas chewers strongly induced volatiles [67].
(Plantaginaceae) *Plantago lanceolata*	*Dysaphis* cf. Plantaginea, *Grammia incorrupta*, *Heliothis virescens*	Secondary metabolites	🟩 Chewers had stronger effects and upregulated many compounds. Aphids mainly downregulated compounds [23].
(Poaceae) *Zea mays*	*Spodoptera littoralis*, *Rhopalosiphum maidis*	HIPVs	🟩 Chewers induced many volatiles, whereas aphids induced no measurable emissions (even after heavy infestation) [68].
(Solanacae) *Lycopersicon esculentum*	*Macrosiphum euphorbiae*, *Helicoverpa zea*	Oxidative enzymes, herbivore performance	🟩 Aphid feeding induced POD and LOX, but had no effect on PI and reduced PPO activities; the chewers induced PPO, PI and LOX, but did not induce POD. Prior aphid feeding had decreased resistance to *S. exigua*. Prior chewer feeding increased resistance to *S. exigua* [69].
(Solanacae) *S. lycopersicum*	*Macrosiphum euphobiae*, *S. exigua*	Transcriptional responses, biochemistry, herbivore performance	🟩 Aphids changed the expression of more genes than caterpillars, yet caterpillar defense induction was higher (PIs). Prior aphid feeding decreased resistance. Prior chewers increased resistance via JA-regulated genes. Aphid feeding had weak JA pathway responses [35].
(Solanacae) *Solanum tuberosum*	*M. persicae*, *Leptinotarsa decemlineata*	HIPVs, oxylipin synthesis	🟥 Chewers induced fewer genes (no JA-dependent responses), whereas the phloem-feeders induced JA-dependent responses. Volatile signatures and biochemical precursors associated with stress signaling were distinct [70].
(Solanacae) *N. attenuata*	*Manduca sexta*, *S. littoralis*, *Trichoplusia ni*, *Myzus nicotianae*	Transcriptional responses	🟩 Chewers induced JA-dependent genes, whereas the phloem-feeders reduced some JA-dependent genes and increased SA-dependent genes [33].

[a] Each comparison is from a single study.

[b] Color-coding reflects consistency with the hypothesis that the phloem-feeders induced a weaker defensive response than the chewers (green). Yellow indicates no consistent pattern and red indicates rejection of the hypothesis.

white mustard (*Sinapis alba*) [37]. Specialist feeding and mechanical damage induced threefold increases of the glucosinolate–myrosinase system, whereas generalist feeding induced up to twofold increases in glucosinolate only. Although these studies did not have replication at the level of specialists and generalists, because of the additional controls, we can speculate that specialists might have different mechanisms based on their strategy to evade (diamondback moth) or sequester (turnip sawfly) the plant's defenses. Although the herbivore treatments alone in both experiments would have demonstrated differences between the two species, having relative bases of comparison allows for a stronger interpretation. Ultimately a link between these differential induced responses and the impacts on the herbivores would be needed to assess which parties benefit.

One of our major predictions is that generalist herbivores use mechanisms to suppress plant defenses more so than specialists, allowing them to feed on a broad range of species (Figure 2). This hypothesis was advocated some time ago with regards to behavioral trenching, a method by which some generalist herbivores attack plants that exude latex [16]. Generalists that trench were able to feed on a diversity of host plants with latex, whereas generalists that did not trench had poor performance on these same plants. Recent developments confirm other, less visually apparent, mechanisms by which generalists can also suppress plant defense [38].

Mandibular glands of the noctuid caterpillar *Helicoverpa zea* were found to secrete salivary glucose oxidase (GOX) [38,39], which has been implicated as an effector responsible for suppression of defense by eliciting an SA burst (which, in turn, attenuates JA and ET levels). When the ability of caterpillars to introduce GOX to their host plants is removed (via ablating the saliva-producing spinnerets), tobacco (*Nicotiana tabacum*) plants mount a response that reduces herbivore performance, thus demonstrating a benefit for generalists to reduce the ability of the plant to respond to herbivore attack [40]. A recent survey of GOX levels in 85 species (across 23 families of Lepidoptera) found that highly polyphagous species have relatively higher levels of GOX compared with more specialized species [39]. Thus, the production of GOX as a suppressor of induced plant defenses appears to follow our prediction of generalists being more suppressive of plant defense than specialists.

An additional example of generalists suppressing plant defense was found in *Arabidopsis* plants infested by the phloem-feeding silverleaf whitefly (*Bemisia tabaci*). Whitefly feeding increased SA-responsive gene transcripts, whereas JA- and ET-dependent pathways were repressed or not modulated [41]. Mutant plants with higher activity of JA defenses or impaired in SA defenses slowed nymphal development, whereas those that activate SA and impair JA increased nymphal development [41]. Thus, generalist whitefly feeding strategies appear to benefit the whiteflies at the expense of plant defense. Given the similarity of this result with that of the generalist potato aphid on tomato discussed above [35], we advocate a critical comparison of plant responses to generalist versus specialist aphids. All of the examples of comparisons thus far have been between the generalist green peach aphid (*M. persicae*) and the specialist cabbage aphid (*B. brassicae*) on Brassicaceae, and none have linked plant responses with aphid performance (Table 1).

But wait, are specialists not specialists?

Given that specialist herbivores share an intimate evolutionary history with their host plants, are specialists more manipulative as herbivores than generalists? The answer to this question is complicated by three issues: (i) specialists can be somewhat tolerant of defenses (and, thus, might not need to be manipulative); (ii) specialists can maximize their fitness in nonobvious ways (e.g. phenology, location of feeding); and (iii) from a coevolutionary standpoint, plants might recognize specialists (particularly those with strong fitness impacts on the plant) and defend appropriately. Of course there are examples of specialists that manipulate their hosts [42,43]. Insect gallers perhaps epitomize highly manipulative specialist herbivores. The conventional view is that gallers reprogram both primary and secondary plant metabolism to their benefit [43]. Indeed, most gallers are highly specialized, more so even then their endophagous (but nongalling) relatives [44].

Thus, specialists can either be highly manipulative or not so manipulative. As discussed above, directly comparing specialist induction to some mechanical damage and to elicitor-free control should aid in addressing this issue. More generally, we are in need of direct contrasts of specialists and generalists, testing whether generalists are more sensitive to particular defenses and, hence, can manipulate them effectively.

Plants in charge? Fatty acid amino acid conjugates and beyond

Plants are able to perceive a wide range of herbivore-associated elicitors resulting in the activation of specific plant responses, although the adaptive value of such specificity is unclear [39]. Most elicitors and their respective responses differ from responses to mechanical damage and appear to be restricted to particular plant–insect associations [45]. There have been four documented elicitors produced by insects: β-glucosidase [46], fatty acid amino acid conjugates (FACs) [47], inceptins [48] and caeliferins [49]. The most broadly investigated and described elicitors to date have been FACs from lepidopteran larvae (generalists and specialists) and these constituents (typically obtained from oral secretions or regurgitate) are thought to betray the insects presence (and perhaps identity) to the plant [45,47,50]. The first well-characterized FAC was volicitin [*N*-(17-hydroxylinolenoyl)-L-glutamine], which was identified from the beet armyworm [47] and induces direct and indirect plant defenses in several plants [51]. FACs (particularly volicitin) have a strong impact on plant hormone levels as well as on the induction of plant volatiles in a variety of plant species, unlike caeliferin and inceptin, two newly identified elicitors that appear to be more restricted in the plants for which they are active [48,52].

We presume that insect elicitors, although potentially harmful to the insect in the plant–herbivore interaction, are produced (and not lost because of natural selection) because they are an essential part of the primary metabolism of the insect. For example, FACs in the noctuid moth *Spodoptera litura* play an active role in nitrogen assimilation by regulating the amount of glutamine in the larval midgut [53]. A recent FAC screen of 29 Lepidoptera species found that some species do not produce these elicitors [51]. Additional categories of elicitors are combinations of plant and insect constituents, which might be a highly stable mechanism for plant recognition of attack. For example, inceptins are derived from fragments of digested plant tissues. Peptides released from proteolytic fragments of chloroplastic ATP synthase were found in the oral secretions of the fall armyworm (*S. frugiperda*) [48], thus giving the plant a direct role in the perception of a specific attacker.

It is unclear if generalist and specialist herbivores differ in their elicitors. A study has shown that the transcriptional responses of *Nicotiana attenuata* to attack from two generalist herbivores [the tobacco budworm (*Heliothis virescens*) and the beet armyworm (*S. exigua*)] was more similar than that of the tobacco hornworm (*M. sexta*), which is a specialist herbivore, and that this difference was linked to their FACs (although in this case, the two generalists were closely related and thus shared many traits) [54]. Regurgitates of the generalists were virtually identical [55], whereas that of the specialist differed, lacking volicitin and dominated by fatty acid–glutamic acid conjugates that were not present in the regurgitates of the generalists [56,57]. FACs from the specialist *M. sexta* are involved in suppressing the nicotine response in tobacco, but do not suppress indirect defensive responses (VOCs), and this has been interpreted as adaptive on the part of the plant [58,11]. It would be interesting to evaluate the degree of specificity of insect recognition in plants and to assess whether plants tend to have more fine-tuned degrees of recognition (e.g. via mechanisms specifically associated with FACs or saliva produced by labial and mandibular glands) for specialists and more broad feedback mechanisms (plant-derived byproducts of herbivore digestion, e.g. inceptins or regurgitants) for generalists.

Concluding remarks

For plants to 'be in charge' we assume that after integrating signals from a given attack they will activate pathways that provide the most defensive response. The predictions of the specialist–generalist paradigm suggest that there can be consistency in herbivore elicitation and plant recognition among different types of attackers. Yet, to date, evidence for distinct groupings of generalists and specialists is not so clear, in part because of methodological limitations. A ubiquitous problem with interpreting the specialist–generalist paradigm is that there are two sides to every story (that of the herbivore and of the plant), there are also potentially different predictions based on the type of specialist (sequestering or not?) and the fact that coevolutionary interactions can modify the dynamics in space and time. Nonetheless, we are optimistic. As detailed in this review, we advocate the use of real species level replication, strong controls and links between measures of plant responses with insect performance. It is premature to kill the specialist–generalist paradigm, but perhaps also too early to celebrate its generality.

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