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Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions

M. L. FORISTER,^{1,5} L. A. DYER,¹ M. S. SINGER,² J. O. STIREMAN III,³ AND J. T. LILL⁴

¹*Department of Biology, University of Nevada, Reno, Nevada 89552 USA*

²*Department of Biology, Wesleyan University, Middletown, Connecticut 06459 USA*

³*Department of Biological Sciences, Wright State University, Dayton, Ohio 45435 USA*

⁴*Department of Biological Sciences, George Washington University, Washington, D.C. 20052 USA*

Abstract. Ecological specialization is a fundamental and well-studied concept, yet its great reach and complexity limit current understanding in important ways. More than 20 years after the publication of D. J. Futuyma and G. Moreno's oft-cited, major review of the topic, we synthesize new developments in the evolution of ecological specialization. Using insect–plant interactions as a model, we focus on important developments in four critical areas: genetic architecture, behavior, interaction complexity, and macroevolution. We find that theory based on simple genetic trade-offs in host use is being replaced by more subtle and complex pictures of genetic architecture, and multitrophic interactions have risen as a necessary framework for understanding specialization. A wealth of phylogenetic data has made possible a more detailed consideration of the macroevolutionary dimension of specialization, revealing (among other things) bidirectionality in transitions between generalist and specialist lineages. Technological advances, including genomic sequencing and analytical techniques at the community level, raise the possibility that the next decade will see research on specialization spanning multiple levels of biological organization in non-model organisms, from genes to populations to networks of interactions in natural communities. Finally, we offer a set of research questions that we find to be particularly pressing and fruitful for future research on ecological specialization.

Key words: *diversity; host range; insect–plant interactions; niche breadth.*

INTRODUCTION

One of the defining features of life on Earth is the fact that all organisms are ecologically specialized to some extent with respect to abiotic conditions and biotic resources (Futuyma and Moreno 1988, Thompson 2005). Any organism has a subset of environmental conditions in which it can thrive, and particular types of food, defense, and breeding resources that it must obtain for survival and reproduction. The ubiquity of ecological specialization makes it relevant to nearly every facet of organismal biology. Recently, the study of ecological specialization has resurged as a key component of ecological speciation and adaptive radiation (Schluter 2000, Rundle and Nosil 2005). However, the evolution-

ary causes of ecological specialization have not been synthesized to the same degree.

It has been just over 20 years since the publication of a pivotal review on the evolution of ecological specialization by Futuyma and Moreno (1988). In the intervening two decades, empirical and theoretical work on specialization has flourished (Schluter 2000, Funk et al. 2006, Ravigné et al. 2009, Scriber 2010). Developments have been sufficient in volume and importance that we find it opportune to review and synthesize the field. Our twofold goal is (1) to highlight empirical and theoretical results from the last two decades that have addressed questions considered pressing by Futuyma and Moreno (1988); and (2) to identify questions and perspectives that we believe will be important and fruitful in coming years. In summarizing recent developments and attempting to shed light on future advances, we focus on four topics: (1) genetic architecture, (2) behavior, (3) interaction complexity, and (4) macroevolution. We cover these four topics within a conceptual framework

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⁵E-mail: forister@gmail.com

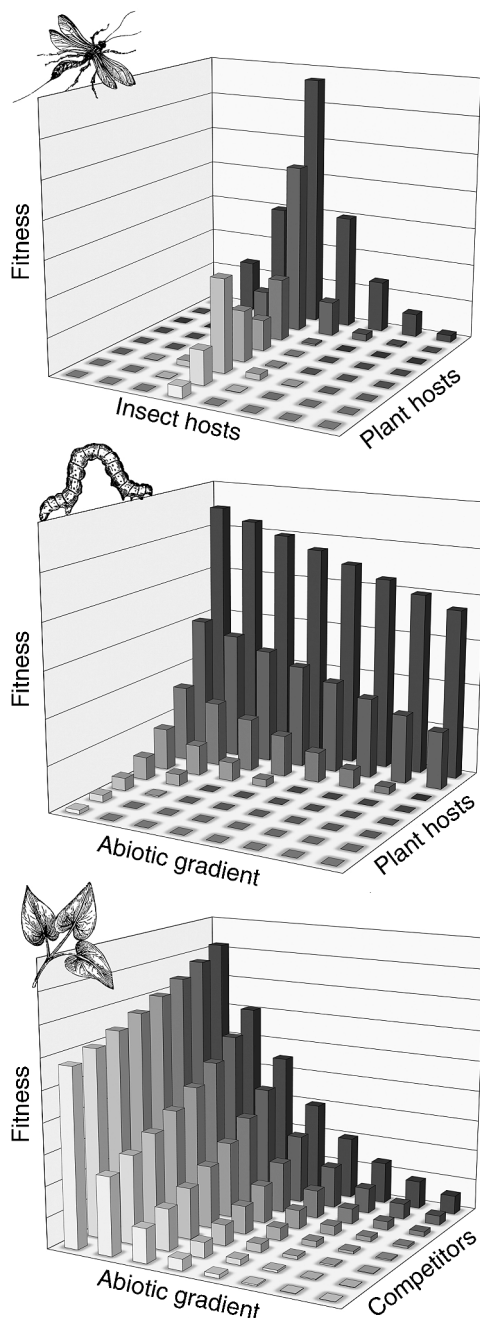


FIG. 1. Dimensions of specialization and interactions across trophic levels, illustrated with a hypothetical plant (lower panel), herbivore (middle panel), and natural enemy of the herbivore (top panel). Two resource dimensions are shown for each panel, with fitness on the vertical axis. The plant is a specialist along the abiotic gradient, while relatively generalized with respect to competitors (though in the presence of certain competitors a more narrow abiotic range is viable). The herbivore is a host specialist, but generalized with respect to the abiotic gradient, while the enemy (top panel) is specialized for both insect and plant hosts.

that emphasizes two unifying themes. First, we stress the idea that specialization must be studied with reference to specific traits, organisms, and environments. Second, we highlight the importance of interactions for understanding specialization at all levels of biological organization, from epistasis in gene networks to multitrophic interactions in communities. We draw primarily on systems that include plants, herbivorous insects, and their enemies, which have provided some of the classic models of specialization, and have historically been used to generate ideas that can be extrapolated to other systems and organisms. Furthermore, these systems are ideal for examining specialization, as many of the mechanistic aspects have been well-studied, such as oviposition behavior or the sequestration of plant secondary compounds by insect herbivores.

SPECIALIZATION: DEFINING THE PROBLEM

As ecological specialization touches on so many areas of biology, many problems or questions could be defined. However, we begin by following Futuyma and Moreno (1988) in attempting (1) to explain specialization of traits at the level of individual populations or species (i.e., why traits show specificity with respect to the environment); and (2) to explain the distribution of ecological specialists and generalists in space and time, which is a central question in both biogeography and macroecology as well as macroevolution. Both of these goals clearly require a working definition of specialization. Futuyma and Moreno (1988) utilized a qualitative framework, in which an herbivore such as the Colorado potato beetle that attacks at least 20 species of plants is more generalized than its congeners in the genus *Leptinotarsa*, which have each been recorded from a single or at most two host plants (Jacques 1988). Specialization must be defined with reference to a particular environmental factor. Therefore, it is an ecological property, reflective of the interaction between particular traits of an organism and a specific aspect of the environment, rather than an all-encompassing or typological property of an organism (see Fig. 1 for an illustration of levels of specialization along different axes and among trophic levels). A particular species might be behaviorally specialized with respect to one trait, such as prey choice, but functionally generalized with respect to another, such as thermal tolerance (Irschick et al. 2005). Once the axis of specialization is defined, specialization and generalization become relative terms and comparisons are only useful within this framework. A specialist in one comparison might be more or less generalized in another comparison, and continuous measures of specialization have been developed that offer promise in analyzing what is clearly a continuum as an evolutionary process (Blüthgen et al. 2006, Devictor et al. 2010, Novotny et al. 2010). Specialization can also be evaluated in a phylogenetic context, such as by analyzing the level of specialization in a lineage in relation to environmental parameters (e.g., Rodríguez-

Castañeda et al. 2010). Finally, specialization of traits can be defined and studied across a range of scales, from populations to communities and individuals (Bolnick et al. 2003).

GENETIC ARCHITECTURE

By “genetic architecture” we refer to the mapping of genotypes to phenotypes, which includes interactions among genetic elements involved in the expression of phenotypes. Historically, the most common genetic approach to explaining ecological specialization, as described by Futuyma and Moreno (1988), has been to assume a cost of adaptation, specifically a negative genetic correlation between alleles associated with the use of different resources. This is often modeled as genetic loci associated with host plant utilization, and a suite of alleles, each of which confers high performance on one host and reduced performance on another (Ravigné et al. 2009). Thus specialization is “built in” to the system, as optimization of fitness for a population in a constant environment results from fixation of alleles associated with one host. A generalist carries alleles associated with different environments, but never the optimal combination for any one environment (the “jack of all trades is a master of none”).

Futuyma and Moreno (1988) raised the suggestion that genetic trade-offs in host use might not be common, and thus might be an insufficiently general explanation for specialization. This suggestion has been borne out: cross-host correlations of juvenile performance (measured, for example, with siblings reared on different host plants) are nearly always positive or not significantly different than zero. A positive correlation results from families with high performance on one host having high performance on a second host, as opposed to a negative cross-host correlation, which would be consistent with genetic trade-offs. Thus variation in performance among families suggests variation in general “vigor” but not host-specific trade-offs (Fry 1996). While these studies have most often used the least powerful designs (e.g., full-sib experiments; Camara 1997), the large number of times that investigators have tried and failed to find negative cross-host correlations in performance suggests that simple genetic trade-offs in performance are either rare or difficult to detect (Joshi and Thompson 1995, Whitlock 1996, Scriber 2005, Futuyma 2008, Agosta and Klemens 2009, Rasman and Agrawal 2011). These conclusions are not without caveats that have been raised since Futuyma and Moreno (1988). In particular, some authors have suggested that a focus on juvenile performance might be too narrow to detect trade-offs in host use. Scheirs et al. (2000) found that adult performance in a dipteran leafminer associated with different hosts could explain oviposition preference, as adults maximized their own realized fecundity but not juvenile performance.

Even without the complications of studying multiple life history stages, more sophisticated quantitative and

population genetic perspectives have underscored the problems with searching for genetic trade-offs: A small number of loci exhibiting trade-offs might be sufficient to prevent optimization of fitness across multiple resources, but that small number of loci might be extremely difficult to detect given variation in performance among families (Fry 1993). Furthermore, Joshi and Thompson (1995) have suggested that trade-offs in host use will be most readily detected under a restricted set of circumstances, namely a population at genetic equilibrium utilizing two host plant species. Finally, a number of possibilities for the evolution of specialization have been presented that do not rely on trade-offs (Whitlock 1996, Kawecki 1998, Holt 2003). As long as cross-host correlations are less than one (though they need not be negative), selection should lead to an increase in fitness on the more commonly used host, a situation which favors alleles conferring specialized preference behavior (Fry 1996).

Beyond the search for simple genetic trade-offs, the field of specialization would benefit from a perspective encompassing broader issues of genetic architecture, as has been developed in other fields of evolutionary biology (Futuyma 2010, Schluter et al. 2010). In particular, the issue of complexity of adaptation is relevant to ecological specialization (Welch and Waxman 2003). Features of organisms can be thought of as being more or less complex with reference to the number of unique genetic elements involved; for example, wings and eyes are potentially more complex than horns and claws. In this context, we can ask how many independent genetic traits (e.g., detoxification, recognition, and other traits) underlie the ability to utilize a particular host plant species (Forister et al. 2007, Nosil and Sandoval 2008). The extent to which these traits are or are not genetically correlated should affect which hosts can be more readily incorporated into the diet of an herbivore. Fisher (1930) proposed that it will be most difficult for natural selection to move a population from one adaptive peak (e.g., host plant) to another when the relevant adaptation is a complex trait (Orr 2000). As an alternative hypothesis, genetic complexity underlying host use might facilitate adaptation by providing a larger target for mutation (Griswold 2006).

The newly available 12 *Drosophila* genomes have facilitated an unprecedented level of comparative work relevant to the genetics of specialization (Whiteman and Pierce 2008). In particular, analyses of suites of genes associated with chemoreception have suggested that specialization is associated with elevated rates of loss-of-function mutations and some evidence of positive selection. The host specialist *D. sechellia* has lost genes associated with deterrence (bitter receptors), which may have previously (in an ancestor) conferred deterrence to what is now the host of *D. sechellia* (McBride 2007, McBride and Arguello 2007, Dworkin and Jones 2009). These now nonfunctioning genes may also have been associated with deterrence for a non-host that was

important in an ancestral environment but is no longer encountered by *D. sechellia*. Similar loss of function in genes associated with the detection of bitter compounds was reported for another host specialist, *D. erecta* (McBride and Arguello 2007). Such a process has been called adaptive decay (Ostrowski et al. 2007) or genome decay (Dworkin and Jones 2009), and has been studied in other contexts, such as the loss of visual traits in cave-dwelling organisms (Jeffery 2005). For chemoreception genes that remain intact in these *Drosophila* species, elevated rates of amino acid substitution are evident, particularly in genes expressed in larvae (McBride and Arguello 2007). It is noteworthy that the paths to specialization reflected in these studies, involving gain and loss of function, do not necessarily rely on simple trade-offs among the ability to use different hosts. At present, similar resources are available for few insect-plant systems (Whiteman and Jander 2010), though this is changing with the advent of genomic technologies (Hudson 2008, Vera et al. 2008, Gompert et al. 2010, Renn and Siemens 2010).

BEHAVIOR

In their discussion of ecological specialization, Futuyma and Moreno (1988) made a distinction between behavioral and morphological/physiological (M-P) traits. They cited evidence that behavioral specialization is more evolutionarily labile than M-P traits, and state “behavior is often the mechanism by which specialization is exercised.” These arguments have gathered support over the last two decades (e.g., Caillaud and Via 2000, Ravigné et al. 2009) as the importance of key behavioral traits such as host acceptance has become evident. Recent theoretical work predicts the evolution of specialization under a wider range of conditions than seen in previous models (e.g., Wilson and Yoshimura 1994), specifically when habitat choice evolves jointly with habitat-specific performance traits (Ravigné et al. 2009). Correspondence between behavior and performance (i.e., the preference–performance correlation) has been long-debated in herbivorous insects, though recent evidence suggests that a positive association might be common (Gripenberg et al. 2010). This line of reasoning assumes that behavioral traits are evolutionarily labile, which has also been borne out by recent genetic work. The well-studied evolutionary ecology of oviposition preference by Edith’s checkerspot butterflies offers a paradigmatic example of rapid behavioral adaptation and specialization (Singer et al. 1993, Singer and Thomas 1996, McBride and Singer 2010). Several studies show that allelic variation at one or few genetic loci can alter behavioral responses to resource cues. A recent review of the genetic basis of host-plant preference in phytophagous insects shows that preference might be predominantly determined by a relatively small set (1–5) of genetic loci (Matsubayashi et al. 2010), which could facilitate rapid adaptive change by Fisher’s (1930) complexity argument.

The proximate basis of behavioral specialization is not only genetic, but also environmental. Yet environmentally induced behavioral plasticity does not necessarily preclude the evolution of behavioral specialization. The last two decades have seen an explosion of research on the role of phenotypic and behavioral plasticity in the evolution of ecological traits (e.g., Odling-Smee et al. 2003, West-Eberhard 2003). According to the theory of genetic accommodation and subsequent assimilation (cf. West-Eberhard 2003), the occupation of marginal environments enabled by phenotypic plasticity (accommodation) can facilitate evolutionary adaptation to such extreme environments. Through fitness costs of plasticity or genetic stochasticity in small, geographically marginal populations, phenotypic plasticity can be lost with ensuing local adaptation and ecological specialization (assimilation) in the marginal population. Similarly, plasticity of behavior can influence the evolution of specialization through niche construction (Odling-Smee et al. 2003). That is, behavioral response to the local circumstances partly determines the environment, hence the selective regime, to which the organism and its heritable phenotypes are exposed. For example, the species-specific shelter-building behaviors exhibited by caterpillars in many families of Lepidoptera provide these insects with opportunities to alter their chemical and physical environments (Berenbaum 1978, Lill and Marquis 2007), potentially facilitating adoption of novel hosts or habitats that may otherwise be unavailable.

The behavioral basis of ecological specialization demands consideration of bidirectional feedbacks (Hailoin and Strauss 2008) as well as organismal constraints. Bidirectional feedbacks are increasingly entering into the research paradigms of evolutionary ecologists because it is clear that causation often goes in both directions, between ecological factors and evolutionary processes (Schoener 2011), and behavioral mediation of such bidirectional feedbacks is likely to be common. For example, the evolution of olfactory and behavioral specialization can dictate host use and ecological specialization in *Drosophila melanogaster* (Matsuo et al. 2007). However, ecological circumstances can also limit an individual organism’s range of behavior, and thus promote the evolution of specialization as M-P traits adapt locally (Ravigné et al. 2009) or genetic assimilation proceeds (West-Eberhard 2003). Similarly, behavioral and M-P traits interact at the level of the individual organism to constrain or expand the breadth of resource use (West-Eberhard 2003, Nylin and Janz 2009). For example, the specialized “trenching” behaviors of some insect herbivores can promote diet expansions by subverting defenses of lactiferous plants (Dussourd and Denno 1994) but these behaviors require specific mandible phenotypes for their expression.

The neural constraints or information-processing hypothesis presents a different mechanism for potential feedbacks between ecological and evolutionary factors.

Its premise is that the limited information processing ability of the central nervous system imposes constraints on attention to cues and decision-making (Bernays and Wcislo 1994, Bernays 2001). Individual organisms with a relatively specialized or narrow behavioral repertoire will perform better and achieve greater fitness than relatively generalized individuals (Egan and Funk 2006). The net fitness benefit of ecological specialization is thus expected to be greatest in lineages with limited neural capacity, such as arthropods. In phytophagous insects, performance advantages of specialists have been demonstrated through higher quality oviposition decisions (Janz and Nylin 1997) and faster decisions about host-plant acceptance (Bernays 1998, Bernays and Funk 1999) relative to decisions made by generalists.

INTERACTION COMPLEXITY

At the time Futuyma and Moreno (1988) reviewed the evolution of ecological specialization, the dominant synecological paradigm was the study of pairwise interactions, with limited consideration of multispecies interactions with indirect effects. Since then, the development of evolutionary ecological theory (e.g., Schluter 2000, Strauss and Irwin 2004, Fussmann et al. 2007) and empirical evidence showing the importance of more complex interactions (e.g., Dyer and Letourneau 2003, Werner and Peacor 2003, Schmitz et al. 2004, Strauss and Irwin 2004) necessitates a reevaluation of how interaction complexity influences the evolution of ecological specialization (Poisot et al. 2011). Given recent developments, we argue that the indirect and combinatorial effects entailed in complex, multispecies interactions are likely to be paramount agents in the evolution of ecological specialization. A simple example of interactions affecting resource use and specialization is illustrated in Fig. 1. The herbivore (middle panel) is a host specialist, but is generalized with respect to an abiotic gradient. Assuming the plant (lower panel) is the optimal plant for the herbivore, the insect herbivore could be restricted (via interaction with the plant) to a narrow portion of the abiotic gradient (exactly which portion of the abiotic gradient could in turn be affected by interactions between the plant and competitors). This creates a situation in which the herbivore could adapt to the abiotic gradient that is optimal for the plant, becoming fundamentally specialized along both resource and abiotic axes. Thus interaction complexity increases the likelihood of facing ecological opportunities and trade-offs that spur specialization (Singer and Stireman 2005).

As discussed above, genetically based fitness trade-offs in physiological, morphological, and behavioral traits have received little support (Blows and Hoffmann 2005). This lack of support is at least partly a result of testing relatively simple systems that offer limited opportunities to observe fitness trade-offs (Rasman and Agrawal 2011). As one solution, Scheirs et al. (2005) argue compellingly for a more comprehensive account-

ing of fitness across life stages of phytophagous insects associated with different host plants. We further emphasize the likely importance of interaction complexity as a determinant of host-plant associated fitness, (e.g., tri-trophic niches; Singer and Stireman 2005, Fordyce and Nice 2008, Forister et al. 2011).

In such complex interactions, indirect effects on fitness may be important agents of selection in and of themselves, as seen in a pioneering study of complex pathways of selection for chemical defense of *Brassica nigra* plants, in which selection on sinigrin concentrations depended on the combinatorial effects of intra- and interspecific competition as well as herbivory from sap-feeding aphids and leaf-chewing mollusks (Lankau and Strauss 2008). In a notable example of host specificity based on complex, indirect interactions, Kaminski et al. (2010) show that facultatively myrmecophilous *Parrhasius polibetes* butterflies select and perform best on host plants occupied by myrmecophilous treehoppers due to enemy-free space provided by ants. Additionally, combinations of direct effects can generate fitness trade-offs favoring ecological specialization. Nosil, Sandoval, and colleagues analyzed the multidimensional process of selection for host-plant specialization in *Timema* stick insects as it relates to host-associated divergence and ecological speciation (e.g., Sandoval and Nosil 2005). In this system, predation from visual predators coupled with host-plant quality generate stronger divergent selection for host specialization than selection from predation alone, indicating complex causes of ecological specialization.

MACROEVOLUTIONARY CONSEQUENCES OF ECOLOGICAL SPECIALIZATION

Because ecological specialization limits the breadth of resources an organism relies on and potentially results in increased isolation among populations, it is expected to have macroevolutionary consequences for lineage diversification. There has been much theoretical and empirical examination of these consequences (e.g., Futuyma 2001, Winkler and Mitter 2008, Colles et al. 2009), yet little consensus has emerged due to the quandary that specialization can serve as a catalyst, spurring rapid and extensive diversification and, conversely, it may doom lineages to extinction. One way that specialization can facilitate diversification is by allowing the division of resources into more discrete niches, effectively providing ecological opportunities that lineages can evolve to exploit (Schluter 2000, Funk et al. 2002, Gavrillets and Losos 2009). Tropical cucurbit vines may host dozens of specialized herbivorous fly species rather than a single generalist species (Condon 2008). Clearly, a world of specialists has the potential to be far more diverse than one of polyphages. The ecological isolation that specialization confers can also directly facilitate species divergence by encouraging population subdivision and restricting gene flow (Price 1980, Berlocher and Feder 2002, Rundle and Nosil 2005, Funk et al. 2006). Thus,

ecological specialization is central to models of adaptive radiation (Schluter 2000), which may underlie much of the generation of life's diversity (Simpson 1953, Glor 2010).

As an alternative hypothesis, specialization may also incur a macroevolutionary cost; it should reduce genetic variation in populations due to selection for more efficient resource use, compromising their ability to adapt to changing environmental conditions and leaving them at the mercy of resource fluctuations (i.e., the "dead end" argument; Simpson 1944, Moran 1988, McKinney 1997, Biesmeijer et al. 2006, Colles et al. 2009). Furthermore, specialization often results in limited population size or restricted geographic range, which should exacerbate loss of genetic variation and increase susceptibility to extinction (Colles et al. 2009). Indeed, both paleontological and neontological studies indicate that specialists are more vulnerable to extinction (McKinney 1997, Smith and Jeffery 1998, Labandeira et al. 2002).

Futuyma and Moreno (1988) identified two fundamental questions concerning specialization and macroevolution: (1) Does specialization influence rates of diversification and extinction? and (2) Are there differential rates of evolution between generalist and specialist states? The importance of specialization in diversification is suggested by the finding that phytophagous insects are more diverse than their relatively generalized, non-herbivorous sister clades (Mitter et al. 1988), and by the strong association that exists between host shifts and speciation in many herbivorous insect groups (Winkler and Mitter 2008, Winkler et al. 2009, Fordyce 2010a). However, these studies do not assess the influence of specialization per se on diversification, and few studies have addressed this issue directly. Winkler and Mitter (2008) used simple comparisons of clade richness to address the prediction that specialization leads to increased diversification, but did not find evidence for the expected importance of specialization.

With respect to differential rates of evolution between generalist and specialist states, two related processes may be expected to produce an apparent bias in transition rates from generalists to specialists on phylogenies: (1) If specialized taxa lose genetic variation to use alternative hosts, they may be constrained to give rise to only additional specialized lineages; and (2) if specialized lineages are more likely to face extinction relative to more eurytopic taxa, they will tend to be found at the ends of shallow branches on phylogenies (Futuyma and Moreno 1988, Kelley and Farrell 1998). Some studies have indeed found evidence for a bias toward transitions from generalists to specialists, suggesting a constraining effect of specialization (e.g., Kelley and Farrell 1998, Crespi and Sandoval 2000). However, this is by no means the rule (e.g., Janz et al. 2001, Morse and Farrell 2005, Colles et al. 2009), and most analyses suggest that host range is labile; specialists evolve from generalists and vice versa (Schluter 2000, Nosil 2005, Stireman 2005, Winkler and Mitter 2008).

Regardless, these results must be taken as tentative, due to biases in ancestral state reconstruction (Nosil and Mooers 2005, Stireman 2005).

One reconciliation of the opposing macroevolutionary consequences of specialization is found in the Oscillation Hypothesis of Janz and Nylin (2008, Janz et al. 2006). This hypothesis posits that lineages undergo repeated cycles of transient host range expansion and subsequent contraction. A key feature is that specialized lineages retain plasticity in host use, and thus avoid evolutionary cul-de-sacs. Although it is difficult to effectively test, some studies of phytophagous insects have found results consistent with the Oscillation Hypothesis (e.g., Janz et al. 2006, Nylin and Janz 2009, Jahner et al. 2011, Slove and Janz 2011) and its applicability to other taxa is being explored (Hoberg and Brooks 2008, Agosta et al. 2010). Similar models have been proposed that focus on the dependency of speciation modes on the "tolerance" of lineages to different resources and resource heterogeneity (Nyman 2010). Support for the Oscillation Hypothesis tends to focus on relatively young, actively radiating lineages, and an open question is how long genetic variation permitting host expansion can persist in specialized lineages.

The increasing availability of phylogenetic reconstructions has spurred many tests of the dependence of diversification rates on traits, and a wide variety of methods have been developed to do so. Powerful statistical approaches have been developed (e.g., Paradis 2005, Ree 2005, Rabosky 2006) that expand our ability to test for effects of ecological specialization on diversification beyond sister group comparisons. Recently developed methods can test for effects of binary or continuous characters, can consider the influence that biased diversification has on character reconstruction, and can potentially allow variation in speciation rates to be distinguished from variation in extinction (e.g., Maddison et al. 2007, Paradis 2008, FitzJohn 2010; see Rabosky 2010 for challenges associated with estimating extinction rates). Many also tend to be time-explicit, examining lineage accumulation to detect shifts in diversification rates (e.g., McKenna and Farrell 2006, Rabosky 2006, Fordyce 2010b). Hardy and Cook (2010) examined whether galling taxa (typically highly specialized) exhibit increased diversification relative to non-gallers using both sister group comparisons and maximum likelihood analysis of rate shifts. These authors found no consistent effect of galling and no indication that specialization was associated with diversification. With the current availability of data (phylogenies) and analytical tools, the time is ripe for further explicit analyses of the evolution of host range and macroevolutionary diversification.

CONCLUSIONS AND FUTURE DIRECTIONS

We have emphasized a framework for studying specialization that relies on focused investigations specific to particular traits and environments (Fig. 1)

rather than absolute categories of “specialist” and “generalist.” We have also stressed the value of understanding interactions, which is highlighted in a number of areas of future research that we outline next.

What is the distribution of specialization in natural communities?—The distribution of ecological specialization in assemblages or guilds (e.g., graded variation, bimodal distribution) has rarely been rigorously quantified in natural, diverse communities (but see Dyer et al. 2007, Novotny et al. 2010). Documenting these patterns and how they associate with other environmental variables would provide insight into the evolutionary processes driving ecological specialization. The distribution of ecological specialization can also be investigated with respect to key ecological dynamics; for example, as the diversity of consumer specialists increases, the effects of consumers on other trophic levels are increased (e.g., Sinclair et al. 2003).

How is specialization correlated across the different facets or traits of a particular organism?—One possibility is that host-specific insect herbivores will also have predictably narrow (and specialized) environmental tolerances, though this has not to our knowledge been tested (specialization is correlated across axes in the top panel of Fig. 1, but not in the middle panel). Whether specialized interactions of one type (e.g., trophic) are associated with specialization in other types (e.g., abiotic) is not only of basic interest, but may also help predict which species will be most sensitive to a shifting global climate (Yang and Rudolf 2010).

How does complexity of genetic architecture influence the evolution of ecological specialization?—The advent of genomic technologies promises to shed light on a number of issues including the following: Do complex epistatic interactions constrain the evolution of diet breadth? What role do gene duplications play in the evolution of novel traits associated with diet breadth (Demuth and Hahn 2009)? Will specialization associated with elevated loss-of-function mutations as reported from *Drosophila* be generalizable to other specialists (Whiteman and Pierce 2008)? An important unresolved issue related to genetic architecture involves conditions that favor the evolution of genetic, ecological specialization vs. generalism through plasticity (DeWitt et al. 1998). It has been suggested that environmental predictability is a key determinant of specialization vs. plasticity (Donaldson-Matasci et al. 2008), and herbivorous insects provide ready opportunities for examining this issue (Futuyma 1976).

How do generalist habits evolve?—The Oscillation Hypothesis has recently drawn attention to the possibility that lineages could alternate between generalist and specialist phases (Janz and Nylin 2008), which highlights how little we know about the process of niche expansion. For example, does a generalist habit evolve through the modification of existing genetic elements toward a generalized genotype or through the accumulation of independent genetic elements associated with

different resources? Trade-offs among fitness components across resources or through time (e.g., among seasons or generations) could generate equal fitness, on average, across resources, favoring the use of multiple resources by ecological generalists. If the variance in fitness within resources is greater than the variance in fitness across resources (e.g., host plants), resource generalization is favored (Michaud 1990). Thorough tests of this hypothesis are currently lacking, and more mechanistic studies are needed; however, it garners support from scattered evidence of such trade-offs in a variety of study systems (reviewed in Singer 2008).

Why is specialization not a dead end?—Despite dire theoretical predictions, many empirical studies have found that specialization does not doom lineages to extinction and transitions to generalized habits may be frequent (e.g., Nosil 2005). Does intraspecific variability among hosts maintain genetic variation, allowing host expansions? Does a geographic mosaic of interactions maintain variation (Thompson 2005)? Or do truly host-specific populations face frequent extinction such that most “specialists” we observe are actually oligophages?

How do symbionts influence ecological specialization of their hosts?—The growing realization that symbionts are ubiquitous and influential implies that previous attempts to frame the problem of specialization might be missing this key component (Hyde and Soytong 2008, Janson et al. 2008). Aspects of specialization from genetic architecture to interaction complexity could all fall under the influence of viruses, bacteria, and fungi residing in hosts (Rudgers et al. 2009, Gibson and Hunter 2010, Vogel and Moran 2011).

How does the network structure of species interactions in a community affect the distribution and evolution of specialists and generalists?—Recent advances in systems biology have provided the tools for visualizing multitrophic connections among large suites of species (Poulin 2010). Among the patterns revealed is a nestedness of interactions, such that more specialized species tend to interact with sets of more generalized species (Bascompte and Stouffer 2009). Is this pattern of nestedness common across various environmental gradients and community types? Ultimately, profitable theoretical links may be made between network structure in communities and epistatic networks of gene interactions (Tyler et al. 2009).

What is the role of epigenetic effects in specialization?—Epigenetic effects, including methylation and transposable elements, clearly have the potential to influence diet breadth and environmental sensitivity across generations (Adams et al. 2003, Johannes et al. 2008). In model vertebrate species, the mother’s diet, for example, influences gene regulation in offspring (e.g., Lillycrop et al. 2008). Though maternal effects on host use have been examined (e.g., Fox 2006), most epigenetic dynamics have yet to be considered in insect–plant systems within the context of specialization (Bossdorf et al. 2008, Richards et al. 2010).

What are the community consequences of ecological specialization?—Potential consequences of specialization are broad and beyond the scope of the present discussion, but in closing we note a few possibilities as a fecund area for research. For example, there is the role of specialist herbivores in maintaining plant diversity (the Janzen-Connell hypothesis; Janzen 1970, Connell 1971, Carson et al. 2008), and the hypothesis that natural enemies are most effective at regulating herbivores in communities or periods of time when specialists are the most damaging consumers (Whittaker and Feeny 1971, Cornell and Hawkins 2003, Dyer et al. 2004). Increased levels of specialization in insect herbivores also appear to select for chemical dissimilarity or divergence in plant communities (Becerra 2007). At the macroevolutionary scale, specialization might not only elevate rates of diversification in herbivores as discussed above, but might also lead to patterns of congruent history across trophic levels (Ehrlich and Raven 1964, Janz 2011).

Substantial progress in understanding the evolution of ecological specialization has been made in recent decades, and, as has often happened in the history of ecology, we have found that the simplest conceptual and quantitative models are insufficient. The way forward involves an integration of a more realistic genomic framework, a better understanding of complex selective forces, and consideration of interplay between genotype and phenotype and between ecological and evolutionary processes.

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