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# What We Don't Know About Diet-Breadth Evolution in Herbivorous Insects

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## Abstract

Half a million species of herbivorous insects have been described. Most of them are diet specialists, using only a few plant species as hosts. Biologists suspect that their specificity is key to their diversity. But why do herbivorous insects tend to be diet specialists? In this review, we catalog a broad range of explanations. We review the evidence for each and suggest lines of research to obtain the evidence we lack. We then draw attention to a second major question, namely how changes in diet breadth affect the rest of a species' biology. In particular, we know little about how changes in diet breadth feed back on genetic architecture, the population genetic environment, and other aspects of a species' ecology. Knowing more about how generalists and specialists differ should go a long way toward sorting out potential explanations of specificity, and yield a deeper understanding of herbivorous insect diversity.

## 1. INTRODUCTION

One out of every three described eukaryote species is a herbivorous insect. That comes to approximately half a million species. Most are diet specialists (Jaenike 1990, Forister et al. 2015), and the species richness and diet specificity of herbivorous insects are often seen as two sides of the same coin. Understanding the diet specificity of herbivorous insects is tantamount to understanding their species diversity, but at present, diet specificity is poorly understood. Progress may have been slowed by the fact that most investigations have aimed to test only a few of the potential explanations of specificity, especially since some of the most-studied explanations simply do not seem to work (e.g., Futuyma & Moreno 1988, Poisot et al. 2011, Forister et al. 2012). By far, the most frequently tested explanation is that there are genetic costs for generalism stemming from antagonistic pleiotropy at a few diet-determining loci: Alleles that are good on one host are bad on another (Ravigné et al. 2009). But evidence of these costs has been elusive (e.g., Agosta & Klemens 2009), and their theoretical basis has been eroding (e.g., Joshi & Thompson 1995, Remold 2012). By comparison, much less attention has been paid to a raft of alternative explanations. Constraints on diet-breadth evolution could operate at levels of biological organization ranging from genes to ecosystems. In this article, we catalog these potential constraints and review the evidence for each (**Table 1**). Our hope is that by doing so we will expose areas in need of research and will foster a broader view of the potential causes of diet-breadth variation.

In our view, progress may also have been slowed by a poor understanding of how diet generalists and specialists differ in ways other than diet breadth. Therefore, after we catalog the potential causes of host-use specificity, we discuss how changes in diet breadth might affect the rest of a species' biology. First, to set up our discussion of the causes of specificity, let us consider the causes of unspecificity.

**Specialist:** a species with a narrow niche; here often used to refer to a herbivore that feeds on relatively few host plants

**Pleiotropy:** a condition in which a single locus affects more than one phenotype

**Allele:** one of several variant DNA sequences at a single genetic locus

**Diet breadth:** the diversity of a herbivorous insect's host-use relationships

**Generalist:** a species with a broad niche, with respect to some dimension such as diet; here often used to refer to a herbivore that feeds on diverse host plants

## 2. CAUSES OF DIET EXPANSION

Without constraints, and when competition abounds, negative density-dependent selection should drive the evolution of the niche breadth of a species to match the variation in its environment

**Table 1 Empirical evidence from herbivorous insect systems for potential constraints on diet breadth evolution[a]**

| Potential constraints on diet breadth | | Evidence for | Evidence against |
|---|---|---|---|
| **Genetic constraints** | Antagonistic pleiotropy | Carroll & Boyd 1992, Sandoval 1994, Hawthorne & Via 2001, Nosil & Crespi 2006, Gompert & Messina 2016 | Futuyma & Moreno 1988, Fry 1996, Agosta & Klemens 2009, Zhen et al. 2012, Gompert et al. 2015, Smilanich et al. 2016 |
| | Epistasis | Zhen et al. 2012 | Zhen et al. 2012; Peterson et al. 2015, 2016 |
| **Population constraints** | Insufficient genetic variation | Futuyma et al. 1995 | Gompert et al. 2015 |
| | Genetic drift | Gompert et al. 2014, Grosman et al. 2015, Hardy et al. 2016 | No evidence |
| | Genetic draft | No evidence | No evidence |
| | Ecological drift and draft | No evidence | No evidence |
| | Slow host-use adaptation | No evidence | Forister et al. 2015 (host use is more evolvable in generalists), Oppenheim et al. 2018 (fast evolution of polygenic traits) |
| **Ecological constraints** | Competitive exclusion | Liu & Stiling 2006 | Joshi & Vrieling 2005 |
| | Allee effects | Rhainds 2010 | No evidence |

[a] This table is not exhaustive and excludes theoretical evidence as well as empirical evidence from systems other than herbivorous insects.

(Maynard Smith & Hoekstra 1980, Futuyma & Moreno 1988). Generalists should evolve in heterogeneous environments. Specialists should evolve in homogeneous environments. In fact, this is precisely what we see in simple systems; in experimental evolution studies of bacteria, algae, and viruses, niche breadth does tend to evolve to match environmental heterogeneity (Rainey et al. 2000). Broad niches can also be adaptive without intense competition; they can hedge against environmental uncertainty. After first describing how competition may or may not drive diet expansion in herbivorous insects, we turn to competition-free diet expansion.

**Host use:** describes the parasitic relationships between a herbivorous insect and its host plants—fundamentally trophic but encompassing many other aspects of a herbivorous insect's ecology

**Negative density-dependent selection:** a condition in which rarity is selectively advantageous

## 2.1. From Competition to Broad Diets

Left to itself in a mixed community of plants, and without constraints on adaptation, a herbivorous insect population should evolve a broad diet in response to negative density-dependent selection (Rainey et al. 2000). Of course, that depends on herbivorous insects actually competing for resources. Whether such competition occurs was once controversial. Because of intense top-down pressure on herbivorous insect populations from their natural enemies, herbivorous insects were thought to rarely compete for food. This is the Green World Hypothesis (Hairston et al. 1960): The world is green, more or less. Therefore, host plants are not a limiting resource for insect herbivores. If the Green World Hypothesis is correct, then competition for host resources would be an unlikely driver of the evolution of broad diets. But it is becoming increasingly apparent that the Green World Hypothesis is wrong.

Without a doubt, herbivorous insect populations are under intense top-down regulation by their natural enemies (Vidal & Murphy 2018). But herbivorous insects still compete for host resources (Kaplan & Denno 2007, Bird et al. 2019). The resolution of this apparent paradox is that much competition is indirect (Holt 1977)—via the induction of plant defenses and the recruitment of natural enemies—and that indirect competition can be strong even at low population densities (Bird et al. 2019). The upshot is that, in natural settings, competition between herbivorous insects can be subtle but consequential nevertheless. There are costs for high population density; induced plant defenses reduce the effective food supply, and nonlinear density-dependent increases in enemy pressure reduce the effective refuge supply. Even in a green world, herbivorous insects compete for hosts that have their defenses down and that afford refuge from natural enemies. Pervasive indirect competition between herbivorous insects implies selection for broader diets, to the extent that novel hosts have lower densities of competitors than occupied hosts. In some cases, indirect competition might be an even more potent force than direct competition; because it can kick in at low population densities, it may affect populations sooner and more often.

## 2.2. From Environmental Uncertainty to Broad Diets

Plant communities change over time. Specialist herbivores are more exposed to the potential downside of these changes. In the most extreme cases, an insect species could follow its host to extinction. Short of that, the specificity of a herbivorous insect's diet will largely determine how changes in a plant community affect its long-term fitness. In theory, the long-term fitness of a genotype is extremely sensitive to how its short-term fitness varies over time (Orr 2009); even if generalism is suboptimal most of the time, it can persist by virtue of being much less bad during the worst of times. This idea is borne out by microbial experimental evolution studies (Rainey et al. 2000) and geographic variation in host-use specificity. Plant communities are more volatile in some places than others, which seems to correspond to geographic variation in the diet breadths of herbivorous insect species. For example, most trophic guilds appear more host specific in the aseasonal tropics than in seasonal temperate areas (Forister et al. 2015; but see Janzen 1981 and Hardy et al. 2015 for counterexamples).

Individual plants also change over time. Sooner or later every plant dies, and over a plant's lifetime, it can vary considerably in nutritional quality and the danger it poses to an insect herbivore. Even in stable plant communities, herbivorous insects often need to disperse from one host plant to another. (Even a sessile herbivore, such as a gall inducer or leaf miner, needs to colonize new hosts.) Since plant communities tend to be species rich, hosts are embedded in a matrix of nonhosts. Generalism is a way of minimizing the risk of not finding a host. To be sure, many herbivorous insect species have evolved sophisticated host-finding systems (Jaenike 1990), and in fact, generalism is especially pronounced and pervasive in herbivorous insects that are especially poor host finders, for example, wind-dispersed scale insects (Normark & Johnson 2011). But sophisticated host-finding systems could have costs: (*a*) They could take resources away from growth and reproduction. By increasing the genetic complexity of host use, they could also (*b*) hinder adaptive host-use changes and (*c*) increase the target size and thus the rate of deleterious mutations (see Section 4.1, below). Species that have solved their host-finding problems with generalism have fewer of these costs to pay.

**Epistasis:** a condition in which a single phenotype is affected by more than one locus

**Genetic drift:** change in allele frequency due to chance

**Genetic draft:** change in allele frequency due to linkage to a locus under selection

In summary, generalism has its advantages. Nevertheless, in most natural systems, specialists prevail. Most plant communities are complex. But at any given location, most herbivorous insects have narrow diets (Forister et al. 2015). Something must oppose selection for broad diets or select for narrow ones. What pushes species to specialize against the pull of selection for generalism?

## 3. CAUSES OF DIET CONTRACTION

Above, we assert that negative density-dependent selection on herbivorous insects should promote diet generalism in any diverse plant community, unless there are constraints on diet adaptation. In fact, such constraints are the basis of all theoretical models of specialization (e.g., Maynard Smith & Hoekstra 1980, Kawecki 1998). They either make diversifying selection ineffectual or transform it into divergent selection. Instead of the evolution of broad diets, we get the diversification of specialist species. In essence, all that it takes for a specialist to evolve from a generalist is for the tools of generalism to stop working (Fry 1996).

We see three major classes of constraints that could stand in the way of the evolution of broad diets, each corresponding to a level in the hierarchy of biological organization (**Figure 1**). The first is genetic constraints. Diet breadth may be constrained either by (*a*) epistasis, where some mutations are good only in certain genetic environments (Zhen et al. 2012), or by (*b*) antagonistic pleiotropy, where an allele that is good on one host is bad on another (Paaby & Rockman 2013). Note that such constraints stem from their effects on host-use phenotypes, particularly those relating to host-use preference and performance (Levins & MacArthur 1969, Van Tienderen 1991, Bernays 2001, Gripenberg et al. 2010). The second is population constraints: (*a*) A population may lack the genetic variation necessary for selection to promote an optimal generalist phenotype (Bennett & Lenski 1993, Blows & Hoffmann 2005, Gompert et al. 2015), (*b*) selection for generalism may be swamped by a variety of neutral processes, including genetic drift and draft (Holt & Gaines 1992, Kawecki et al. 1997, Forister & Jenkins 2017), and (*c*) generalists may adapt more slowly to new hosts than specialists (Whitlock 1996, Kawecki 1998). The third is ecological constraints. One population may stand in the way of another evolving a new host association; many of the potential host resources in an environment may have already been claimed or may be too dangerous to access (Yoder et al. 2010).

In addition to these constraints, there is the potential for positive selection for host-use specificity, although this could be cast as a response to demographic constraints on host-use evolution. Specifically, rarity can lead to positive selection for host-use specialization if it makes mate finding

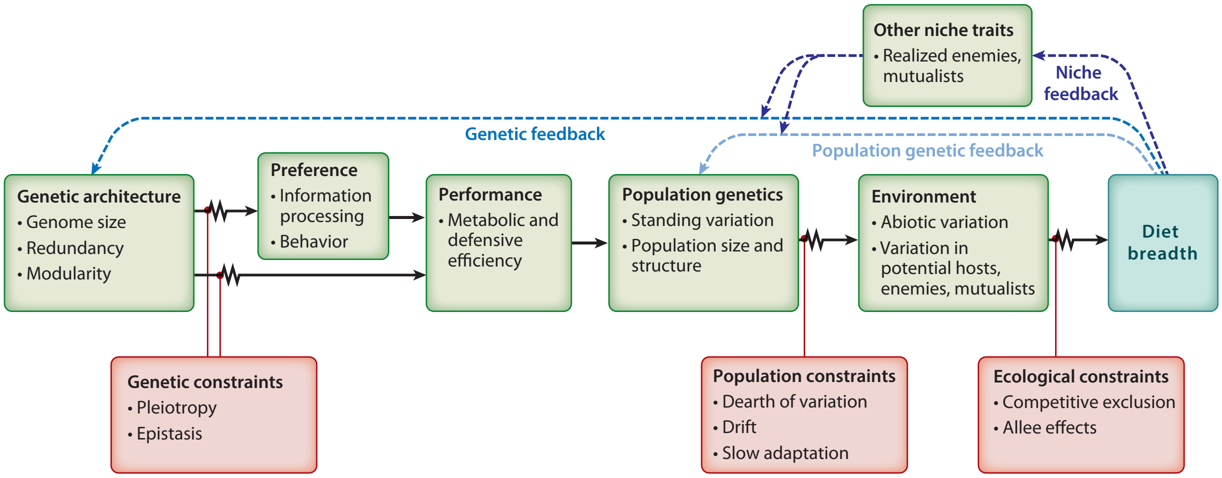

**Figure 1**

Conceptual overview. Diet-breadth evolution is governed by constraints—indicated by resistor symbols (zigzags) and red boxes—at the levels of genes, populations, and ecosystems. Diet breadth can also feed back on genetic architecture, population genetics, and other niche traits (in ways that can change the dynamics of diet-breadth evolution).

more efficient (Colwell 1986, Jaenike 1990), or if dense aggregations of herbivorous insects can overwhelm their host's defenses (Kaplan & Denno 2007).

Some combination of these constraints explains why there is no single supremely generalized herbivorous insect species that eats all plant species. Which constraints are most important? Let us consider each.

## 3.1. Genetic Constraints

The evolution of diet breadth in herbivorous insects could be governed by two kinds of genetic constraint: epistasis and pleiotropy.

**3.1.1. Epistasis.** Some potentially beneficial mutations work only in certain genetic environments. Each mutation increases the potential utility of one set of subsequent mutations and decreases the potential utility of another set. For example, the fitness effects of mutations at a gene for host plant preference may depend on alleles at a gene for physiological tolerance to host plant toxins, which could lead to exclusive evolutionary paths of host-use adaptation (Nosil & Flaxman 2011). How important is such historical contingency for the evolution of diets in herbivorous insects? If epistatic constraints are strong, that should show up in the phylogenetic patterns of host-use evolution. We should see strong negative evolutionary correlations in host use, as adaptation to one set of host plants reduces the probability of adaption to another; we should find clades with exclusive host-use modules. But comparative phylogenetic analyses suggest that such negative correlations are rare. For example, in true bugs (Hemiptera) and moths and butterflies (Lepidoptera), almost all of the significant evolutionary correlations in host use are positive; for example, evolving to use fabaceous hosts increases, rather than decreases, the probability of evolving to use asteraceous hosts (Peterson et al. 2015, 2016).

**3.1.2. Pleiotropy.** A mutation that improves one function can degrade another. This antagonistic pleiotropy could drive the evolution of niche specificity, as it appears to have done in the experimental adaptation of *Escherichia coli* populations (Cooper & Lenski 2000). As mentioned above, this is the most frequently cited explanation for the evolution of diet specificity in herbivorous insects (Futuyma & Moreno 1988, Jaenike 1990, Joshi & Thompson 1995, Ravigné et al. 2009). Because of pleiotropy, adaptation to one host comes at the cost of reduced performance on another. In fact, researchers sometimes imagine that these trade-offs are so steep and inexorable that it is impossible for a generalist to outperform a specialist (e.g., Richmond et al. 2005, Dapporto & Dennis 2013). That is all it would take to convert diversifying selection to divergent selection.

**Conditionally neutral:** selectively neutral in a particular environment; here used to characterize genetic diversity that is neutral on a subset of the host plants used by an herbivore

The problem is that there is strikingly little genetic evidence of such pleiotropy-driven trade-offs, despite extensive investigation (Futuyma & Moreno 1988, Fry 1996, Agosta & Klemens 2009, Gompert et al. 2015; but see Hawthorne & Via 2001, Gompert & Messina 2016). This lack of evidence could be due to the difficulty of recognizing the signs of trade-offs that govern the evolution of a polygenic, complex life-history trait (Joshi & Thompson 1995). But the theoretical grounds for expecting pleiotropy to drive the evolution of a polygenetic trait are shaky (Joshi & Thompson 1995, Sgrò & Hoffmann 2004, Remold 2012). And, in contrast to what we observe in *E. coli*, other experimental evolution studies of microbial systems have failed to find pleiotropic costs for generalism (e.g., Kassen & Bell 1998). Clearly, antagonistic pleiotropy is not inevitable. Moreover, any constraint on adaptation imposed by negative pleiotropy could be released by epistatic changes.

For a vivid example, consider the case of convergent evolution of $Na^+$,$K^+$-ATPase insensitivity to cardenolides in the community of insects that feed on milkweeds (Zhen et al. 2012). Many mutations can cause cardenolide insensitivity, but the dozens of species that have evolved it have fixed, in parallel, a small subset of these potential mutations. A possible explanation is that the mutations most apt to be promoted are those that minimize antagonistic pleiotropy (Stern 2013). But these pleiotropy problems appear solvable by epistasis; among milkweed eaters, gene duplication has allowed for functional divergence across gene copies, which reduces pleiotropy and expands the pool of genetic loci at which adaptation occurs (Zhen et al. 2012). Pleiotropy can constrain how genes adapt to a specific selective pressure, without necessitating the evolution of niche specificity per se. For example, Zhen et al. (2012) found that generalist milkweed feeders do not evolve cardenolide resistance through target-site insensitivity. They use some other strategy, for example, enzymatic detoxification. Generalists play a different game.

We see two promising lines of research to clarify the role of pleiotropy in herbivorous insect diet specialization. The first is the use of genome-wide association studies to determine how many loci tend to have sizable effects on performance across hosts, and what proportion of those loci are negatively pleiotropic (as recommended by Vertacnik & Linnen 2017). Such studies of *Timema cristinae* (Comeault et al. 2014), *Lycaeides melissa* (Gompert et al. 2015), *Rhagoletis pomonella* (Egan et al. 2015), and *Callosobruchus maculatus* (Gompert & Messina 2016) found that the genetic architecture of host-use-affecting traits varies considerably; some traits appear to be governed by a handful of large-effect loci, while others are governed by more than 100 loci, each with a relatively small effect. Moreover, it seems that the fitness effects of these genes tend to be conditionally neutral, affecting performance on one host plant species but not others. Such genes probably impose minimal constraints on the evolution of diet breadth. Therefore, the question is to what extent a few antagonistically pleiotropic loci can drive the evolution of a polygenic trait. This brings us to our second promising line of research, the use of individual-based simulation studies to better understand the effects of negative pleiotropy on the evolution of a polygenic trait (Haller et al. 2019).

To be clear, genetic constraints flow from trade-offs between phenotypes—in this case between phenotypes related to host-use preference and performance. As we have seen, detecting the genetic signatures of phenotypic trade-offs can be difficult. Do we have more direct evidence of phenotypic trade-offs? We start with performance, then look at preference.

#### *3.1.2.1. Performance.*

Some gross phenotypes work only in specific host environments. For example, stick insect color morphs that reduce bird predation on one host can increase it on another (Sandoval 1994, Nosil & Crespi 2006). Likewise, decreasing the length of a soapberry bug's proboscis improves performance on some hosts and decreases performance on others (Carroll & Boyd 1992). Such biomechanical trade-offs likely select for specificity at the level of plant growth form or tissue type, and they surely account for some of the diet specificity we see across herbivorous insects. But most insects have trophic and defensive morphologies that would seem to work on a much broader array of hosts than what they actually use. Further specificity requires further explanation, and for the most part, such explanations have hinged on metabolic trade-offs (Ehrlich & Raven 1964). What evidence supports such metabolic trade-offs?

First we consider chemical defense. Many herbivorous insects sequester the toxins of their hosts and use them for their own defense. If specialists were better at reusing their hosts' chemical defenses, that could help explain the prevalence of specificity. But meta-analyses indicate that generalists and specialists are just as likely to benefit from host defensive chemicals (Smilanich et al. 2016); thus, it is doubtful that this would select for diet specificity.

More often, biologists consider the metabolism of host plant detoxification; specialists are thought to detoxify their host's defensive chemicals with greater economy. In fact, a recent meta-analysis suggests that on shared hosts, specialists tend to grow faster than generalists—although researchers have looked mostly at lepidopterans, have not found consistent differences between generalists and specialists in fecundity or survival rates, and have yet to account for the phylogenetic nonindependence of performance variables (Rothwell & Holeski 2020).

More support for the greater metabolic efficiency of specialists is offered by butterflies that feed on plants defended by furanocoumarins. Specialists and generalists alike have furanocoumarin-detoxifying cytochrome P450 enzymes, and specificity at the level of diet appears to be matched at the level of enzymes; specialist P450 homologs are more efficient and less flexible (Li et al. 2004). But we know of no applications of the approaches used by Li et al. (2004) to other systems. Furthermore, it is not clear how the efficiency of secondary metabolism scales up to the level of organisms, or whether energy limitations govern herbivorous insect fitness. For the most part, researchers have found that, even on highly toxic plants, detoxification accounts for a small part of a herbivorous insect's energy budget, and boosting detoxification activity might not dampen growth and reproduction (e.g., Neal 1987, Castañeda et al. 2009). When toxins do reduce performance, it is typically by reducing feeding rates, prolonging development, and reducing feeding efficiency (Appel & Martin 1992, Bastias et al. 2017). A meta-analysis might be fruitful.

#### *3.1.2.2. Preference.*

Because of sensory system or information processing constraints, herbivorous insects might not be able to tell good hosts from poor hosts (Levins & MacArthur 1969), and by accepting a broader range of hosts, a generalist may increase the odds of using a poor one. The Information-Processing Hypothesis posits that by reducing the complexity of the host-discrimination problem, specialists are better at it. Less-distracted, more-decisive species waste less time searching for hosts, and thereby attract less attention from predators (Bernays 2001). For example, in aphids, more-specialized forms more accurately settled on hosts that are good for them (Bernays & Funk 1999). More broadly, meta-analyses have found that female host preference was positively correlated with offspring survival, and that this effect was strongest for specialists (Gripenberg et al. 2010). In sum, at least the starting premises of the Information-Processing Hypothesis seem to hold. Of course, just because specialists are better at choosing their best host does not mean that they will outcompete a generalist on it (but see Rothwell & Holeski 2020). Better host-use decisions in specialists could simply reflect that, for specialists, poor decisions have harsher consequences and are more strongly selected against. Conversely, a loose correlation between preference and performance in a generalist would not be so bad if they do reasonably well on any host. A comparative phylogenetic analysis of the effects of diet breadth on performance would help clarify this issue, as would individual-based simulations of the joint evolution of performance and preference when those traits are polygenic.

**Cryptic genetic variation:** genetic diversity that is neutral in one environment but subject to selection in another; here used to refer to genetic diversity in a specialist that is neutral on the specialist's usual host plant but that affects its fitness on alternative host plants

## 3.2. Population Constraints

Let us turn now to how diet-breadth evolution could be governed by population-level constraints.

**3.2.1. Insufficient standing variation.** Natural selection requires genetic variation. In some microbial and insect populations, it seems that the genetic variation needed for some types of niche evolution is absent. For example, *E. coli* populations have been experimentally adapted to a range of temperatures, but no known genotypes survive above 43°C (Bennett & Lenski 1993). Likewise, populations of *Ophraella* beetles appear to lack genotypes that can survive on most of the plants they might encounter (Futuyma et al. 1995). One thing that might make such genetic diversity shortages especially likely is the complexity of host-use phenotypes and genetic architectures (Forister et al. 2007). Therefore, prevalent specialism may be due to prevalent genetic poverty.

**3.2.2. Drift and draft.** Specialization could occur through genetic drift. This is more likely in smaller populations (Lynch et al. 2011), and specialization via drift might be expected whenever small populations are isolated from broadly distributed, generalist ancestors. This hypothesis could not be rejected by comparative phylogenetic analyses of scale insects (Hardy et al. 2016), but neither could an alternative hypothesis, in which specialization is driven by local selection on subpopulations of a generalist (Stireman 2005). Progress might best be made with population genetic approaches. Do specialists tend to be derived from generalist ancestors? Do we see signs of more genetic drift in specialists?

Genetic drift could also keep populations specialized, as diet expansion could be stymied by the buildup of cryptic genetic variation that is neutral on a current host but detrimental on a potentially new host (Kawecki et al. 1997). This idea has some support from experimental evolution in microbial systems. For example, Reboud & Bell (1997) found that adaptation of *Chlamydomonas* algae to light or dark environments came at a cost of performance in the nonselected environment. But a generalist lineage—one that performed as well in each environment as the specialist—evolved when exposed to temporally fluctuating light levels. Thus, the cost of adaptation to each environment was due not to antagonistic pleiotropy but rather to the accumulation of mutations that were neutral in the selected environment but deleterious outside of it. We have at least some evidence that this applies to plant–insect systems (Gompert et al. 2014). For example, following a natural switch to a novel host, populations of the geometrid moth *Thyrinteina leucoceraea* lost fitness on old hosts faster than they improved fitness on novel ones (Grosman et al. 2015).

Taken to the extreme, this hypothesis predicts that specialization is an evolutionary dead end. The longer a species is specialized, the more cryptic genetic variation builds up that is neutral on the current host but deleterious on others. Can cryptic genetic variation build up to such an extent that essentially no host switching is possible? If so, this does not appear to be typical. Several comparative phylogenetic studies have found that diet breadth is evolutionarily labile and that apparent specialists are often latent generalists, maintaining the genetic capacity to use ancestral hosts (Janz et al. 2001, Nosil 2002, Hardy & Otto 2014, Hardy et al. 2016). Thus, cryptically deleterious genetic variation may more often impede host-use adaptation than completely block it. It depends on how long it takes for ancestral host-use capacity to fade, something we could learn more about with phylogenetic estimates of ancestral host use coupled with comparative phylogenetic analyses of performance across hosts.

Genetic drift is not the only neutral process that could stymie diet expansion. Another is genetic draft, also called genetic hitchhiking—a diet-shrinking allele could increase in frequency by virtue of being linked to another allele that confers a selective advantage for some other trait (Neher 2013). In an analogous spatial process, a diet-shrinking allele could increase in frequency by occurring in a local population that is expanding (Barton & Whitlock 1997). Alternatively, specialization might evolve by ecological drift (Forister & Jenkins 2017). Imagine a host-structured metapopulation fixed for an allele that confers the ability to use two host species, one of which is rare. If demographic stochasticity caused the extirpation of subpopulations on the rare host species, realized diet breadth would contract without any change in allele frequency. Likewise, allopatric speciation could cause diet specialization via a kind of niche vicariance, that is, the partitioning of host environments and diet-affecting alleles across nascent species (Forister & Jenkins 2017). For example, many of the commonalities in the scale insect fauna of Australia and New Zealand are thought to be the result of West Wind Drift (Hardy et al. 2008); the wind blows east across the Tasman Sea to New Zealand and brings with it propagules of the Australian biota (Sanmartín et al. 2007). In most cases, scale insect species that establish a population in New Zealand will encounter few of their ancestral Australian host plants. As a specific example, the eucalyptus mussel scale (*Lepidosaphes multipora*) in New Zealand feeds on three of the seven host species that it feeds on in Australia (García Morales et al. 2016). Diet contraction is linked to the evolution of geographic range disjunctions.

**Ecological drift:** change in abundance of a species due to chance

**Metapopulation:** a set of populations of a single species, linked by at least occasional gene flow

In summary, the neutral processes that could undo broad diets in herbivorous insects are many. But apart from ample evidence of niche vicariance, rigorous empirical demonstrations are few.

**3.3.3. Generalists are slow to adapt.** Even if generalism were the ideal phenotype, it might take too long to evolve. Relative to specialists, generalist populations could be slow to adapt to certain hosts. Simple population genetic models predict that adaptation to a specific resource will be faster in specialists because a greater proportion of a specialist population will be exposed to selection on that resource (Holt & Gaines 1992, Whitlock 1996, Kawecki 1998). For example, Whitlock (1996) considers the fate of conditionally neutral alleles, that is, genetic variants that are advantageous on one host plant and neutral on others. He shows that, all else being equal, the rates at which such an allele is promoted and fixed are governed by the probability with which an individual in a population will encounter a given host. Thus, such alleles will be more rapidly promoted and fixed in specialists. Likewise, in comparison to generalists, specialists are expected to more rapidly purge alleles that are deleterious on a particular host. We are unaware of strong empirical evidence that generalists are slow adapters. Perhaps this is a question for experimental evolution or comparative phylogenetics.

Similar reasoning could be applied to genetic environments; less epistatic variation might cause more consistent selection on a diet-affecting locus and, hence, more rapid evolution. In fact, some classic theory (Fisher 1930) and individual-based simulation models (e.g., Gavrilets & Vose 2007) predict that adaptation and niche divergence will be faster when traits are controlled by few loci and, thus, that the scope for epistatic variation is limited. But all bets are off with additional genetic architectural complexity, or with a positive covariation between genetic architectural complexity and standing genetic diversity. Without epistasis, standard quantitative genetic models tell us that adaptation will be faster with more additive genetic variance, which should increase with the number of contributing loci. Moreover, empirical research suggests that polygenic traits can evolve quite rapidly (e.g., Oppenheim et al. 2018). Therefore, a big question is how much epistasis is involved in the evolution of herbivorous insect diet traits (Carroll 2007).

**Allee effect:** a condition in which rarity is selectively disadvantageous

## 3.3. Ecological Constraints

On top of genetic and population-level constraints, ecological constraints could also be important for the evolution of diet breadth.

**3.3.1. Costs of high density.** According to the classical theory of adaptive radiation, the biggest constraint on niche breadth is antagonism between species (Yoder et al. 2010), which becomes apparent when the constraints are released. Niche expansion is sparked by an ecological opportunity that distances a population from its enemies or competitors—opportunities such as the extinction of an antagonist, the colonization of a new environment, or the evolution of a key innovation (Simpson 1949). For a time, the growth of populations that realize such opportunities goes unchecked; then, individuals mainly compete with conspecifics, causing strong density-dependent selection for niche expansion (MacArthur et al. 1972). So the story goes. Eventually niche expansion is succeeded by niche divergence, but in the classical adaptive radiation theory this step depends on a shift from ecological constraints to phenotypic and genetic trade-offs.

Adaptive radiation is at the heart of the oft-invoked Escape and Radiate Hypothesis (Ehrlich & Raven 1964), a coevolutionary version of adaptive radiation which posits that herbivorous insects diversify after evolving to exploit some previously protected group of host plants. As for the more general adaptive radiation theory, it assumes that the diversifying selection in the new host environment is due to release from community-level constraints. Popular though the Escape and Radiate Hypothesis may be, comparative studies indicate that it poorly predicts phylogenetic patterns of host use and species richness in herbivorous insects (Hardy & Otto 2014, Braga et al. 2018). For example, in butterflies, the evolution of major new host associations appears to negatively affect species diversity (Kaczvinsky & Hardy 2020). What evidence do we have that ecological antagonism constrains the evolution of herbivorous insect diets?

Studies of invasion biology show that escape from the old antagonists can indeed spark niche expansion. For example, niche expansion in cane toads in Australia has been linked to depauperate Australian natural enemy communities (Tingley et al. 2014), and the pest status of many invasive insects has been hypothesized to be due to their release from natural enemy pressure. Nevertheless, evidence for the generality of this enemy-release effect is mixed (Colautti et al. 2004, Liu & Stiling 2006). We know the most about invasive weeds. Where weeds have been introduced, they tend to be fed upon by fewer and less specialized insect herbivores (Liu & Stiling 2006), but the generalist herbivores in their introduced ranges can be voracious (e.g., Joshi & Vrieling 2005). In summary, although the importance of community-level constraints on niche breadth flows from first principles of ecological theory, evidence for them is surprisingly scarce.

**3.3.2. Costs of low density.** Up to this point, all of our explanations of host-use specificity entail constraints that oppose selection for broad diets. By contrast, certain challenges associated with being rare—that is, Allee effects—could lead to positive selection for host-use specialization (Colwell 1986). One such challenge is finding a mate. If mating occurs on or near host plants—a rule for many herbivorous insects—host-use specificity gives mate searchers a more specific target. By similar logic, host-use specificity could be promoted by exploitative facilitation, for example, when dense herbivore populations are better able to overwhelm their hosts' defenses (Kaplan & Denno 2007).

What evidence do we have for Allee effects in herbivorous insects? Do polyphagous species have more trouble finding mates? The research into female insect mating failure was reviewed by Rhainds (2010); most studies find no evidence of it, but some do, and in some cases, mating failures can be pronounced. Rhainds (2010) did not attempt to explain the variation in female mating failure quantitatively. A phylogenetic regression of mating failure against diet breadth could be revealing. As for exploitative facilitation, currently there is no evidence that diet specialists more effectively team up against their host plants (Bird et al. 2019).

### 3.4. Constraint Integration

Constraints on diet breadth are surely interdependent. For example, in the adaptive radiation framework, a mutation that allows a population to access a new resource can release it from ecological constraints on diet breadth. But such a mutation could also release genetic constraints, and all of the above changes could cause changes in population size and structure that release population genetic constraints on diet breadth. Insofar as a species' biology is integrated across levels of biological organization, the constraints on a species' biology are also integrated.

## 4. DIFFERENCES BETWEEN GENERALISTS AND SPECIALISTS

Simple population genetics theory clearly predicts the effects of diet breadth on the rate of host-use adaptation: Specialists should adapt faster. Much of that clarity stems from the simplifying assumption that the only difference between a generalist and a specialist is the breadth of their diets. But generalists and specialists could differ in many other ways, and many of these differences are likely to affect host-use adaptation. Consider the power-law-fitting frequency distribution of diet breadths across plant-eating insect species (Forister et al. 2015). Such a distribution implies some underlying positive feedback process. It implies that the probability that any new host will be added to an insect's diet is proportional to the size of its current diet. This accords with comparative phylogenetic evidence that novel host associations evolve faster in generalists (Hardy & Otto 2014). Generalists not only have broader diets; they have more evolvable diets.

Here we consider four types of potential differences between generalists and specialists that could affect host-use adaptation and explain how diet breadth changes diet evolvability: differences in (*a*) genetic architecture, (*b*) phenotypic plasticity, (*c*) population size and structure, and (*d*) community interactions (**Figure 1**). Furthermore, we argue that ecological changes tend to favor species that are good at managing stress, and that a fundamental aspect of generalism is open-ended stress management.

### 4.1. Genetic Architectural Differences

In Section 3.1.2, we note that a major question about the evolution of diet breadth is how complex the underlying genetic architectures are. A related question is how genetic architectural complexity covaries with diet breadth. In particular, one might predict that generalists would tend to evolve genetic architectures that reduce the scope for pleiotropic and epistatic constraints on host use (Zhen et al. 2012, Stern 2013).

Because of pleiotropy and epistasis, the genetic complexity of a trait could have complex effects on the rate at which it can adaptively evolve (Forister et al. 2007). On the one hand, with more genes, we have more targets for adaptive mutation (Griswold 2006). That should increase the rate of adaptation. On the other hand, we have more ways in which a mutation that is good for one thing can be bad for another. That should decrease the rate of adaptation (Fisher 1930), but to a degree it depends on two features of genome architecture: redundancy (e.g., the number of genes per gene family) and modularity (i.e., the organization of genes into sets of coregulated functional groups that are loosely coupled to other such groups) (Hansen 2006). Both redundancy and modularity should promote adaptability by limiting the scope of pleiotropy and epistasis. With more genetic redundancy comes greater potential for functional divergence. With more modularity comes a lower chance of antagonistic pleiotropy and a smaller set of epistatic constraints that must be satisfied for a mutation to be beneficial.

The diverse host plant environments experienced by generalists could select for more redundant and modular genetic architectures, which in turn could facilitate adaptation to yet more diverse hosts. As it stands, we have little empirical evidence. Nothing has been published on the relationship between diet breadth and genetic modularity. Such a relationship could be tested with phylogenetic contrasts of gene expression modularity across species, for example, quantified with weighted gene coexpression network analysis (Langfelder & Horvath 2008). We have a little more to go on for the relationship between diet breadth and genetic redundancy. For example, in a comparison of genomes of species varying in diet breadth, Gouin et al. (2017) found that the most polyphagous species (*Spodoptera frugiperda*) had the most diverse gene families involved in detoxification of xenobiotics.

### 4.2. Phenotypic Plasticity Differences

Phenotypic plasticity can be adaptive or nonadaptive; that is, environment-induced changes in gene expression can move a trait value closer to or farther away from an optimum value (Ghalambor et al. 2007). Across a handful of herbivorous insect species, studies of host-induced plasticity in gene expression suggest more adaptive plasticity in generalists and more nonadaptive plasticity in specialists (Govind et al. 2010, Hoang et al. 2015, Ragland et al. 2015). As an example of nonadaptive plasticity, consider larvae of the snowberry-feeding fruitfly species *Rhagoletis zephyria* that are experimentally raised on apples. The novel host induces changes in the gene expression of several hundred loci and results in low fitness for the flies (Ragland et al. 2015). Most of the gene expression changes seen in the *R. zephyria* larvae are opposite in direction to the evolved gene expression changes seen the species' apple-adapted close relative *R. pomonella*.

How might such plasticity affect host-use evolution? Adaptive plasticity can improve the fit between a generalist genotype on a new host environment, and nonadaptive plasticity can worsen a bad fit between a specialist genotype and a novel host environment. In fact, this worsening of ecological fit has been linked to some of the most rapid rates of adaptive evolution ever recorded (Ghalambor et al. 2015), and experimental evolution of host use in herbivorous insects has repeatedly shown an early phase of rapid selection against nonadaptive plasticity (Hoang et al. 2015, Ragland et al. 2015). At first glance, these findings seem to support the idea of there being differences in genetic architecture between generalists and specialists that lead to more evolvable host use in generalists. More research along these lines would be illuminating.

### 4.3. Population Genetic Differences

Natural selection is more efficient in larger, less structured populations (Lynch & Conery 2003). Such populations maintain more potentially adaptive genetic variation, fix more beneficial alleles, and more efficiently purge deleterious ones. Currently, we do not know whether, in general, more polyphagous herbivorous insect species have larger and less structured populations. But this appears true of at least some lineages, for example, scale insects (Ross et al. 2013). In his consideration of rates of host-use adaptation, Whitlock (1996) notes that if population size increases linearly with diet breadth, it would negate some of the expected adaptive speed advantage of specialists. It is possible that on a particular plant species, a generalist population could be larger than that of a specialist. This might be true if generalist metapopulations occur more evenly across resources patches and can more efficiently find and colonize host species, as is the case for tropical communities of armored scale insects (Peterson et al. 2020). In this case, the effects of population size could shift the relative rates of adaptation in favor of generalists.

Whitlock's (1996) models predict the fate of alleles that are conditionally neutral across host species. If generalist species do tend to have larger effective population sizes, when it comes to general vigor alleles—that is, genetic variants that are beneficial across host environments—larger population sizes in generalists would give them an adaptive edge; more such alleles will arise in each generation, and more of them will be promoted to fixation. Even if specialists respond more nimbly to adaptive challenges posed by specific hosts, generalists would be likely to adapt more rapidly to challenges that are common across hosts. Genome-wide association studies could potentially detect alleles that improve fitness across hosts and determine whether such alleles are more frequent in more-generalist herbivorous insects.

Because generalists are less fastidious about where they put their eggs and what they try to eat, they may be more likely to attempt to feed on a new host when it is encountered (Holm et al. 2018). Even if specialists adapt more rapidly to a novel host, this could be offset if a generalist tends to have an adaptive head start. Generalists could evolve more new host associations simply because they more often experiment with new hosts.

### 4.4. Community Interaction Differences

In this section, we consider how the evolution of a broader diet in a herbivorous insect population might change the nature of its interactions with host plants, natural enemies, and symbionts.

**4.4.1. Interactions with host plants.** In response to insect feeding, plants emit volatiles that attract herbivore enemies and directly inhibit herbivore development. A meta-analysis has shown that, in comparison to generalists, specialists tend to induce more such volatiles (Rowen & Kaplan 2016). Moreover, in at least some systems, plant volatiles vary according to the diet breadth of the inducing insect herbivore (Danner et al. 2018). The upshot is that as herbivorous insects evolve broader diets they may also evolve qualitatively different interactions with each of their host plants. Do plant species tend to have more similar responses to their generalist enemies? If so, this might flatten the adaptive landscape for generalists and promote more rapid diet evolution.

On the insect side of the interaction, what little evidence we have suggests that there are distinct generalist and specialist trophic approaches. In the brush-footed butterfly *Vanessa cardui*, there are two main host-induced gene expression patterns: one induced by a clade of presumably ancestral hosts and another induced by an array of distantly related hosts thought to have been more recently colonized (de la Paz Celorio-Mancera et al. 2016). We would need to look at gene expression across hosts of other herbivorous insect species to know whether this is a general pattern, but the notion of generalism as open-ended host use—as opposed to the accumulation of specific ad hoc host-use adaptations—is consistent with phylogenetic evidence that generalism facilitates the colonization of novel hosts (Nylin & Janz 2009, Hardy 2017).

**4.4.2. Interactions with natural enemies.** Evolutionary game theory suggests that more-specialized natural enemy assemblages could exert more diversifying selection on host use in herbivorous insect populations (Brown & Vincent 1992), as specialized enemy assemblages may tend to leave more enemy-free space in an environment. We suspect that generalist insect herbivores may tend to have more-specialized natural enemy assemblages, a suspicion that could be tested with analysis of quantitative trophic interaction networks. If so, there could be a positive evolutionary feedback between herbivore diet breadth and the extent to which natural enemies apply diversifying selection on diet.

**4.4.3. Interactions with endosymbionts.** Another aspect of a herbivorous insect's ecology that is likely wrapped up with the evolution of its diet is its symbiotic relationships with microbes. How might we expect endosymbiosis to affect the evolution of diets in herbivorous insects? At this point, it is hard to say (Singer & Stireman 2005, Janson et al. 2008). To a certain extent, endosymbiosis simply adds to the complexity of an insect herbivore's genetic environment, in much the same way as gene duplication. Thus, symbionts could cause new pleiotropies or the release of old ones. But symbiosis may be more likely than gene duplication to spark genetic conflict and increase the odds of divergent mutation-order host-use specialization (Brucker & Bordenstein 2012, Crespi & Nosil 2013). In contrast, if the associations between herbivorous insects and certain microbial symbionts vary over ecological time, the diversity of potential insect–microbe interactions would be yet another layer of environmental heterogeneity that might select for generalism. Evidence of such functional microbiome turnover is scarce but not completely lacking. For example, in the fall armyworm, *S. frugiperda*, insecticides select for an insecticide-degrading gut microbiome (de Almeida et al. 2017). Thus, diet heterogeneity could select for herbivorous insect genotypes with open-ended mechanisms of managing their microbiota. If the diverse hosts of generalist insects expose them to more diverse microbes, this could ramp up selection for open-ended microbe-management systems, which could then feed back on host-use evolution.

## 4.5. Hedging Against Shocks

We have considered several putative differences between specialists and generalists that could make generalists more evolvable. Now we consider two extrinsic facets of adaptive challenges that could favor generalism: (*a*) Ecological opportunities are probably shocking, and (*b*) generalism is a hedge against shocks.

**4.5.1. Ecological opportunities are probably shocking.** The ecological opportunities that might spur diet evolution are likely to be harsh jolts to a population. Imagine a population of herbivorous insects that has gained a foothold on an island. The odds are high that in the beginning, the match between herbivore genotypes and each possible host plant is far from optimal. It could be that the initial shock of an ecological opportunity flattens an adaptive landscape (Lahti et al. 2009, Yoder et al. 2010). If so, in addition to the diet expansion we expect from the loosening of community-level constraints, we would expect further diet expansion due to reduced fitness disparity across potential host plants. During times of niche transformation, selection might not tend to strongly favor any specific niche. Alternatively, it could be that a novel environment exposes a herbivore population to a range of host-use suboptimality with peaks and valleys as pronounced as they were in the old environment. Progress could come from studies of introduced species. Are fitness disparities across potential hosts less pronounced in adventive populations?

**4.5.2. Generalism is a hedge against shocks.** Throughout its evolutionary history, an insect species will be exposed more often to stress of some kind than to stress of any particular kind. Many of these stresses will share some higher-order similarity, for example, the disruption of normal redox signaling. With some recycling of the logic of the population genetic models that predict faster rates of adaptation in specialists than generalists, we could make this prediction: The efficiency of selection in an environment should be proportional to how often it is encountered. By the same token, the efficiency of selection could be proportional to how often a particular environmental feature is encountered across mixed environments. In the case of the evolution of stress-compensation mechanisms, we might expect selection to most efficiently promote systems that respond to the most generic aspects of stress or that can maintain homeostasis in the most open-ended ways. A potential example of such a system can be found in certain armored scale insect species, in which overall body size varies greatly across hosts, depending on their quality, but the sizes of fitness-critical structures such as reproductive organs are invariant (Hill et al. 2011).

Much remains to be discovered about the evolution of diet breadth in herbivorous insects. Of course, this review has likely missed much of what is known. But we hope that, by pointing out some of the more glaring gaps, we have alerted some readers to fruitful opportunities for further research.

## SUMMARY POINTS

1. Explanations of herbivorous insect species richness tend to focus on the adaptiveness of diet specificity. But we find it impossible to view specificity as being adaptive outside the context of what constrains diet evolution.
2. Researchers have tended to focus on genetic constraints—specifically, antagonistic pleiotropy—that seem rarely to govern diet-breadth evolution; empirical evidence for antagonistic pleiotropy is scant, and new insights into the genetic architecture of herbivore host use loosen its theoretical underpinnings. That being said, at least some diet specificity can be attributed to gross morphological trade-offs.
3. In contrast, we find ample evidence that diet specificity can evolve because of genetic drift, a dearth of genetic diversity, and an excess of cryptically deleterious genetic diversity. Given a set of genetic, population genetic, and community constraints on diet breadth, diet specificity can surely be adaptive. But much of the diet specificity of herbivorous insects seems to be nonadaptive.
4. Diet specialists and generalists differ in many ways other than diet breadth, and many of these differences could feed back on diet evolution.
5. What data are available suggest that in generalists the genetic architecture of host use is more complex, phenotypic plasticity is more adaptive, and induced host plant defenses are less pronounced. But relevant data are scarce, and we see potential for several additional key differences, such as in the modularity of gene expression networks, the effective sizes of populations, the rate at which metapopulations colonize resource patches, the type of induced plant defenses, the diversity of natural enemy assemblages, and the diversity and turnover of microbial associations.
6. In other ways, specialists and generalists may be more similar than previously thought. In particular, we find it doubtful that generalism comes at the cost of slow adaptation, poor competitiveness, or lackluster defensive phenotypes.
7. Progress toward a deeper understanding of the evolution of diet breadth in herbivorous insects will surely follow a deeper understanding of how specialists and generalists differ.

## DISCLOSURE STATEMENT

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