Do Natural Enemies Impose Selection on Herbivore Diet Breadth?

Andrew Hennessy, Emily Leggat, Aditi Prasad, Sydnie Rathe, Ben Silverstone, and Michael Singer

Department of Biology
Wesleyan University, Middletown, CT 06459

Introduction

Why dietary specialization is so prevalent among insect herbivores is a longstanding and fundamental question in ecology and evolutionary biology. Natural selection from plant chemical defenses in insect-plant coevolution is the conventional explanation for plant-specific diets of insect herbivores. In 1988, a bold alternative, called the enemy-free space hypothesis, was proposed by Bernays and Graham. They hypothesized that generalist predators of insect herbivores (e.g., ants, wasps, and birds) selected for specific diets in insect herbivores by selecting for anti-predator traits dependent on dietary specialization (e.g., sequestration of specific plant toxins, specific camouflage on host plants). The enemy-free space hypothesis predicts that dietary specialization is associated with superior anti-predator defenses in insect herbivores.

Thirty-two years after this initial publication, we performed a literature review of tests of this prediction to analyze the veracity of the enemy-free space hypothesis. In addition, we focused on studies of four herbivore traits that were originally or more recently considered under selection by predators: ability to sequester plant chemicals; camouflage; efficiency of feeding behavior; and the ability to suppress plant volatiles known to signal predators and parasites.

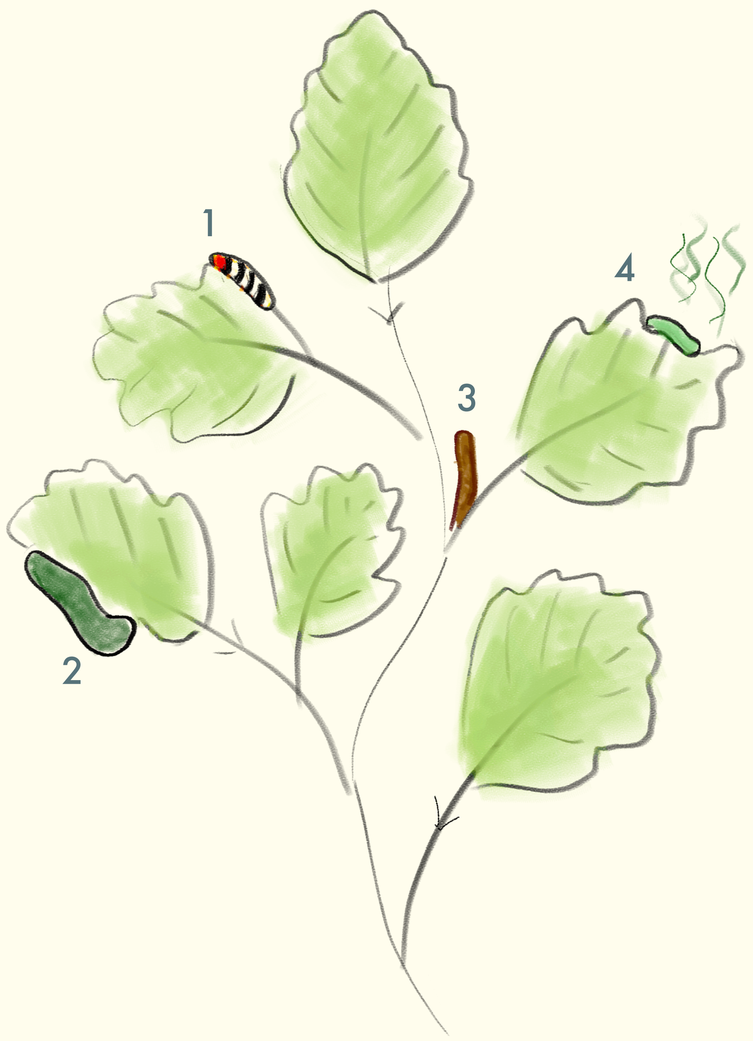

Fig. 1. Caterpillars interacting with their host plant. Numbers correspond with the numbered sections to the right.

Fig. 2. A parasitoid wasp ovipositing into a caterpillar (left), and a camera-shy salticid spider eating a gypsy moth (right).

1. Sequestration of Plant Toxins

Plants typically possess specific allelochemicals that they produce to protect against herbivory. Some herbivores, mainly those that specialize on one or a few related plant species, can tolerate the specific chemistry of their host plants and even sequester them to deter predators.

In our review of the literature we found that dietary specialist insect herbivores sequester allelochemicals more often and use them more effectively towards anti-predator defense than their generalist counterparts. As predicted by the enemy-free space hypothesis and demonstrated by more actively sequestering species, we even found that predators can discriminate between herbivores with different diet breadths based on low concentrations of sequestered chemicals. While these allelochemicals may provide protection from generalist predators, they may be used as search cues by specialist natural enemies, such as parasitoids, leading to a trade-off between reduced mortality from generalist predator versus increased mortality from specialist predators and parasitoids.

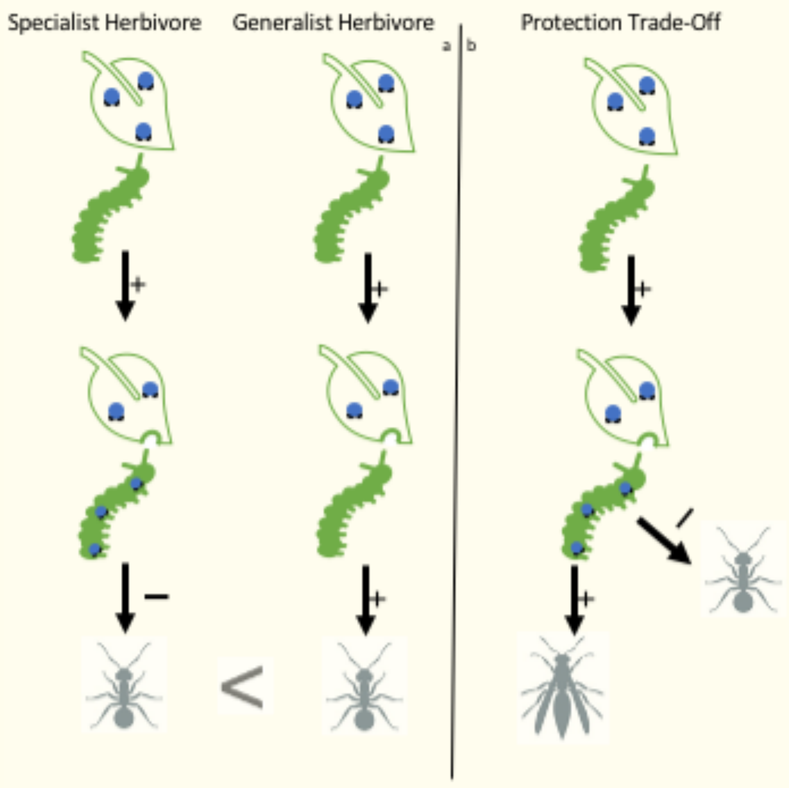

Fig. 3. a: A generalist predator will prefer the undefended prey and in this case cause selection for dietary specialization. b: Specialist sequestering herbivores face a trade off in protection because their defense chemicals deter generalist predators but provide protection as hosts for parasitoid and may even serve as search cues for some highly specialized natural enemies.

2. Efficiency of Feeding Behavior

Several lines of evidence argue that neuro-sensory mechanisms can mediate the enemy-free space advantages of dietary specialist over generalist herbivores. By using fewer sensory cues to assess their host plants, dietary specialist herbivores can more efficiently process neurosensory inputs, leading to more rapid decision-making compared to their generalist counterparts. It is hypothesized that this putative increase in efficiency of feeding behavior leaves specialists less vulnerable to predation.

Studies comparing feeding behavioral efficiency of specialist and generalist insect herbivores showed a clear advantage to specialists in most cases. However, very few studies have tested the prediction that this increased behavioral efficiency of specialists results in reduced predation.

3. Specific Camouflage

Insect herbivores may possess morphological and behavioral traits that enable them to be camouflaged to their specific host plants. Our review found that specialist insect herbivores are more effective at utilizing camouflage on their hosts than generalists, as predicted by the enemy-free space hypothesis. The morphological match between insect and plant was better for specialists even though some generalists can develop specific camouflage through polyphenism. More stereotypical hiding behavior on specific parts of the host plant was seen as evidence for superior behavioral camouflage by specialists. Both the morphological and behavioral camouflage traits predicted reduced predation.

Fig. 4. A pawpaw sphinx moth caterpillar (*Dolba hyloeus*) masquerading as a leaf on one of its hosts, winterberry holly (*Ilex verticillata*)

4. Volatiles

Plants respond to herbivory by emitting volatiles in order to attract herbivore enemies. Some herbivores have the ability to suppress these induced responses, but in our review we found little evidence suggesting that dietary specialists are better than dietary generalists at suppressing herbivore-induced plant volatiles. Instead, there were more studies demonstrating no relationship between dietary specialization and the ability to suppress induced plant volatiles.

Conclusions

- The anti-predator benefits conferred to specialist herbivores through sequestration of plant toxins and camouflage support the enemy-free space hypothesis, but may also make them more susceptible to parasitoids and other predators with different hunting methods.
- Dietary specialist herbivores show more efficiency feeding behaviors, but the enemy-free space advantage of such behavioral efficiency is unknown.
- In the existing literature there is no correlation between the ability to suppress herbivore-induced plant volatiles and dietary specialization.

Future Directions

- There have been limited studies directly measuring herbivore diet breadth against predation and/or parasitism. More research could further illuminate when and if the enemy-free space hypothesis explains herbivore-plant interactions.
- Further research could investigate how enemy diet/host breadth could influence herbivore diet breadth.

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