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Editorial

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One contribution to a Special feature 'Evolution of specialization: insights from phylogenetic analysis'.

Evolutionary ecology of specialization: insights from phylogenetic analysis

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In this Special feature, we assemble studies that illustrate phylogenetic approaches to studying salient questions regarding the effect of specialization on lineage diversification. The studies use an array of techniques involving a wide-ranging collection of biological systems (plants, butterflies, fish and amphibians are all represented). Their results reveal that macroevolutionary examination of specialization provides insight into the patterns of trade-offs in specialized systems; in particular, the genetic mechanisms of trade-offs appear to extend to very different aspects of life history in different groups. In turn, because a species may be a specialist from one perspective and a generalist in others, these trade-offs influence whether we perceive specialization to have effects on the evolutionary success of a lineage when we examine specialization only along a single axis. Finally, how geographical range influences speciation and extinction of specialist lineages remains a question offering much potential for further insight.

1. Introduction

Specialization is a repeated pattern in living systems, suggesting that there are general mechanisms underlying its evolution. Clearly, every species interacts with only a small subset of all other species and in only a subset of habitats. Thus, some constraints on associations have simple explanations: biogeography and range limits preclude pairs of species, or a species and a particular suite of environmental variables, from being in the same vicinity. We do not currently have precise information on the extent to which range limits enforce the levels of specialization that we see in nature [1,2]. Despite this large knowledge gap, we have clear instances where species have access to many potential mutualists or habitats, yet have evolved adaptations that restrict their proportional usage [3,4]. The evolution of these adaptations may themselves directly affect the speciation process [5] or simply be associated with macroevolutionary and macroecological patterns (e.g. diversification through correlated characters or reduced geographical extent [6]). This Special feature serves to highlight our current knowledge of how evolution has produced clades and communities notable in their variation in the level of specialization, despite a paucity of well-characterized pathways that might produce such variation [7]. We focus especially on studies that employ a macroevolutionary perspective to investigate (i) the evolutionary success of specialists and (ii) how specialization is shaped by variation along multiple morphological and environmental axes.

(a) The evolution of specialization

Is specialization a dead-end? A once-held view was that the evolution of specialization was a one-way street, with transitions back to a broader niche breadth being restricted [8]. Recently, however, a growing number of studies of specialization indicate that transitions from specialization to generalization are possible [9,10]. However, examinations of transitions in a phylogenetic context sometimes provide conflicting results. In birds, transitions in the level of specialization are rare [11]. Yet in plants, there are many examples of reversals in specialization

[12]; for example, pollinator breadth exhibits little phylogenetic signal [13]. Phytophagous insects also exhibit equivocal results with transitions occurring in either direction [14,15]. Thus, evidence is mounting that specialization is not an absolute 'dead-end', even though a disproportionate number of transitions may be in the direction of generalist to specialist in some systems. However, the conditions and processes that lead to biases in transition rates in one direction or the other remain poorly understood.

The envisioned pathway that would produce biased transitions from generalization to specialization involves the idea of trade-offs, which however have proved elusive to demonstrate empirically. The trade-offs might operate at the physiological level through antagonistic pleiotropy [16]. For instance, C4 plant photosynthetic pathways have greater efficiency in hot, dry environments, but lower photosynthetic rates in shaded, moist environments [17]. Ecology could enhance the evolution of specialization through producing further genetic trade-offs. If a certain environment were more common (e.g. dry environments in the above example), deleterious mutations that affect the performance in other environments might accumulate [18]. If these changes represented loss-of-function mutations, reversals towards a generalist state would be rare. Whether physiological or genetic trade-offs occur in tandem or independently is not well characterized, nor is there much compelling evidence of irreversibility [12].

Notably, the difficulty of defining and detecting specialization hampers our ability to pinpoint its pathways and trade-offs. In the evolution of specialization of plants on pollinators, for example, steep trade-offs (where adaptations improving the attraction or use of one pollinator decrease the attraction or use of others) will generally favour specialization [19]. Studies on plant–pollinator specialization, in particular, have provided many examples showing how caution must be exercised in inferring fitness trade-offs from morphological traits ('phenotypic specialization', e.g. long corolla tubes [20]). Classically, floral corolla tubes were one trait conceived as an appropriate indicator of reduction in biotic partnerships (narrow corolla tubes suggesting efficient pollination by hummingbirds and poor pollination by bees and vice versa for wide corolla tubes [21]). Many cases of apparent specialization on certain functional groups of pollinators have been observed to be, in fact, ecologically generalized (e.g. flowers with wide corollas are visited by insect and birds [22–24]).

Characterization of trade-offs is further complicated because they can occur at different scales and involve different aspects of a species' biology [25] (see *Axes of specialization*). This complexity has led to the somewhat perplexing view that trade-offs are uncommon, at least in within-species comparisons [25]. Intriguingly, the elusive nature of trade-offs spurred investigation of whether they were an essential condition—a theoretical study by Muchhala *et al.* [26] demonstrated that the selective cost of lost pollen alone is sufficient to drive specialization even in the absence of trade-offs. To date, there have been few phylogenetic comparisons, yet analyses of host–pathogen and plant–pollinator associations suggest that the ability to incorporate a certain plant species into diet breadth is correlated with phylogenetic distance [27–29]. This suggests that specialization on clades of hosts or mutualists is widespread and that the use of certain hosts is indeed lost over evolutionary timescales. Notably, this pattern is not only consistent with trade-offs, but also consistent with ecological models of the loss of selection for interacting with hosts or mutualists that are outside of a species' range.

From a macroecological perspective, there is one additional reason to expect the appearance of dead-ends with transitions to the specialist state [6]. If specialists occupy a narrow niche, they often also occupy smaller ranges [1], and endemics are more susceptible to extinction [6,30]. While some data suggest that the evolution of specialization is associated with evolutionary success in plants [31], habitat specialization is correlated with increased extinction risk in birds and bumblebees [32,33]. If specialists go extinct more frequently, most specialists will appear as young lineages on phylogenetic trees [34] that have had less opportunity to transition to a generalist state [10]. Species occupying a smaller range can also be less likely to speciate [35,36]. Both of these processes would produce a pattern whereby there are more extant generalist lineages, each with the potential to transition to a more specialized state. Yet there are examples that show empirical support for the opposite as well, with generalists exhibiting higher extinction risk, at least in Odonata [37].

In this volume, we examine how 'evolutionary success' in terms of speciation and extinction rates varies with specialization and document transitions between specialization and generalization. Specialization and generalization in the diversification of lepidopterans were examined for evidence of the musical chairs versus the oscillation hypotheses [38]. Following a 'musical chairs' model we might see that specialist clades were more often transitioning between hosts, but remaining specialized, whereas in the 'oscillation' model we would predict that niche-breadth shifts (e.g. in phytophagy in lepidopteran clades) from generalist to specialist would be more common. Rather than a pattern of unidirectional shifts to specialization in lepidopteran clades, Hardy and Otto find more support for the musical chairs hypothesis [38]. In addition, they find a negative relationship between host-plant breadth and diversification rates, with generalists diversifying at lower rates because of their broad niches. This calls into question whether specialization can ever be considered a dead-end, at least in phytophagous insects. While transitions to a more generalist state might be rare, host switching within specialist clades is common and generates more species that are specialized, such that lowered diversification rates will not be apparent. These patterns held despite the finding that extinction rates were considerably lower in polyphagous lineages, suggesting that specialists could potentially appear as evolutionary dead-ends due to declines in persistence, but not due to trade-offs that prevent transitions back to a more generalized state.

The musical chairs hypothesis may be clade-specific, as other patterns have been seen in some plant–pollinator relationships. The shift from a specialized relationship (e.g. pollination by few resin-collecting bees) to a generalized relationship (e.g. pollination by many pollen-feeding insects) can be followed quickly by a reversal to a more specialized relationship (e.g. pollination only by 'buzz-pollinating' bees) [39]. This last example is consistent with the oscillation hypothesis, which postulates that generalist lineages give rise to specialist daughter species, but over time specialists can gradually add functions and become more generalist. Similarly, in an analysis of pollinator breadth in passionflowers, Abrahamczyk *et al.* [40] find that shifts are not disproportionately from generalization to specialization. Instead, reliance on the sword-bill hummingbird (*Ensifera ensifera*) appears to have evolved early on in a clade that then generated many new species by allopatric isolation, some of which escaped from specialization by reducing their floral tubes, thereby

being able to rely on a broader set of bird or bat pollinators. In contrast to the idea that shifts in specialization result in speciation (pollinator shifts), Abrahamczyk *et al.* [40] find more evidence favouring biogeographical shifts spurring the process of lineage splitting. In *Tritoniopsis revoluta* (Iridaceae) Anderson *et al.* [41] report that pollinators vary geographically across the plant's range and are closely associated with variation in floral traits, suggesting a strong role of distribution and range in how biotic specialization influences speciation (see Range extent, specialization, and diversification).

In summary, the studies in this Special Feature indicate that specialization is not a certain 'dead-end' from an evolutionary perspective. First, transition from specialization to generalization is possible and even prevalent in certain ecological contexts. Second, specialization in traits related to foraging or reproduction can be associated with increased evolutionary success of some specialist clades, especially in specialist clades that experience greater transition rates to different specialist states ('musical chairs' pattern described above [38]). Specialization also need not by itself be the driver of speciation. In the sword-bill-pollinated clade of passionflowers, Abrahamczyk *et al.* [40] find that specialized pollination is not the driver of speciation but instead the precondition for successful species persistence in small populations, which then adapt locally and evolve into separate species.

Hardy & Otto [38] raise the interesting point that the question of whether specialization influences speciation depends on how specialization is defined: 'One grey area is how to define the relevant niche with respect to diversification, as generalists along some axes (e.g. resource use) may be specialists along others (e.g. in host-pathogen interactions). While theoretical models have shown that speciation is more likely when phenotypes are multi-dimensional... this raises a challenge for empiricists who must identify the phenotypic axes exhibiting the strongest diversifying selection in order to detect relationships between niche breadth and speciation'. Other authors in this Special Feature also tackle the issue of multi-dimensional axes of specialization.

(b) The axes of specialization

Specialization can be defined in a number of ways, and there are many ways to expand the 'Jack of all trades, master of none' paradigm. One way to define specialization is the breadth occupied by a species on niche axes. Most species probably are a generalist on some axes and a specialist on others [16]. For example, some species of *Dalechampia* (Euphorbiaceae) exhibit apparently compensatory specialization/generalization on two pollination niches axes: specialization on the temporal axis (shorter duration of blooming season) is associated with generalization in the number of pollinator species used and vice versa [42]. A growing body of evidence suggests that, while physiological trade-offs are uncommon, constraints may act to allow for specialization along alternate facets of a species' life history, e.g. where an advantage with one biotic partner or in inhabiting one niche comes at the expense of dealing with another [43–45]. Limits on floral specialization may also accrue from conflicting selection generated by herbivores or by abiotic factors. For example, specialization on large bees may select for large petals or bracts, but this may be countered by selection by herbivores (that use the same cues to find host tissues) [46], selection for water conservation in xeric environments [47,48] or selection for rapid seed production in seasonal habitats [49–51].

Expanding the number of axes to include both biotic and abiotic specialization can also provide insight into the underlying forces that spur the evolution of specialization. For example, pollinators often select for larger corolla size, but such increases exert a large cost in terms of water loss in dry environments [47,48,50], as noted above. Without information on the physical-environmental niche, it would be hard to ascertain why more species do not display large flowers. Examining these trade-offs in a phylogenetic framework can be a powerful approach to understanding the constraints on the evolution of specialization. Litsios *et al.* [52] provide evidence in this Special Feature of a negative correlation between environmental tolerances (in temperature, salinity and pH) and host specificities in clownfish and anemone mutualisms, which would likely confound phylogenetic analyses of diversification along any single specialization niche axis. Further, if differential specialization across resource axes is widespread, it may be a large contributor to the local coexistence of specialist and generalist species [52], and provide insight into the puzzling observation that specialists often do not outcompete generalists [53].

Despite finding that multiple axes contribute to specialization and interact to influence its evolution [16], we have little information on whether abiotic or biotic factors are more likely to drive specialization, or whether dispersal and geographical range provide environmental heterogeneity to spur initial transitions to specialization. Muschick *et al.* [54] examine these questions in this volume using the radiation of cichlids in Lake Tanganyika, testing the idea that specialization along multiple niche axes occurs according to a common sequence of transitions. In these cichlids, subdivision of trophic traits occurs in the early stages of adaptive radiation, while sexual communication traits diversify late in the radiation. The phylogenetic analysis of Muschick *et al.* [54] also provides limited support that specialization along biotic niche axes (diet) precedes specialization along abiotic niche axes (macrohabitat).

(c) Range extent, specialization, and diversification

Environmental heterogeneity is a key factor both in the evolution of specialization and in the evolutionary success of the resulting lineage [7]. For example, if spatial heterogeneity is such that the abundance of a commonly used host changes rapidly over space (beta-diversity is high), this should accelerate the evolution of specialization [41]. Much of the work in this area is done with herbivorous insects, with some studies suggesting that generalization is positively associated with large range size [55] and others finding cases where a specialist can have a much larger range if its host species is widespread [56]. Models of the evolution of specialization that incorporate environmental heterogeneity and associative mating indicate that these variables can result in a decrease in gene flow between environments and contribute to speciation [7]. Anderson *et al.* [41] examined pollinators in different parts of a plant species' range and found a close association between floral traits and the traits of the pollinators in the region but did not find strong evidence that these patterns greatly influenced gene flow and dispersal. Presumably, if selection pressures were consistent for generations, speciation could occur, yet pollinators may be too variable between years [57]. Further work on the interplay between dispersal, range, and beta-diversity would lend insight into how specialization evolves and persists as well as the propensity of these factors to lead to speciation.

Widely dispersing organisms are more likely to have opportunities to expand their geographical range [58]. Species occupying large ranges should experience divergent selection pressures upon their constituent populations; heterogeneity of selection pressures may in turn provide selection towards generalization across the entire species (leading to its scoring as a generalist in a phylogenetic trait reconstruction that might use just one accession to represent the species), but selection for different specialists at the local population level. Bonetti & Wiens [59] find evidence in amphibians, however, that the causal arrow could point in the opposite direction, with species with wide climatic tolerances (e.g. generalists along a climate niche) having the ability to persist in a greater number of locations and thus be exposed to a greater number of conditions in another niche axis. Range size could then influence the heterogeneity in selection pressures from biotic partnerships, allowing specialization to evolve in other niche axes. Bonetti & Wiens [59] find trait associations consistent with these expectations, with species having broad tolerances for variation in temperature and precipitation rather than trade-offs in these tolerances. For example, specialization along the climatic niche can reduce range size and set-up conditions conducive to the evolution of specialization along other niche dimensions. Thus, we can also observe positive associations in the levels of specialization between different axes of specialization rather than trade-offs.

(d) Conclusions and future directions

Forister *et al.* [60] list a number of interesting unanswered questions in the evolutionary ecology of specialization. While they concentrated on plant–insect associations, we attempt here to examine the process in a range of invertebrate and vertebrate systems (butterflies, bees, hummingbirds, amphibians, fish lineages). The problem of how to define specialization remains. Generally, our view of trade-offs appears to be widening, and this broadened perspective has the consequence of making trade-offs more readily apparent. Whether or not trade-offs are observed depends on how widely we cast the net; trade-offs do appear to be an important characteristic of specialization if we allow that they may operate between very disparate facets of a species' life history (e.g. pollination and herbivory). Furthermore, the issue of dispersal and range size presents further complicating factors, influencing the number and combinations of conditions encountered (and therefore the trade-offs observed). Recent studies indicate that the association between range size and niche breadth may vary in its strength depending on niche position as well as the axes of the niche (dietary or habitat) examined [61], suggesting that the complexity of these factors will provide an active area of research for some time.

From a conservation perspective, specialists are some of our most charismatic species, with the sword-billed hummingbird and the *ca* 50 species of plants that completely depend on it for pollination being a striking example. Thus, specialist species often receive greater conservation attention than do generalists [62]. Although there is evidence that specialists can exhibit

superior competitive strategies in their element (for foraging and/or reproductive assurance) [63], there is also evidence that their greater reliance on a smaller subset of species puts them at greater risk of extinction [64]. From a macroevolutionary perspective, specialist clades may play a particularly important role in generating additional species at high rates due to host switching (the musical chairs process; see [38]), and this process would tend to make many specialist species appear 'young' on phylogenies. With the current conservation focus on the phylogenetic uniqueness of a given species [66], one implication is that the 'young' nature of many specialists may put them at lower prioritization for conservation. Additionally, while there is little evidence to suggest that specialization is irreversible or associated with lower speciation rates, specialist clades can experience higher extinction rates. Elevated speciation rates may buffer specialist clades from being lost to extinction to a certain extent [67], but further research should examine which specialist clades may be at the limits of the compensatory effects of speciation and experiencing net declines in species richness.

Network studies are providing some valuable insight into how specialization varies among communities. However, while connectance (the number of links between trophic levels compared to the maximum possible) is often equated with stability, loss of specialists will appear as increased connectance in networks [68]. Additionally, gain of a high proportion of weedy generalist species in numerous communities will result in lowered beta-diversity and more homogeneous community composition over larger spatial scales [69]. While these two outcomes would suggest that we lose biodiversity despite increasing stability in networks, there are at least two reasons to suggest that specialists may be as robust as generalists to environmental perturbations. First, specialist species often rely on generalist partners (i.e. networks tend to be asymmetrical and nested) [70,71]. Second, as exemplified in clownfish in this Special Feature, generalist–specialist trade-offs across multiple resource axes will act as a buffering force, such that specialists in bipartite networks may be habitat generalists, thus providing a further balancing mechanism that allows for coexistence of species [52]. Recent studies have incorporated macroevolutionary and phylogenetic approaches into network studies to reveal the influence of shared traits on forming network interactions [28,64], and the new metrics currently emerging [72] will likely further provide an important link between the influences of evolutionary history, traits, and environmental heterogeneity.

In summary, specialists can experience greater evolutionary success compared to their generalist counterparts, possibly due to the very trade-offs that often drive specialization. In cases where we observe specialization along a number of different niche axes, historical range size may provide insight into how suites of specialized traits arise in lineages. Some of these insights would be impossible to gain without using a macroevolutionary perspective, and the studies in this issue highlight how comparative phylogenetic analysis sheds light on general principles underlying the evolution and persistence of specialized interactions.

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