Jack-of-all Trades or Master of One:
Advantages and Disadvantages of Herbivory Specialization in Insects

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Abstract

Insects are among the most voracious terrestrial herbivores and are the most detrimental plant pests. Insect herbivory has put high amounts of selection pressure on plant species to evolve physical, behavioral, and chemical defenses that attempt to prevent this herbivory. In turn insects develop workarounds to plant defenses. This “arms race” is not infinite and generally results in the insects becoming specialist feeders on one or a group of related plant species. However, not all insect species evolve to become monophagous feeders, instead some remain more or less polyphagous generalists, avoiding well-defended plants and feeding more broadly. For the most part, insects are forced to become some sort of specialist to compete, whether it be on a single host plant species, a group of closely related host plant species, or a family of host plant species. Specialization does not come without its costs, some of them quite hidden. Most likely, the complexity of insect and plant interactions may be such that each interaction must be individually studied before any rules can be established for optimal feeding strategies, but there may be evidence that the generalist or specialist feeding strategy are a more ideal strategy. This paper will examine both anecdotal and direct evidence exploring insect feeding behavior and the evolutionary steps necessitated by specialist feeding strategies.
Introduction

Arthropods are the most abundant terrestrial fauna as well as the most diverse. Plant-dwelling insects alone are estimated to comprise nearly a quarter of all terrestrial biodiversity \(^1\). Of these plant dwelling insects, most have been found to be more or less plant host specific \(^2\). Species restricted to a single host plant species or a small group of closely related species are called specialists. Presumably, specialist insects are experts at circumventing their host plant’s physical and chemical defenses and outperform other herbivorous insects that are not specialists, so called generalists.

In 1964, Ehrlich and Raven suggested the possibility of evolutionary arms races between plants and their herbivores, especially in the context of herbivorous insects \(^3\). High levels of herbivory pressure would select for plants with defensive mechanisms in the form of physical, behavioral, and chemical defenses. Herbivorous insects would then have evolutionary pressure to develop workarounds for these defensive measures and the insect and plant would enter a cycle of one-upmanship \(^4\). Specialist insects should exert far more of this pressure than generalist counterparts because they should be more intensively feeding on plant hosts.

Driving this evolutionary arms race are two biotic variables that account for the largest effect on individual fitness in herbivorous insects; 1) food resources and 2) natural enemies \(^5\). In most trophic chains, herbivorous insects lay between the producers (in this case plants) and carnivores (especially carnivorous insects). When feeding, herbivorous insects are 100x more likely to be eaten then while resting, making foraging the most important aspect of herbivorous insect behavior; possibly second only to reproduction \(^5\). This creates an interesting combination
of selective forces which, in a general sense, shape herbivorous insect species into very specific behavioral and chemical niches and result in high levels of specialization.

Despite herbivorous insects becoming highly specialized, plant defenses can still remain an effective deterrent to all herbivorous insects, specialist or not. On the other hand, even with high levels of defenses, most plants can still be consumed by at least one species of insect \(^6\text{–}^9\). This essay aims to elucidate several ideas central to understanding the ecological and evolutionary impacts of herbivorous insect specialization. These impacts range from individual arms races between insects and their plant hosts to shaping entire food chains. To begin, it is best to start with an in depth look at the advantages and disadvantages of specialization.

**Advantages and disadvantages of specialization.**

It is hypothesized that specialist feeders trade the ability to utilize many plant species for food for an ability to tolerate, if not completely resist, their plant host’s defenses \(^9\). For this to be true there are three suggested and testable hypotheses that measure the degree to which any given insect is specialized. First, a specialist feeder should be less impacted by host plant defenses when compared to a generalist feeder \(^10\). These comparisons are best done if the specialist and generalist are closely related species with similar feeding styles (also called feeding guilds). Additionally, the specialist should also be able to more easily detect and locate the host plant when compared to the generalist species. Second, the specialist species should use defense circumvention mechanisms that are specific to the host plant’s defenses while the generalist species may use an array of mechanisms, or at least mechanisms that allow for broader tolerance to many plant defenses. This is especially important in clades of plants with unique and particularly toxic compounds such as the *Brassicaceae* with glucosinolates or
Asclepias with alkaloid containing latexes\textsuperscript{11–15}. Thirdly, plant hosts should respond differently to a specialist and a generalist feeder. The assumption here is that specialists have evolved mechanisms that prevent host plant defenses from being activated, where as the generalist has not evolved the stealth required to manipulate the plant host’s defense responses\textsuperscript{10}.

If these three hypotheses are proven true for any given herbivorous insect, they show a clear advantage to a specialist feeder versus a competing generalist feeder when both are feeding on the same host plant species. In nature; however, it does not appear that the highest level of host plant specialization is ever truly achieved. That is to say, rarely does a specialist insect feeder succeed in fully exploiting its plant host. To understand how specialists fail to obtain full specialization we have to take each hypothesis in turn.

The notion that specialist insects are immune to the host plant’s defense is often incorrect regardless of the amount of specialization. In most cases the specialist is merely more tolerant to the defense mechanism and high doses of defense compounds can still negatively impact the insect\textsuperscript{10,16}. Indeed, when purified defense compounds are applied to specialist insects directly there are almost no examples of complete immunity\textsuperscript{15,17,18}. Also confounding the first hypothesis is the fact that there are many cases in which generalist species are still able to eat host plants and circumvent plant defenses. Therefore, overcoming plant defenses is not reserved for specialist feeders and overcoming plant defenses is not always the best criteria for determining whether or not an insect is indeed a specialist.

In general, specialist herbivorous insects focus all of there plant defense detoxification efforts on the plant defenses that are present in their host plants, while generalists have to adapt to a wider range of plant defenses that are found across many species of host
Indeed this is the factor that makes a species a specialist, making it impossible to feed on anything other than the host plant. Unfortunately, this hypothesis seems to be a matter of degrees. If we consider the specialist and generalist descriptors as a continuum rather than a true dichotomy, then insect species can have different levels of specialization and therefore different numbers of host plants. True specialists (hyper specialists or monophagus insects) live their entire life feeding on a single plant species. This includes every life stage from egg to adult, and therefore they are completely dependent on their food source. True generalists (polyphagus insects) on the other hand, would be able to feed on multiple phytochemically unrelated plants. It appears as though there are few truly generalist species of herbivorous insects in nature, since most insects have a preference for some clade of plants or another. Most likely due to the wide array of potential herbivory defenses found across the entire Angiosperm clade, a true generalist feeding strategy is unobtainable. There are; however, numerous examples of true specialists (e.g. monarch butterflies on milk weeds). In general, however, it seems that the amount of plant defense detoxification mechanisms contained within a species does correlate with the number of food sources it is likely to consume.

The third hypothesis states that plants should responded differently to specialists or generalists at the transcription, protein, and/or chemical levels of defense. There are many ways for these differences to manifest themselves. Theoretically, generalists have to worry more about inducing plant defenses than the specialist, because of their lower level of resistance to any induced plant defenses. What would kill a generalist should only mildly effect the specialist. It would seem that in most cases the specialist actually does not manipulate its
host’s defense responses because it can tolerate the response. Additionally, generalist feeders typically don’t manipulate the host plant’s response because the host plant is unable to exert a strong enough selective pressure on the generalist insect, which only occasionally feeds on it, for sophisticated host manipulation to evolve\textsuperscript{15,22}. It seems that only in generalists that feed on a discrete number of related plant species that some level of host manipulation can occur\textsuperscript{23}. While the generalists are polyphagus, they are in some ways specialists but to a plant family not species or genus.

Does this then imply that polyphagus generalists manipulate plant hosts more than a specialist? Would that manipulation make the generalist, in fact, more specialized than the specialist\textsuperscript{10}? The answer to this question depends strongly on specific interactions and whether or not the specialist does anything else with the host plant’s defenses. For example, if we consider the \textit{Manduca sexta} caterpillar feeding on plants of the \textit{Nicotiana} genus, it has no need to decrease the host plant defense response, because it is effectively able to ignore the nicotine. On the surface this interaction seems unsophisticated; however, Manduca is able to use the plant derived nicotine for its own defense against wolf spiders. This use of the plant defense for protection shows a much greater level of specialization than a generalist insect that merely decreases nicotine production\textsuperscript{24}.

Despite almost no difference in plant response to generalist versus specialist, host plants are indeed able to recognize what kind of insect is feeding on it and respond. It seems that the most important factor is not levels of specialization but the feeding guild the insect belongs to\textsuperscript{5,10,16}. For example, phloem feeding aphids induce very low levels of plant defense responses because they cause very little cellular damage. Defense responses to aphids are
typically carried out by the salicylic acid (SA) hormone pathways\textsuperscript{25–27}. The leaf chewing insects like caterpillars; however, induce plants to mount very strong defense responses using the jasmonic acid (JA) hormone pathways\textsuperscript{28,29}. This implies that specialist insects are not sensed any differently than their generalist counterparts, only their ability to tolerate those defenses is different\textsuperscript{15,30–32}. To increase the complexity of the interactions, different feeding guilds play off one another. For instances chewing insects can induce JA responses that negatively impact phloem sucking insects and vice versa\textsuperscript{16,33–35}. An unaddressed question that would tie feeding to herbivorous insect specialization is: Do different feeding guilds intrinsically require different degrees of host selection and specialization? For example: is being a phloem sucking insect a more specialist feeding guild than a chewing insect?

**Consequences of Being a Specialist**

Notwithstanding the somewhat obvious advantages of becoming a feeding specialist, there are potentially several drawbacks. First of all, specialist feeding, by definition, is predictable and constant. This consistency makes the insect predictable and allows the plant hosts to evolutionarily fine tune defenses specifically for the specialist or evolve mechanisms that are especially hard for an individual specialist species to adapt to. Specialist insects are especially vulnerable to this if the damage done to the host plant is significant enough to cause strong fitness penalties in the host plant. It may indeed be easier for a host plant to defend against a specialist because the threat is almost guaranteed, it is persistent, and the insect is more or less dependent on the host plant\textsuperscript{10}.

Especially important in this context, are complicated, community driven, defense mechanisms known as third level or indirect defenses\textsuperscript{4,10}. In these plant defense mechanisms,
predators and parasitoids of the herbivorous insect are recruited by the host plant to kill the herbivorous insects. Specialist feeders are more prone to indirect defenses because consistent feeding, generation after generation, allows the time required to evolve these interactions. These third level defenses cannot generally evolve against generalists to the same degree due to the more sporadic nature of feeding. These interactions are generally evolved by the release of volatile compounds by the plant host after it has detected feeding of a specialist. These released volatiles are recognized by predators and parasites and acts as an attractant molecule. As a caveat, plants most likely do not release these volatiles with third level defenses in mind. Most likely, predator insects are also selected to detect the released volatiles, which indirectly helps the host plant; a case of “my enemies, enemy is my friend.” Not only do third level plant defenses kill any insects that the predators can find, they can also select for herbivorous insects with altered feeding habits. Third level defenses may force herbivorous insects to feed at night or only on secluded parts of the plant. This may benefit the host plant evolutionary and shape the entire host plant – herbivorous interaction.

Another unintended consequence of specialization of herbivorous insects is the dependence on the success of the host plant. Unfortunately, for the herbivorous insect this becomes paradoxical. For the insect, it would be best if its host plant would flourish and spread its range. This would allow the specialist to invade new territories and sustain larger populations. Unfortunately, by feeding on the host plant, the specialist decreases the fitness of the host and limits the reproduction of its host. This means the specialist must be very good at finding, colonizing, and eating its host plant but not to the point where the damage threatens extinction of the host plant. Monophagus specialists are especially prone to this. Extinction of
their food source often means extinction of the insect. There are instances where the extinction of the monophagus insect can be avoided by host swapping but these are fairly rare. 

Extinction events of host plants and their feeding specialist are known as co-extinctions. They are a direct result of the specialist depending too much on a single food source. Even if the insect host does not drive its host species to extinction, external factors may decrease host plant populations and therefore specialist populations as well. In rapidly changing environments, this interdependence is especially threatening. There are six factors that may impact a species chances of becoming extinct:

1) Specialized habitat or microhabitat requirements
2) Narrow environmental tolerances or thresholds
3) Dependence on environmental or specific cues/triggers
4) Dependence on interactions with particular species
5) Poor ability to disperse to or colonize suitable new habitats
6) Small population size, area of occupancy or extent of occurrence

Unfortunately for monophagus specialists, most of these factors apply to them. Especially if they are unable to swap hosts or just so happen to live off a host plant species with a narrow range.

The final drawback to specialization is that the specialist’s population structure is completely dependent on the host plant’s population structure. Disruption or fragmentation of the host plant results in the same effect on the specialist. Changes in host plant population structure, such as reduction of the number of host plant stands or an increase in the distance of those stands will decrease the ability of the specialist to traverse between stands and therefore
impact the genetic heterogeneity of the specialist insect$^{38,39}$. Indeed specialists seem especially prone to habitat fragmentation and alteration. A generalist herbivore is more likely to evolve the use of a new host plant. New host plants may act as bridges between two existing plant populations that the generalist can feed on. This bridging of habitats by the addition of new hosts results in a decrease of stand isolation and an increase in habitat connectivity for the generalist$^{40}$. With increased connectivity, there is often a decrease in the rate of local population decline and faster recolonization after extinction events$^{38,41,42}$

Feeding specialization’s impact on plant defenses

Most plants are eaten by more than one species, in fact single large plants (i.e. trees) can be attacked simultaneously by an entire community of insect species. This community is a combination of specialists and generalists, each of which is comprised of multiple feeding guilds. How then are plant’s defenses able to protect the plant? It would seem that most defense mechanisms evolve to counteract as many threats as possible and are purposefully broad. In doing this, plants may be sacrificing the specificity and potential effectiveness of a single defense on a single insect species for a more successful strategy overall. These responses are usually mediated by two or three hormone pathways, as suggested earlier and are almost always systemic. This ensures defense mechanisms are in place before other herbivores detect the wounded plant and therefore potentially weakened plant$^{43}$.

For most plants, it is beneficial to respond as quickly and drastically as possible to herbivory, especially to generalists, for which the defenses should be the most effective$^{10}$. It would also appear that the more varied the defense responses can be, the less likely the insect will have a single mechanism that will counteract all defenses$^{4}$. With a systemic and broad
defense response a plant is able to defend against the most number of potential attackers without investing too heavily in any one defense. Most experiments to date focus on single paired interactions between a feeding insect and its host plant, yet most chemical defenses should be viewed through the lens of community based evolution rather then pairwise, reciprocal coevolution with one insect. Due to the incredibly diverse number of insect threats, no plant can develop a universal defense mechanism against all herbivorous insects.

There are; however, several examples of plants acting to counteract a single, dominant herbivorous insect species especially if the number of insect threats are limited. These actions are elicited by herbivore-associated molecular patterns (HAMPs). HAMPs are particularly important with the leaf chewing feeding guilds that salivate. Species-specific proteins in the insect saliva can be detected and specific pathways up-regulated depending on the feeding species. For example, almost all chewing insects activate the JA pathway. In the case of Manduca sexta feeding on Nicotiana attenuate, a separate defense pathway known as the MPK4 pathway alters the JA response specifically to counter Manduca but the same pathway is not activated when the plant is fed on by the generalist species Spodoptera littoralis. This difference in response between a specialist and generalist feeder is an example of how HAMPs may tailor plant responses to herbivory by different species.

Concluding remarks

The number of interactions between herbivorous insect species and their host plants are staggering. In an attempt to gain an evolutionary advantage, most insect species evolve to be specialists for certain plant hosts, to some degree or another. These specialist interactions are not without their drawbacks. Specialist insect species lose the ability to access multiple
sources of energy and thereby potentially increase the chance of co-extinction with their host plants. Additionally, plants and their communities are shaped by hundreds of these interactions simultaneously, making insect defense mechanisms incredibly diverse and potentially very efficient. It would seem that there are no hard rules when it comes to the evolution of insect feeding behavior but it is clear that evolution favors feeding specialization again and again and that the risk of becoming a specialist is worth the payoff.


13. Traw, B. M. & Dawson, T. E. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black


