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Bridging the Process-Pattern Divide to Understand the Origins and Early Stages of Adaptive Radiation: A Review of Approaches With Insights From Studies of *Anolis* Lizards

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Abstract

Understanding the origins and early stages of diversification is one of the most elusive tasks in adaptive radiation research. Classical approaches, which aim to infer past processes from present-day patterns of biological diversity, are fraught with difficulties and assumptions. An alternative approach has been to study young clades of relatively few species, which may represent the putative early stages of adaptive radiation. However, it is difficult to predict whether those groups will ever reach the ecological and morphological disparity observed in the sorts of clades usually referred to as adaptive radiations, thereby making their utility in informing the early stages of such radiations uncertain. Caribbean *Anolis* lizards are a textbook example of an adaptive radiation; anoles have diversified independently on each of the 4 islands in the Greater Antilles, producing replicated radiations of phenotypically diverse species. However, the underlying processes that drove these radiations occurred 30–65 million years ago and so are unobservable, rendering major questions about how these radiations came to be difficult to tackle. What did the ancestral species of the anole radiation look like? How did new species arise? What processes drove adaptive diversification? Here, we review what we have learned about the cryptic early stages of adaptive radiation from studies of *Anolis* lizards, and how these studies have attempted to bridge the process-pattern divide of adaptive radiation research. Despite decades of research, however, fundamental questions linking eco-evolutionary processes to macroevolutionary patterns in anoles remain difficult to answer.

Subject areas: Molecular systematics and phylogenetics
Keywords: adaptive radiation, *Anolis*, determinism, convergence, diversification

It has long been recognized that the process of adaptive radiation, diversification from an ancestral species into many ecologically and morphologically different forms, may be responsible for much of the Earth's biological diversity (Givnish and Sytsma 2000; Schluter 2000; Glor 2010). Although such groups can be found across space, time, and taxa (Gillespie et al. 2019; this issue), all adaptive radiations are characterized by 2 key features: speciation and phenotypic diversification. The proliferation of species and adaptation to different niches has long considered to be the outcome of divergent natural selection driven by resource specialization, ecological interactions between members of the radiating clade, and environmental adaptation (Schluter 2000). Ideally, adaptive radiation can be studied by examining a gradient of stages, from observing an ancestral phenotype through to communities of closely related and ecologically diverse species. However, for the most part, such gradients do not exist, and much of what we understand about how adaptive radiations evolve is inferred from patterns of present-day phenotypes considered in the context of their phylogenetic relationships.

As is common across much of evolutionary biology, the study of adaptive radiation is, therefore, tantamount to assembling a puzzle without having all the pieces. A general picture may be inferred by making assumptions about the pieces which are missing, but these assumptions come with uncertainty. For many radiations, the processes which drove diversification happened many millions of years ago and thus cannot be directly observed, leaving fundamental questions about adaptive radiations without robust answers: How do radiations arise? Where do new species come from? What processes lead to divergence? The elusive early stages of adaptive radiation encompass many topics which are notoriously difficult to study. Here, we discuss the limitations of different approaches to the study of the early stages of adaptive radiation, and review how research on *Anolis* lizards has attempted to bridge the divide linking eco-evolutionary processes with macroevolutionary patterns.

Studying Process Versus Pattern in Adaptive Radiations

Adaptive radiations have been typically studied using two approaches. Classically, one may observe an established radiation and draw inferences about the past processes which led to the present-day pattern of ecological and phenotypic diversity, informed by understanding of the phylogenetic relationships among species. Alternatively, one may identify and study the evolutionary processes operating on a clade of relatively few species (or forms), which may be currently diverging, with the assumption that the clade is representative of the early stages of a forthcoming adaptive radiation. These two approaches represent either end of the process-pattern divide in adaptive radiation research (Figure 1).

Many researchers have taken the latter approach, focusing on young, species-poor groups as model systems enlightening the processes thought to drive adaptive diversification. Our understanding of natural selection and adaptation has been shouldered by research on stickleback fish (*Gasterosteus aculeatus*; Schluter and Nagel 1995; Rundle et al. 2000), *Timema* stick insects (Nosil and Crespi 2006), Caribbean pupfish (*Cyprinodon* sp.; Martin and Wainwright 2013; Martin 2016), and red crossbills (*Loxia curvirostra*; Benkman 2003). A key problem, however, is that it is unclear if what we learn from many such groups—those yet to radiate into an eco-morphologically diverse collection of reproductively isolated species—is actually representative of what goes on in the early stages of adaptive radiation. The reason, of course, is that we cannot know whether such groups, given a few thousand or million years more of evolution, will blossom into the sort of diversity characteristic of adaptive radiation. Much insight on the ecological and microevolutionary processes thought to spur adaptive radiations is gained from studies of such nascent, species-poor, or nondisparate groups. Yet, it is difficult, if not impossible, to know whether such studies are truly pertinent to understanding the initial stages of adaptive radiation.

What Are the Alternatives?

There are a handful of other ways one might study the process of adaptive radiation. For example, the use of microbial systems to experimentally study questions about evolutionary diversification exploded at the start of the 21st century (Kassen 2009; Steenackers et al. 2016). Such experiments have several advantages over most model adaptive radiations: small organism size and fast rates of reproduction mean that studies can include large sample sizes, span many generations, and comprise multiple replicates (Jessup et al. 2004; Collins 2011). Replicated adaptive radiations among closely related lineages—in other words, independent radiations that have produced very similar outcomes in terms of the diversity of different species present within each radiation and paralleled across radiations—are rare in nature (Losos 2010), representing a classic problem in drawing generalizations across groups; microbial experiments provide an opportunity to overcome this. Microbial

Figure 1. Adaptive radiation research is reliant on inferences. Classically, processes that led to observable patterns in adaptive radiations were drawn from studies of phenotypic and ecological differences among species interpreted in the light of their phylogenetic relationships, such as in the Hawaiian honeycreepers (left). At the other end of the spectrum, the processes that lead to diversification may be studied in clades of relatively few species (or forms) in groups presumed to represent the incipient early stages of an adaptive radiation, but which have not yet reached the ecological and morphological disparity of many established groups, such as in threespine sticklebacks (right). Photographs: J. Jeffreys, A. Hendry.

study systems are also unique in being able to study both process and pattern into relatively deep evolutionary time. For example, the 30-year study of the diversification dynamics of experimental *Escherichia coli* lineages by Lenski et al., now spanning >70,000 generations, provides a unique insight into how—given identical starting conditions—diversification plays out in genetically identical lineages (Blount et al. 2008). Such long-term, replicated studies have provided important insights into how evolutionary diversification may occur and the extent to which such processes are deterministic (Blount et al. 2018). Nonetheless, such studies are limited to the artificial confines of the laboratory. Moreover, most laboratory studies are on a much shorter timescale than the work in the Lenski lab, more on the order of days than decades. For example, our understanding of the relationship between ecological opportunity and adaptive radiation was propelled by experiments with the aerobic bacterium *Pseudomonas fluorescens* in which macroevolutionary patterns were assessed following 3–7 days of diversification (Rainey and Travisano 1998). Long-term microbial experiments are time-, labor-, and money-intensive, but hopefully more such research programs will be established in the near future as their insights to the process of adaptive radiation can be unheralded.

Another approach to understanding adaptive radiation is to contrast different contemporary locations, each containing different sets of species presumed to be representative of a different stage in adaptive radiation (Shaw and Gillespie 2016). Assuming such series are an accurate surrogate for how a radiation unfolds through time, analyses of chronosequences could provide valuable insights into how species proliferate and differentiate through time (Shaw and Gillespie 2016). This "chronosequence" method has been widely used in other subfields of ecology (Terborgh et al. 1997; Foster and Tilman 2000) and has proved particularly insightful for some radiations, such as the Hawaiian arthropods (Roderick and Gillespie 1998; Gillespie et al. 2018; Kennedy et al. 2018), Palau jellyfish (*Mastigias* sp.; Dawson and Hamner 2005), and African rift lake cichlids (Brawand et al. 2014; Wagner et al. 2014). In these systems, islands and lakes of different ages, in which lineages have had different lengths of time to diversify and are composed of unique suites of constituent species, may represent snapshots of distinct stages of the radiation process. These studies rely on the assumption that the species or phenotypes occurring in different communities truly do represent different stages in the same process, an assumption that can be difficult to evaluate (Shaw and Gillespie 2016).

Last, fossils can complement research on contemporary adaptive radiations by providing a window into earlier stages of diversification (Schluter 2000). In this way, fossils can be used to observe those ancestral forms which existed pre-diversification or those intermediate forms which only existed during diversification. The discovery of *Archaeopteryx* from the Late Jurassic, representing the earliest undisputed fossil avian (but see Hu et al. 2009 and Ksepka et al. 2017), provided a bridge for evolutionary biologists to understand the early diversification of birds (Ostrom 1974, 1976; Mayr et al. 2005). Similarly, fine-scale fossil sequences of sticklebacks reveal the temporal pattern in which present-day limnetic populations transitioned away from the heavily armored phenotype of ancestral littoral forms (Bell et al. 1985, 2006; Hunt et al. 2008). Without fossils, it can often be impossible to empirically observe such ancestral phenotypes. However, for most adaptive radiations, a reliable, comprehensive, or particularly useful collection of fossils does not exist; for some groups, no record exists at all.

Classic Approach: Inferring process From Pattern

The classical approach in adaptive radiation research is to study those clades which have already radiated and exhibit high levels of phenotypic and ecological disparity. From these groups, much has been learnt about how phenotypes are distributed across a phylogeny (Givnish and Sytsma 2000; Schluter 2000; Seehausen 2006). However, in such diverse groups, the sequence of past diversification can be complex and difficult to infer. Recent advances in molecular phylogenetics have allowed more detailed and time-calibrated phylogenies to be constructed, providing an opportunity to explore the temporal patterns of diversification. For most of those groups, however, the early stages of radiation remain opaque: they represent events that happened many million years ago, and directly studying the processes that produced and transformed them is generally not possible. In the absence of such observations, inferences are usually drawn based on estimated ancestral states inferred from phylogenetic information; sadly, such inferences are often not particularly reliable, especially given the usual absence of much fossil data to enhance phylogenetic precision (Frumhoff and Reeve 1994; Omland 1999; Webster and Purvis 2002; Losos 2011; Duchêne and Lanfear 2015).

Although the ability to infer ancestral states early in radiations is often minimal, increased availability of genomic data is allowing insights into other aspects of the history of adaptive radiations (Schneider 2008; Seehausen et al. 2014 ; Foote 2018; Marques et al. 2019), such as revealing cases of ancestral hybridization (Alexander et al. 2017). With the increasing availability of phylogenomic data, we look forward to what other inferences about the processes operating during the early stages of adaptive radiation may be possible.

A Case Study: Caribbean *Anolis* Lizard Radiations

One group that is highly diverse in both species and phenotypes is the *Anolis* lizards (anoles) of the Greater Antilles. The result of a single colonization event from South America (Poe et al. 2017), anoles on each of the 4 largest islands in the Greater Antilles—Cuba, Hispaniola, Puerto Rico, and Jamaica—have radiated independently into ecologically and morphologically distinct species that include essentially the same set of habitat specialists, or "ecomorphs" (Williams 1972, 1983; Losos 2009). Here we review how research on anoles—a model system in which both process and pattern has been studied—has attempted to bridge the micro- to macroevolutionary divide and reveal how adaptive radiation likely unfolded. Many fundamental questions, in adaptive radiations in general and anoles specifically, remain difficult to answer. What did the ancestral anole look like? What triggered it to radiate? How did anoles speciate? How did anoles diversify? Here, as an exemplar case of issues we have so far discussed, we explore what macroevolutionary studies of diversification, comparative assessments of convergence, and field studies of ecological and microevolutionary processes have revealed about the origin and early stages of anole radiations.

What Was the Phenotype of the Ancestral Anole?

An intuitive place to start when aiming to understand the origins of an adaptive radiation centers around identifying the phenotype of its progenitor. For anoles, insight into the ancestral phenotype would be valuable to both understand how diversification proceeded, but also to understand whether each replicated radiation stemmed from an initially similar starting point, or whether different ancestral phenotypes nonetheless led to highly similar outcomes. Given widespread convergence across independent anole radiations, this represents a key question relevant to understanding the role of contingency versus determinism in the repeated adaptive radiations of anoles. In theory, fossil evidence could provide the most direct information on ancestral phenotypes. Unfortunately, informative fossils from early on in anole diversification are few. All post-Pleistocene anole fossils so far recovered date from the mid-Miocene (~15–23 mya); these fossils post-date the divergence of most ecomorphs (30-65 mya, Mahler et al. 2010). Similar to present-day phenotypes, these fossils are uninformative about earlier, ancestral forms (Rieppel 1980; de Queiroz et al. 1998; Sherratt et al. 2015).

Attempts to reconstruct the phenotype of the anoles on the Greater Antillean islands using phylogenetic methods have yielded mixed results. Early quantitative assessments using parsimony suggested a hypothetical phenotype representing an ecological generalist, one that was phenotypically intermediate between existing ecomorphs (Losos 1992). Subsequent methodological advances revealed that in many cases of evolutionary diversification, reconstructions of ancestral character states based on phylogenetic inference have very large uncertainties (Schluter et al. 1997); this work specifically revealed that the confidence limits around the ancestral reconstruction for the hypothetical anole ancestor overlapped most ecomorph classes in morphological space, indicating that we can have little confidence in the inferred ancestral state (Schluter et al. 1997), although some ecomorphs can be confidently considered to be unlikely candidates (e.g., crown-giant and trunk; Losos 2009).

An alternative approach to inferring the ancestral phenotype is to observe instances whereby a single species has invaded a novel environment. Such scenarios exist in the Caribbean; some islands only have one *Anolis* species, sometimes called "solitary" anoles (Williams 1969; Poe et al. 2007; Losos 2009). These species may experience selection pressures similar to those experienced by the species ancestral to anole radiations. Throughout the Lesser Antilles, a number of solitary anole species, belonging to 1 of 2 clades, occur; members of the *roquet* series occupy islands of the southern Lesser Antilles, whereas members of the *bimaculatus* series occur on the islands to the north. Although Lesser Antillean islands are smaller than their Greater Antillean counterparts, which produced diverse anole radiations, they represent a similar scenario to an ancestral species, a large and environmentally heterogeneous island lacking any close relatives. On these islands, solitary species are most similar in ecology and morphology to trunk-crown anoles of the Greater Antillean radiations (Losos and Queiroz 1997; Knox et al. 2001). Similar single-species islands exist in the Greater Antilles (e.g., St. Croix, Grand Cayman), providing a complementary perspective on anole adaptation on single-species islands. On those islands, solitary anoles are all descendants of either a trunk-ground or trunk-crown species; in most cases, the solitary anoles exhibit the phenotype of the ancestral ecomorph from which they descend, though in a few cases they have evolved phenotypes intermediate between the 2 ecomorphs (Losos and Queiroz 1997; Knox et al. 2001).

Whether such solitary species are good proxies for the species ancestral to the anole radiations is unclear because colonization has not led to further radiation. An alternative possibility is that the phenotype and ecology of these species is a reflection of which ecomorphs are the best colonizers. Although the ancestral phenotype of the colonizers of the Lesser Antilles is unknown, solitary species on oceanic Greater Antillean islands (i.e., those islands not previously connected to the Greater Antilles during times of low sea level) are almost always descended from trunk-ground or trunk-crown anoles, suggesting that these ecomorphs are the most adept colonists (Losos 2009; Poe et al. 2011), a proposition supported by the observation that the vast majority of successful human-assisted anole invaders in the Anthropocene have also been either trunk-ground or trunk-crown species (Kolbe et al. 2007, 2016; Latella et al. 2011; Poe 2014; Kraus 2015; Stroud et al. 2017; Mothes et al. 2019).

Understanding the phenotype of ancestral anoles remains a major unanswered question concerning anole adaptive radiation. Although ancestral state reconstructions may rule out some unlikely ecomorphs as forebearers to the radiation, most current methods produce highly uncertain estimates of an ancestral phenotype. Various ecological data suggest that trunk-ground or trunk-crown anoles represent forms most suited for dispersal, colonization, and success in depauperate communities; attributes presumably important for ancestors of island radiations. However, the absence of radiation in such species, which find themselves in an apparent ecological opportunity, casts doubt on their validity as candidates. To some extent, uncovering what an ancestral anole looked like may be unanswerable—the data required are unobtainable and currently available methods inadequate.

What Triggered the Start of Anole Radiations?

Tracing back to Darwin, ecological opportunity has been identified as a key to understanding when and how adaptive radiation occurs (Simpson 1953; Schluter 2000; Stroud and Losos 2016). Loosely defined as a species finding access to a "wealth of evolutionarily accessible resources little used by competing taxa" (Schluter 2000), ecological opportunity describes a situation in which an ancestral species finds itself with access to a suite of ecological resources which can be evolutionarily exploited (Simpson 1953; Yoder et al. 2010; Wellborn and Langerhans 2015; Stroud and Losos 2016). Upon gaining access to novel ecological space, a lineage may radiate extensively to take advantage of the many resources now available to it. Ecological opportunity may manifest itself due to colonization of an island (or similar habitat), the extinction of species previously usurping resources, or the evolution of a novel feature providing a lineage the evolutionary capability to access previously unavailable resources (reviewed in Stroud and Losos 2016; but see Erwin 2015 and Martin 2016).

Colonization of large islands is considered the trigger of the Greater Antillean anole radiations. If ecological opportunity prompts adaptive radiation, then one prediction is that rates of phenotypic diversification should slow as species evolve and diversify, limiting the availability of unique ecological niches and decreasing subsequent ecological opportunity (Schluter 2000; Freckleton and Harvey 2006). Phylogenetic analysis confirms this prediction: anole radiations underwent rapid phenotypic diversification early in the radiation, slowing through time as lineages accumulated (Mahler et al. 2010).

The scenario of an ancestral anole arriving on an island with no similar species and radiating exuberantly is attractive, but there is one problem: anoles on mainland Central and South America are also phenotypically diverse, radiating to occupy much of the same ecomorphological space as Caribbean anoles (Pinto et al. 2008; Schaad and Poe 2010; Moreno-Arias and Calderon-Espinosa 2016; Anderson and Poe 2018; Poe and Anderson 2019). Given the great many lizard lineages present in this area—as well as of many other types of insectivorous organisms (e.g., birds, frogs, spiders, mammals)—it is hard to envision ancestral mainland anoles occurring in an area with a surfeit of available resources as predicted for the island ancestors. Future studies investigating the eco-evolutionary dynamics of mainland versus island lineages will be valuable in further understanding the extent to which radiation has been convergent across different biogeographic contexts.

An alternative, or perhaps complementary, possibility that could explain the radiation of anoles is that the evolution of adhesive toepads, which provide great clinging ability (Macrini et al. 2003; Elstrott and Irschick 2004). The evolution of toepads has allowed anoles, both island and mainland, to diversify to use a variety of habitats and resources in ways not possible for non pad-bearing lizards. Such key innovation hypotheses are difficult to test and come with many caveats (discussed in Stroud and Losos 2016), but it is notable that geckos, which have also evolved expanded adhesive toepads, are also extraordinarily diverse (Gamble et al. 2012; though, we must note that a third evolutionary instance of adhesive toepads in lizards, in the Papuan skink genus *Prasinohaema*, has not been accompanied by much diversification; see discussion of toepads and key innovations in Williams and Peterson 1982 and Losos 2009).

How Does Speciation Occur?

Next, we might ask: how does the speciation process work? In what manner did the ancestral anole in each radiation give rise to multiple descendant species? Phylogenetic analysis indicates that the different ecomorphs probably appeared soon after diversification commenced (Mahler et al. 2010). In general, two different speciation pathways could be responsible for the divergence of anoles into multiple coexisting, ecologically distinctive species. On the one hand, sympatric speciation could have been responsible for such a pattern; a single ancestral species diverging through disruptive selection into multiple, ecologically differentiated species (Schluter 2000; Coyne and Orr 2004; Nosil 2012; in the age of genomic data, Foote (2018) has shed further light on the various alternative pathways by which sympatric speciation may occur). Alternatively, speciation might occur in allopatry, the ancestral species becoming divided into multiple, nongeographically overlapping populations that then diverge into different species as a byproduct of adaptation to different environments, differing sexual selection pressures, genetic drift, or other causes (Schluter 2000). Following the evolution of reproductive isolation in allopatry, when the geographic ranges of the species expand bringing them into contact, ecological interactions lead them to diverge in resource use to facilitate coexistence (Brown and Wilson 1956).

The sympatric speciation hypothesis has a simplicity in that it does not require invocation of a hypothetical allopatric phase prior to the sympatry that now exists among the ecomorphs. Further, on some islands, especially Jamaica (Figure 2), it is hard to envision how such allopatry might have occurred (Losos 2009). Based on the sympatry of existing anole species, some authors have presumed that speciation occurred sympatrically (Doebeli and Dieckmann 2000; Shaw et al. 2000). Moreover, a recent simulation approach—one which did not consider the role of biotic interactions—concluded that sympatric speciation was responsible for Greater Antillean anole speciation (Skeels and Cardillo 2019).

On the other hand, the prerequisites for sympatric speciation to occur are challenging, leading many to consider it unlikely, particularly in mobile animals such as lizards (Coyne and Orr 2004). Biogeographic evidence supports this view: on all islands in the Caribbean smaller than Puerto Rico, no sister species of anoles co-occur (Losos and Schluter 2000; Helmus et al. 2014). Looked at another way, many relatively large islands, especially in the Lesser Antilles (e.g., Guadeloupe, Dominica, and Martinique), contain but a single species, even though the islands are large and ecologically diverse; the variation of habitats, vegetation, and microclimates available to resident species would suggest that all ecomorphs could feasibly exist. If sympatric speciation was a process likely to happen in anoles, then it is hard to understand why it has not occurred on these islands.

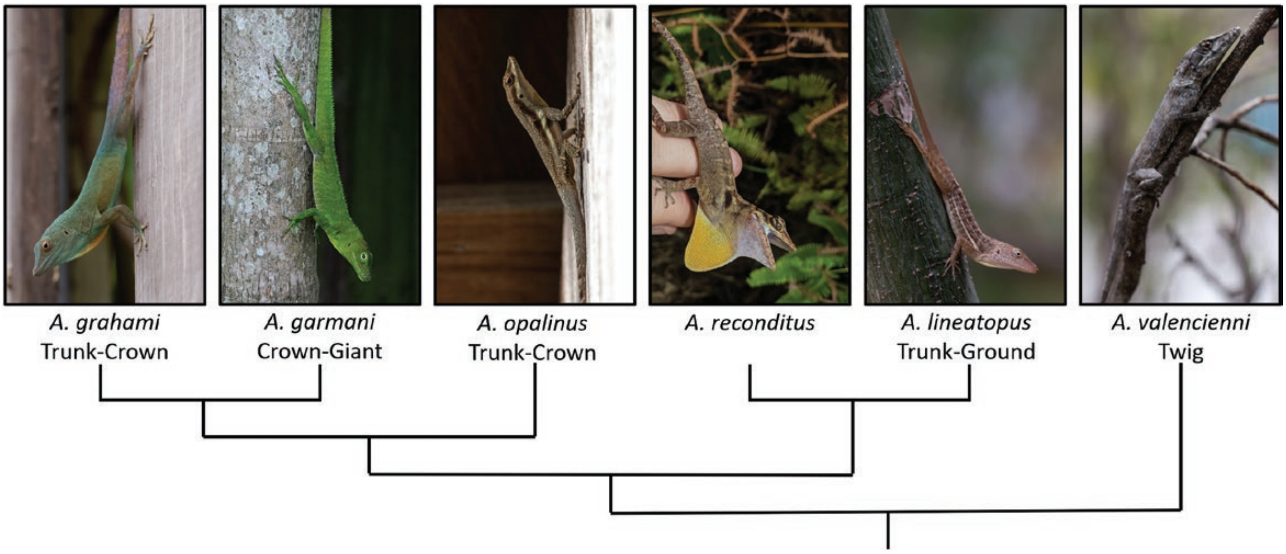

Figure 2. Phylogenetic relationships of the Jamaican *Anolis* radiation. Jamaica, which has a central mountain range and few offshore islands, is the smallest island of the Greater Antilles. Assuming an ancestral colonizer became widely distributed, it is difficult to envision how populations may have become geographically isolated. Sympatric speciation may therefore appear a more parsimonious explanation underlying Jamaican anole diversity, yet little evidence exists to support such a process. Below each species lies its corresponding ecomorph class. Note that *A. reconditus* is not assigned to an ecomorph class and is considered a "unique" anole species, a species that has no convergent counterpart (Losos 2009). Phylogeny from Poe et al. 2017. Photographs: J. Suh, J. Stroud.

The most convincing approach to understanding speciation is to study the process in action; however, such situations are notoriously difficult to identify. One approach long favored by evolutionary biologists—alongside those previously discussed in the Introduction—has been to examine geographically and phenotypically distinct populations, suggesting such a scenario represents intraspecific divergence and perhaps, therefore, the early stages of speciation (Mayr 1963). A well-studied case in anoles is that of the Hispaniolan bark anole species complex (the clade containing *Anolis distichus*, *Anolis brevirostris*, and related species), in which subspecies are eco-morphologically similar but vary greatly in dewlap phenotype (Case and Williams 1984; Williams and Case 1986; Glor and Laport 2012). Divergence of signals used in communication, such as dewlaps, are thought to play an important role in species recognition, meaning differences in such traits may, therefore, be important in reinforcement through assortative mating should populations come into contact (Lande 1981; West-Eberhard 1983; Panhuis et al. 2001; Ng et al. 2017). Ongoing research investigating dynamics of divergence in the *distichus*/*brevirostris* complex promises to continue advancing our understanding of how the speciation process may unfold in anoles.

What Drives Adaptive Divergence?

If speciation in anoles is primarily allopatric, then interactions that occur among nascent species when they come into secondary contact may be a robust force in driving patterns of resource use and evolutionary divergence. When such contact occurs, species may diverge in resource use to facilitate coexistence and circumvent competitive exclusion. As a consequence of changes in ecology, natural selection would be expected to lead to shifts in morphological traits associated with performance and resource acquisition across different parts of the resource spectrum (Figure 3). This is the process of character displacement (Brown and Wilson 1956), often considered responsible for the evolution of much of the ecological and morphological disparity in anole radiations. To begin testing the character displacement hypothesis, one may first ask: what is the evidence that anoles interact ecologically? A large body of literature indicates that, in fact, sympatric anoles often have negative effects on each other. Evidence includes observations that sympatric anoles interact agonistically and frequently partition resources in which they may compete and that rarely do ecologically similar species co-occur; in addition, experimental studies directly reveal negative effects of one anole species on another (Schoener 1968, 1970; Pacala and Roughgarden 1982; Losos et al. 1993; Losos and Spiller 1999; Stuart et al. 2014; Pringle et al. 2019; reviewed in Losos 2009).

Given that sympatric anoles frequently experience negative interactions, we can ask whether such interactions may lead to phenotypic divergence. In other words, is there evidence of character displacement in anoles? One of the first tests of the character displacement hypothesis used a comparative approach to investigate body sizes on islands with one versus two species in the Lesser Antilles. Islands with two species harbor a large and a small species, whereas single-species islands contain an intermediate-sized species (Schoener 1970). Two processes could produce such a pattern: in situ divergence in which the two species diverge to become more different from each other, or nonrandom colonization (known as "size assortment") in which size differences evolve elsewhere and only already-differentiated species can co-occur (more specifically, in the case of anoles, this hypothesis would state that only a small and a large species can colonize and coexist, and that an intermediate-sized species would prevail if it occurred with either a large or a small species). Phylogenetic analyses support the character displacement proposition for anoles in the *bimaculatus* Series in the northern Lesser Antilles (Losos 1990), but whether a similar process occurred in the *roquet* Series of the southern Lesser Antilles is more ambiguous (Giannasi et al. 2000; Losos 2009; Thorpe et al. 2010, 2018).

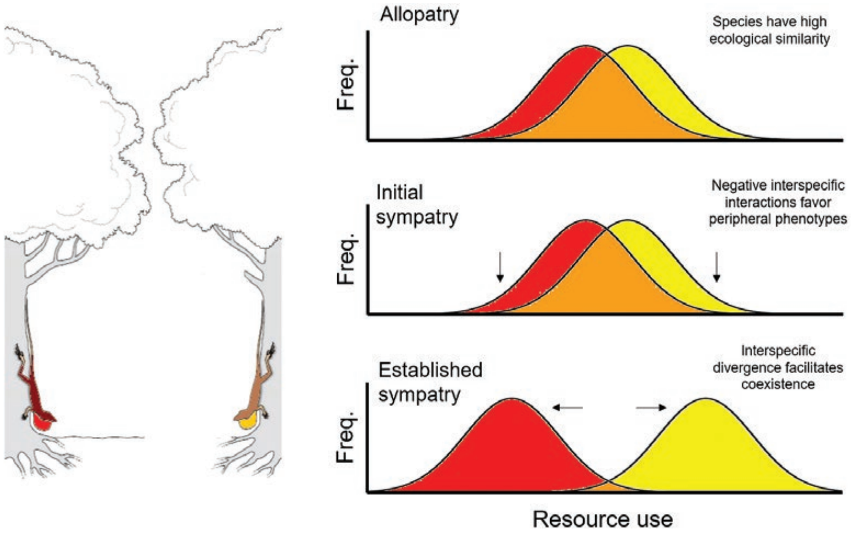

Figure 3. Ecological character displacement may drive the evolution of ecomorphological diversity in *Anolis* radiations. Following the evolution of reproductive isolation in allopatry, here demonstrated by differences in dewlap phenotype (left), ecologically and morphologically similar species are expected to interact strongly in secondary contact. Although ecologically similar in allopatry (right top), when such species come into contact in sympatry (right middle), and in the absence of competitive exclusion, species may diverge in resource use to facilitate coexistence (right bottom). In this scenario, individuals that use portions of the resource spectrum under-utilized by the competing species may be favored by natural selection (arrows; right middle). Subsequently, as species diverge to minimize negative interspecific interactions, natural selection may favor traits better suited to the new portions of the resource spectrum which each species is occupying, leading to morphological divergence. Repeated bouts of ecological character displacement may be responsible for the exceptional adaptive diversity in anole radiations.

Contemporary invasions provide a novel opportunity to investigate the process of character displacement in anoles. On Bermuda, an oceanic island with only one native lizard—a small fossorial skink—3 species of ecologically similar anoles have been introduced and become established over the past century (Losos et al. 1996; Macedonia 2016). Subsequent range dynamics revealed that coexistence between ecologically similar species could only be facilitated through divergence in habitat use; if character displacement in habitat use did not occur, then competitive exclusion through niche incumbency prevailed, revealing the importance of such shifts in broader patterns of community assembly (Stroud et al. 2019). The arrival of a fourth species on Bermuda, the Cuban brown anole (*Anolis sagrei*), may allow further tests of the character displacement hypothesis in this model system (Stroud et al. 2017). Elsewhere, in Florida, USA, the impact of introduced *A. sagrei* on the ecology of native trunk-crown American green anoles (*Anolis carolinensis*) has been studied in great detail in a set of experimental islands. Following invasion by *A. sagrei*, *A. carolinensis* became more arboreal (Campbell 2000). The morphological consequences of this ecological response were revealed in later study on islands in the same area. As a result of increased arboreality in the presence of *A. sagrei*, morphological shifts in *A. carolinensis* were consistent with adaptations for arboreal specialists: in the span of 20 generations, populations of *A. carolinensis* sympatric with *A. sagrei* evolved larger toepads with more subdigital adhesive scales (lamellae) relative to populations of *A. carolinensis* on islands lacking *A. sagrei* (Stuart et al. 2014). In summary, evidence for the occurrence of character displacement as a process facilitating co-occurrence of ecologically similar species and driving adaptive divergence in anoles is revealed both by phylogenetic analysis and by studies of ongoing interactions among species recently brought into sympatry.

Traditionally, interspecific competition has been considered the primary driving force underlying adaptive radiation in anoles. However, predation can also be a potent ecological force affecting the behavior and ecology of anoles (Losos et al. 2004, 2006; Lapiedra et al. 2018; Pringle et al. 2019). In theory, predation could play an important role in driving adaptive radiation (Schluter 2000), but its role as a process during adaptive radiation has been little studied compared with competitive interactions (although see Vamosi 2005; Nosil and Crespi 2006; Meyer and Kassen 2007). Congeneric predation in anoles is widespread and documented both within and between ecomorphs (Schwartz and Henderson 1991; Gerber 1999; Campbell 2000; Gerber and Echternacht 2000; Giery et al. 2013, 2017; Stroud 2013, 2019; Ljustina and Stroud 2016; Walker et al. 2019), suggesting that intraclade predation may have helped shape patterns of adaptive radiation in anoles. The role of predation in adaptive radiation would repay further study, both in anoles and other taxa.

Last, the question may arise of how, following the evolution of different ecomorphs in an anole radiation, such disparity may be maintained through time? Historical inferences of the adaptive landscape have suggested that different ecomorphs have occupied different peaks over long periods of time (Mahler et al. 2013); however, this hypothesis has yet to be tested empirically. In fact, remarkably few studies have attempted to measure natural selection on more than a single species at a given time in adaptive radiations (but see case studies in Galapagos finches (Grant and Grant 2011) and Caribbean pupfishes [Martin and Wainwright 2013; Martin 2016]). A more complete understanding of anole fitness landscapes would provide a useful framework on which to better understand the process of adaptive radiation, from conception to maintenance, and how consistent such landscapes are among convergent communities.

A Cautionary Tale From a Well-Studied Radiation

Despite decades of research having led anoles to become one of the most well-studied cases of adaptive radiation, no easy way exists to circumvent the difficulties of dealing with the fog of time (Williams 1983). Understanding what happened in the past by studying the present is plagued with uncertainty. In anole radiations, evidence suggests that island colonization by an ancestral species was probably the ecological opportunity which spurred radiation, but what that ancestral species looked like remains unclear. Phylogenetic inferences and fossils have so far not provided a comprehensive picture. How speciation occurred is also still unclear—species distribution suggests that sympatric speciation was unlikely, but not being able to view the speciation process poses its limits. Field studies in nature have provided myriad evidence supporting phenotypic shifts in anoles in response to novel biotic and abiotic conditions, illuminating how ecological and morphological disparity may evolve during the early stages of adaptive radiation. However, the debate continues about the extent to which such microevolutionary processes scale up to dictate macroevolutionary patterns.

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