
Phylogenetic methodologies for studying specialization

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Although the concept of specialization has played a central role in the development of ecological and evolutionary theory, important questions about specialization remain largely unanswered. We argue that the traditional division of specialization into evolutionary and ecological factors may be less useful than considering specialization as three components, which may not be mutually exclusive: ecological, behavioral, and functional. Many ecologists assume that these different aspects of specialization are necessarily correlated. However, this assumption has rarely been tested, but could be examined by using a phylogenetic approach. We argue that (1) ecologists should measure these different aspects of specialization within their respective organisms by placing measures of specialization on a standardized scale, and (2) should employ phylogenetic approaches for understanding how these components evolve. We argue that this approach will provide a more coordinated understanding of how specialization evolves.

The concept of specialization has played a key role in the development of ecology and evolutionary biology (Futuyma and Moreno 1988, Schluter 2000, Ferry-Graham et al. 2002). Most concepts of specialization address two questions. First, do individuals in a population display phenotypic or behavioral plasticity for matching the environment (generalists), or do individuals use a subset of available resources or habitats (specialists)? Second, does specialization for a particular habitat or resource always involve a tradeoff in terms of the effectiveness of using other habitats or resources? The concept of specialization is closely allied to the concept of adaptation and biologists sometimes interpret a high degree of adaptation as strong evidence for specialization, but in some cases, authors have shown that specialization and adaptation may not always be equated. For example, cichlid fishes display a variety of morphological and behavioral adaptations for feeding and these adaptations are often interpreted as evidence of specialization for feeding on different prey, but some cichlid species are generalized feeders and prefer available prey for which they are not specialized (Aigner 2001).

We contend that the traditional division of specialization into evolutionary and ecological factors may be less

useful than considering specialization as three components, which may not be mutually exclusive: ecological, behavioral, and functional. Many ecologists might argue that these different aspects of specialization are necessarily correlated, but this assumption has rarely been tested and could be examined by using a phylogenetic approach. In this paper, we argue that (1) ecologists should attempt to measure these different aspects of specialization within their respective organisms, and (2) should employ phylogenetic approaches for understanding how these components evolve. Our focus is on understanding the broad evolutionary scope of specialization at the population or species level of organization (see Bolnick et al. 2002, 2003 for a review of the topic of individual specialization).

Definitions of specialization

Diverse definitions of specialization litter the biological literature, but they typically cluster into two groups, ecological and evolutionary (Futuyma and Moreno 1988, Sherry 1990, but see Ferry-Graham et al. 2002). Ecologists have typically defined a specialist as a species that occupies a relatively narrow niche or restricted range of habitats, or alternatively a species or population that selects resources out of proportion to availability. A second, evolutionary, definition of specialization focuses on how genetic constraints affect character evolution, potentially resulting in tradeoffs among populations or species with respect to the effectiveness of accomplishing few versus many tasks (Huey and Hertz 1984). Rather than arguing the merits of ecological versus evolutionary specialization, we suggest that specialization can be more profitably decomposed into three components, which may not be mutually exclusive: ecological, behavioral, and functional. We do not suggest that these three aspects are distinct from the more traditional above-mentioned evolutionary and ecological aspects. Rather, our division contains many of the above ideas,

but rather places them in a framework in which one can profitably examine evolutionary relationships among aspects of specialization. We therefore propose that studying each of these aspects in conjunction with the phylogenetic context will shed new insights on specialization because evolution in one component (e.g. ecological specialization) may not follow evolution in another component (e.g. behavioral). This goal is achievable, since analytical and technological tools are now available for quantifying all these aspects of specialization.

Ecological specialization

Species vary in their habitat and resource requirements. Hypotheses about the physical, chemical, and biological factors that restrict different species were formalized by Hutchinson's (1957, 1957) n-dimensional niche. Numerous studies have examined how niche volume changes in response to myriad factors (e.g. number of species in a community, body size). Ecological specialization is an individual, population and community parameter that is characterized by a restricted niche volume, and its prevalence will affect other parameters, such as competition and species richness. We largely agree with this definition, but we disagree that one should always apply niche-based ecological concepts towards understanding ecological specialization. While it is tempting to measure ecological specialization only in the context of niche breadth, which is the range of resource types (e.g. numbers of plant species – or genera or families – used by an herbivore) or habitat types, these measures may be meaningless to the species involved. To understand ecological specialization, a simple list of food or prey types is insufficient (Fox and Morrow 1981, Sherry 1990); it is critical to examine the distribution and predictability of resources from the perspective of consumers, along with associated behavioral and performance parameters that help one interpret the distinctiveness and relative importance of resources.

Behavioral specialization

Animals exhibit a range of behaviors to accomplish particular generalized tasks, such as feeding, mating, or escape from predators. We define behavioral specialization as a restricted range of distinct behaviors used for such generalized tasks (Ferry-Graham et al. 2002). Our definition is broad, and assumes that morphological adaptations are necessarily linked to behavior. The importance of incorporating behavioral specialization is that behavior can act as a filter between morphology and performance, resulting in complex relationships between the two (Irschick and Garland 2001). Thus, any complete understanding of specialization must take

into account the extent to which behaviors are constrained by morphology. Prior studies have shown some evidence for a tradeoff between the ability to perform many tasks well, and the ability to perform any one task well (Bernays et al. 2000, Via and Hawthorne 2002), although exceptions exist (Huey and Hertz 1984). Regardless of an organism's effectiveness at performing any task, the available resources or the milieu of enemies and competitors can be more important in determining its degree of behavioral specialization.

Functional specialization

An under-appreciated aspect of specialization is how efficiently a species performs a particular task that is critical to fitness (functional specialization; Ferry-Graham et al. 2002). A recent synthesis (Ferry-Graham et al. 2002) provided detailed examples of functional specialization by focusing on feeding in fish (although their approach is widely applicable). We adopt their definition of a "functional specialist" as being "a species whose morphology (or physiology) constrains it to a subset of available resources" (Table 1 in Ferry-Graham et al. 2002). In other words, functional specialists are taxa that can perform only a few tasks effectively, whereas generalists can perform a variety of tasks effectively enough to persist in their habitat (see also Irschick and Losos 1999 for an example with locomotion in *Anolis* lizards). This notion of a functional specialist has most frequently been tested in studies of temperature and its effects on performance (Huey and Hertz 1984) and studies of plant chemistry and its effects on feeding efficiency (Bernays et al. 2000). However, few studies have explicitly related functional specialization to either behavioral or ecological specialization, particularly in a phylogenetic context (Ferry-Graham et al. 2002). Indeed, many ecologists have assumed that functional specialization will necessarily be correlated with ecological or behavioral specialization, but this assumption is not always borne out (Fox and Morrow 1981, Camara 1997). For example, some biologists have shown that enhanced performance can evolve independently of the ecological aspects of specialization (Lauder 1996, Lauder and Reilly 1996). Other studies have shown that insects can effectively metabolize plant chemicals from plants that they rarely use in nature (Fox and Morrow 1981).

Is a specialist always a specialist?

A critic of our framework might argue that each of the three kinds of specialization (ecological, behavioral, and functional) will necessarily be linked (Fig. 1), but we argue that few studies have tested this assumption.

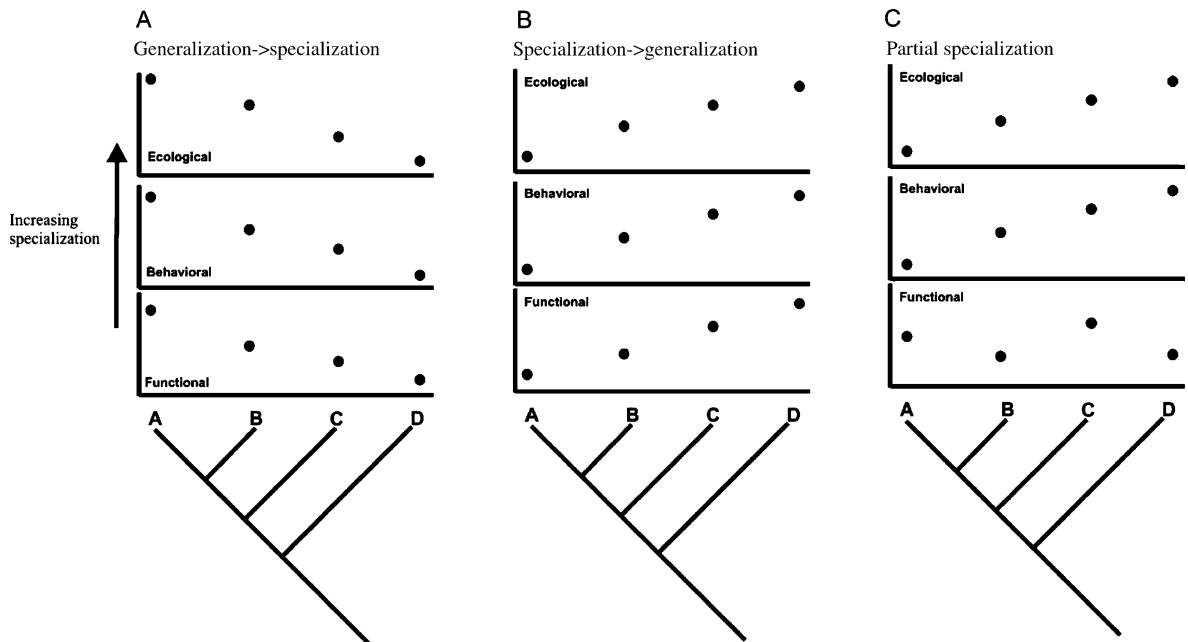


Fig. 1. Coevolution of specialization in two directions. In (A) there is an evolutionary trend for more derived species to be more specialized in all three aspects of specialization. In (B) the evolutionary trend is for more derived species to be more generalized. Note that the evolution of ecological, behavioral, and functional specialization is linked in both cases. (C) depicts “partial specialization” where the three aspects of specialization are not linked.

Indeed, we question whether ecological, behavioral, and functional specialization must necessarily evolve in parallel. Consider the theoretical example of a butterfly species that is a behavioral specialist because it has evolved to deposit eggs only on plants with a particular chemical oviposition cue; the cue is a plant defensive compound that decreases feeding effectiveness but is sequestered by the caterpillar as a defense against its enemies. This butterfly species is not an ecological specialist because specialized oviposition can still lead to a broad ecological niche if: 1) the chemical cues are the same on taxonomically and ecologically disparate plants, and 2) the larval stages can move to and consume other plants. In addition, the ability of the caterpillar to process the chemicals found on the host plant versus other plants (chemical processing performance) can be similar, suggesting that this species is also a functional generalist. Nevertheless, coevolutionary interactions between plant defenses that decrease caterpillar feeding efficiency and caterpillar sequestration that deters enemies could be responsible for the observed behavioral specialization (Dyer 1995). Selection on the plant may be directional towards metabolizing compounds that are difficult to sequester, and simultaneous selection on the caterpillar will result in physiological mechanisms that enhance sequestration and its defensive value. Classic laboratory and field rearing experiments designed to detect physiological tradeoffs (Camara 1997) would not

successfully detect negative genetic correlations in this case. Thus, chemical defenses could limit an herbivore’s diet breadth via behavioral specialization without accompanying functional specialization.

This example shows that one cannot assume that ecological, behavioral, and functional specialization will be positively correlated when comparing different species. However, if researchers were to simultaneously measure these three components in a variety of closely related plant-eating insect species, for example, one could examine evolutionary relationships among these components; below, we outline a procedure for such an analysis.

Phylogenetic approaches

The tremendous growth in molecular systematics and comparative methods has provided a new set of tools to examine ecological questions, but ecologists have too often ignored the power of these approaches for understanding specialization. One unresolved ecological question concerns whether specialization in one aspect (e.g. functional specialization) promotes or constrains the evolution of other kinds of specialization. Within this general concept emerge several hypotheses: (1) one kind of specialization precedes another evolutionarily, (2) specialization in one aspect constrains either the pre-

sence, or the direction of specialization in another aspect, (3) all three kinds of specialization will either evolve together or independently. These hypotheses can be tested profitably using a phylogenetic approach. A first step consists of establishing standardized scales of specialization for ecology, behavior and function within a comparative context. This objective will be challenging if species within a clade carry out distinct tasks (e.g. capture a prey type using speed versus stealth), which would pose a problem for defining levels of functional specialization. Thus, ecologists should focus their efforts on performance abilities that are likely to be important across different species. Thus, studies of specialization among species within a closely related group will be most informative, because of the ability to place all species on a common specialization scale. For instance, in granivorous birds (e.g. Darwin's finches, *Geospiza*, Grant 1986), one can ask whether pair-wise distances between species are distributed linearly on different axes – seed size and type (ecology), seed choice (behavior), and seed-husking efficiency (function).

A second step consists of examining whether specialization in one aspect (e.g. behavior) has evolved concordantly with another aspect of specialization (e.g. function) by using either comparative methods for examining correlations between traits, or ancestral reconstruction methods. At a first pass, one can ask whether all three aspects of specialization are significantly related (uniform specialization), or whether only one or two of the possible three relationships are statistically significant (Fig. 1). One could then use ancestral reconstruction techniques to examine whether evolution in one kind of specialization tends to precede or antecede another kind of specialization (Schluter 2000, Nosil 2002, Fig. 2). For example, one possible outcome would be a trend for specialists to evolve from generalists simultaneously in all three aspects of specialization (Fig. 1A), which would provide the most substantial evidence for a group of species being “highly” specialized. Research on Darwin's finches and cowbirds provides a sample of the utility of this approach. Phylogenetic analyses using microsatellite data suggest that the generalized Cocos finch was derived from a relatively specialized ancestor (a *Certhi-dea*-like warbler-finch; Petren et al. 1999). Similarly, within the clade of brood-parasitic cowbirds (*Molothrus*), more evolutionarily derived species tend to be more ecologically generalized in terms of using more host species (Lanyon 1992). The outlined methodology could also be used for answering other questions, such as: (1) does specialization affect speciation and diversity (Bolnick et al. 2003)? (2) Are some community interactions (i.e. herbivory, parasitism) more prone to specialization than others, and under what circumstances? For example, do herbivores show greater specialization for plant feeding versus defense against natural enemies?

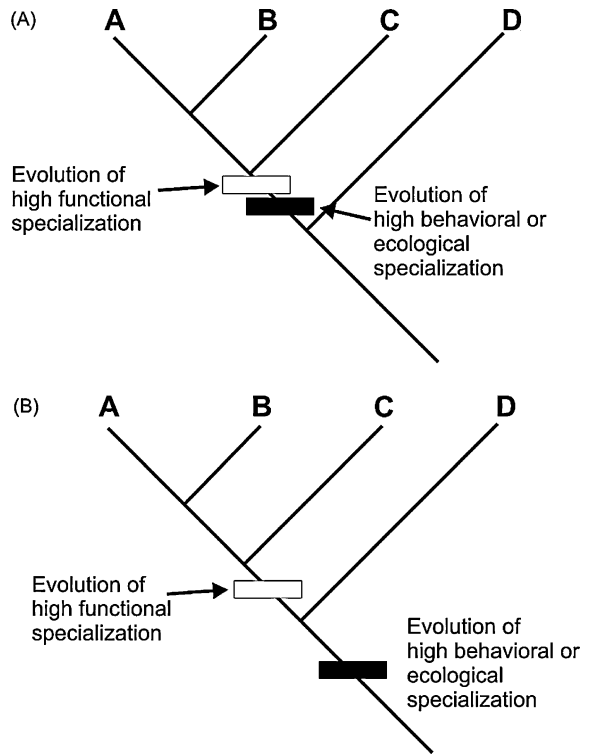


Fig. 2. Two (of many) possible outcomes for the evolutionary sequence of different kinds of specialization. (A) ecological, behavioral, and functional specialization all evolve simultaneously. (B) the evolution of ecological and behavioral specialization occurs simultaneously, but precedes the evolution of functional specialization.

(3) Do some community interactions exert greater effects on specialists than on generalists?

In conclusion, we argue that these, and other, important questions regarding specialization could be examined using the approach outlined above, or a variant of it. A potential critique of our approach here is that we have not provided any empirical examples of this approach. We have not provided empirical analyses for the primary reason that we are not aware of any studies that have examined specialization in these different components (particularly on a standardized scale that could be used in Fig. 1, for example), and/or have used phylogenetic approaches to study how these different components evolve. We suggest that future research in the general area of specialization should evaluate a priori how to measure multiple aspects (i.e. behavior, ecology, function) on various species within their clade of interest. This approach will also induce (perhaps even force!) ecologists into collaborations with functional biologists and evolutionary biologists.

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