

NATURAL HISTORY, ECOLOGY, AND EVOLUTION OF A REMARKABLE ADAPTIVE RADIATION

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What is an adaptive radiation? In its simplest form, it is the explosive diversification of a monophyletic lineage in response to the acquisition of a key innovation or colonization of new niches. What examples come to the mind of most students of evolutionary biology? Presumably, we all have our favorite example, but I would venture that most top five lists would include one or more of: Darwin's finches on the Galapagos islands, African rift valley cichlids, Hawaiian honeycreepers, Hawaiian silverswords, and Greater Antillean *Anolis* lizards. These radiations are textbook classics because of the impressive diversity of form and function in their descendant lineages and/or because they have been studied thoroughly over relatively long periods of time. With the extremely well researched and entertainingly written *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*, Losos (2009) makes a rather convincing case that the latter group, along with their Lesser Antillean and mainland counterparts, may represent the ideal marriage of diversity to explore and study system tractability. To be fair, Losos does not directly make this bold claim; rather it is an impression one easily gets after reading the book.

Chapter 1 begins with a brief introduction to the field of evolutionary biology, especially as it pertains to inferring historical events from fossil and phylogenetic evidence. In it, Losos makes a

cogent defense of inferential approaches, aimed at those who take the narrow-minded view (again, these are my words here) that only experimental work constitutes (good) science. At the end of the chapter, Losos provides some insight into his introduction to the field and what motivates his continued interest in anoles. It is here that we first encounter a thread that will weave through the entire book, which is: although much is known about anoles, even more striking is how much remains undiscovered. Unlike some researchers who appear reluctant to bring other researchers into the fold (or, even, actively discourage others from working on "their" system), Losos (p. 10) extends an open invitation: "There's plenty of room in the *Anolis* world for more researchers, and I will consider this book a success if it helps to produce a new generation of anole biologists." Hear, hear! Throughout the book, Losos ends each chapter with a "Future Directions" section, sometimes brief, other times fairly substantial. Not wanting to steal his thunder, I largely do not touch on their contents, but I will say that they alone make this book a must read for new researchers in the field.

With the scene set, the book really gets going in subsequent chapters. In Chapters 2–4 (the first of four informal sections), Losos introduces the diversity and distribution of anoles. Chapter 2 aims to define what anoles are, in terms of general phenotype, where they are found, and a short discussion of reproduction isolation and species concepts as they pertain to anole species. Having known the most about the ecomorphs (a term now widely used in ecology and evolution, it was first applied by the renowned *Anolis* biologist, Ernest Williams, in this context [see Footnote 72 in

Losos]) prior to reading this book, the discussion of anole dewlaps (extensible structures located on the anterior ventral surface of lizards) especially caught my eye. Dewlaps are not unique to anoles, but they may reach their greatest diversity in size, color, and pattern in this group. Later in the book, Losos returns to the potential role of dewlaps and associated head bobbing in anole speciation. The other surprise was the remarkably adhesive toepads of anole lizards—although geckos receive the most attention, anoles can apparently hold their own. Although species concepts can be vague in theory and even more difficult to apply in practice, the aforementioned dewlaps and head-bobbing displays appear to be remarkably good at maintaining distinct gene pools in sympatry. Hybridization is rare and introgression almost unheard of in anoles. Although this complicates some experimental approaches (e.g., using F_1 hybrids to study ecological speciation hypotheses), it generally adds to the tractability of working with anoles.

Chapter 3 covers the anoles that evolutionary biologists at large are probably most familiar with, that is, the Greater Antillean ecomorphs. Crown–giant, trunk–crown, twig, trunk, trunk–ground, and grass–bush are a part of the general lexicon of evolution, but Losos really brings them to life with succinct written descriptions, informative graphics, and a series of vibrant color plates. Not content with simple descriptions of ecomorphs, Losos then asks two questions: are the ecomorphs “real” and, assuming they are, is six the correct number of classes? Although there is an overlap among species, especially among extremes of their respective classes, several lines of evidence collectively suggest that the ecomorphs are valid integrated syndromes of several classes of traits. Losos then carefully examines the case for more and fewer ecomorphs classes and finds little to warrant any arrangement other than the existing six groups.

In the last chapter of the first section, Losos describes what he refers to as the “other four anole faunas”—namely, Greater Antillean unique anoles, anoles of the smaller islands of the Greater Antilles, anoles of the Lesser Antilles (Anguilla in the north to Grenada in the south), and mainland anoles (i.e., those of Central and South America). Collectively, these groups comprise the bulk of anole species diversity. These faunas may appear on first glance to be mere sideshow exhibits; however, a careful reading of this chapter is warranted, as they often provide informative parallels and contrasts to various aspects of the Greater Antillean anole story. The mainland anoles are especially interesting in this light, being regionally and locally diverse, but there is (as of yet) no evidence suggesting the same predictable set of ecomorph classes coexisting on the mainland; however, the possibility of other repeated phenotypes remains (and invites further research).

In the second major section (i.e., chapters 5–7), Losos delves into the phylogenetic context of anole diversity. Chapter 5 is largely a discussion of the strengths and limitations of the phylogenetic approach, which is a very active component of modern

ecology and evolution and one that Losos himself has actively contributed to in various forms. I have long been sold on the comparative/phylogenetic approach to studying diversification and adaptation, but appreciated his summary of why the reconstruction of putative ancestral traits is problematic at best and potentially misleading at its worst. He concludes the chapter with a discussion of the history of attempts at reconstructing the *Anolis* phylogeny, which will probably appeal the most to specialists in the area.

Chapter 6 is a somewhat short, but very interesting, foray into the origination and spread of the *Anolis* lineage. Although some of the details are in flux, it appears that anoles began diversifying around 65 million years ago (mya) (but possibly only 40 mya) on the mainland, with subsequent colonization of the various islands of the West Indies. One rather interesting wrinkle to the usual mainland–island colonization story is phylogenetic evidence for subsequent recolonization of the mainland from the West Indies to the mainland by the Norops clade. The outstanding issues in anole biogeography involve obtaining better divergence time estimates and tying these to a more resolved history of the geologically dynamic Caribbean region.

The main topic of Chapter 7 pertains to a central question in evolutionary ecology: how did anole diversity evolve within and among different regions? Focusing first on the ecomorphs of the Greater Antilles, Losos lays out the evidence in favor of repeated, independent evolution of each ecomorph class on each island it currently inhabits. The other notable component of this chapter is a consideration of the size-based evolutionary divergence observed on the Lesser Antilles: anole species on one-species islands are almost always intermediate in body length to those on two-species islands, which are themselves markedly divergent in body length. Although there is a long (and occasionally contentious) history of study of these patterns, Losos neatly summarizes the relative evidence for character displacement, sympatric speciation, and taxon cycles for generating and maintaining them.

After laying out the historical perspective in the preceding chapters, Losos provides a detailed examination of a variety of aspects of anole biology in Chapters 8–13. These chapters actually constitute two subsections, with the first building the foundation for the second. Chapter 8 is an overview of basic anole individual and biology, touching on reproduction, diet, enemies, and a brief mainland–island comparison. Perhaps surprisingly, much remains to be known about the “basic ecology” of all but a few well-studied species. Chapter 9 is a nice introduction to the interrelated topics of territorial behavior, mate choice, sexual dimorphism, and sexual selection. In Chapter 10, Losos discusses habitat use, but it may not be what you expect: in addition to the obvious vegetation axes, anoles also partition their habitats along temperature, moisture, and light gradients.

Still within the “anole biology” section, Losos applies a more synthetic approach in the next three chapters, focusing on the

ecological aspects of adaptive radiation and natural selection. Chapter 11 begins with a nice overview of the process of adaptive radiation, which is followed by evidence from a number of lines, which all indicate that anoles interact strongly in sympatry (setting the stage for evolutionary divergence due to such interactions). For example, Losos reviews studies of reduced niche breadth in species coexisting with several others and, conversely, ecological release when those species occur in allopatry. Many readers will appreciate the consideration of enemy–victim interactions in structuring communities, a topic that has consistently received less attention than competition for limited resources. This theme is again touched on in the Future Directions discussion at the end of the chapter. In Chapter 12, we learn of what we do (and do not) know about microevolutionary processes in anoles including the strength and targets of natural selection in the wild and in experiments, associations between morphological and environmental variation, heritability, and phenotypic plasticity. Finally, in Chapter 13, Losos tackles the macroevolutionary aspects of the repeated evolution of ecomorphs and convergence of similar phenotypes living in similar habitat. Here, we are treated to an in-depth look into the life of anoles and their solutions to the challenges faced by ectothermic vertebrates living in and around trees, while trying to find food, avoid being eaten, becoming overheated or dehydrated, and finding mates. Although many evolutionary biologists will be familiar with many of the findings here, Losos brings to life the way in which these data were observed and gathered.

In the last major section of the book, Losos tackles perennial favorites: speciation, adaptive radiation, and adaptive landscapes. Chapter 14 covers many of the mechanisms by which speciation may occur in anoles. One particularly interesting case study is that of a north–south gradient in dewlap color in *A. caudalis*, which may have evolved to prevent hybridization with two parapatric anole species in the same species group. Such tantalizing evidence suggests that there is more to anole speciation than partitioning of food resources and adaptation to different vegetation structures. Chapter 15 is the first of two chapters examining how the adaptive radiation of anoles may have proceeded and what factors may be associated with variation in diversification rates. As with almost all adaptive radiations, we know much less about how and why certain groups radiated more than others. I was surprised by his conclusion (p. 334), at least as it applies to species richness of genera/families, that “the key innovation hypothesis of toepad evolution seems well supported.” With $N = 3$ sister groups, and significant imbalance being the norm rather than the exception in the tree of life, I think the jury is out on that point. Granted, Losos conceded a high “speculation-to-empiricism” ratio at the end of the chapter, so perhaps he was hoping others would take up this and related challenges. Finally, in Chapter 16 Losos returns to the five anole faunas, asking how well an adaptive landscape point of view explains their relative diversities. He begins with a solid

introduction to adaptive landscapes and the concept of historical contingency. Two notable sections include a discussion of the “missing” ecomorphs on some Greater Antillean islands and the possible role of predators in the different outcomes on the Greater Antilles and the mainland. Although I am admittedly biased, the potential for fruitful research in the latter area appears very high.

Losos ends the book, in Chapter 17, by: (1) summarizing how and why anoles are special, (2) detailing the sad fact of threat to various *Anolis* species, and (3) looking forward to the future of research on anoles. The reminder of threats to this adaptive radiation is sobering, but welcome; surely, biologists have some obligation to not only study, but also help protect, their favorite organisms.

Before I conclude, I wanted to make a few comments on the presentation and general content of the book. First of all, it really is a beautiful book, from the cover design, data figures, and color plates (of which there is no shortage) of lizards. Throughout, it is clear that this was a labor of love. Second, Losos made a conscious decision to supplement the main text with footnotes in situ, rather than relegating additional information to the end of chapters. With 477 footnotes, the casual reader may be tempted to skip them more or less entirely, but they do so at the risk of missing some interesting tidbits (for example, Losos succinctly explains the utility and limitations of using fossils [in isolation] to infer trait and lineage evolution in Footnote 107) and, in some cases, rather humorous anecdotes (e.g., in Footnote 306, we are told that he conducted a phenotypic plasticity experiment simply to quiet some “pesky botanists [but ended up proving their suspicions correct]). I occasionally found them distracting but, by and large, I think that most readers will value the included information. Finally, I would be remiss if I did not draw attention to the References list—at 74 pages (or ~15% of the total), it is an impressive compilation of research on anoles and related literature on macroevolution, adaptation, and speciation.

Who should read this book? It would make a valuable addition to the library of a broad audience of readers, including junior graduate students looking for unsolved questions to tackle, more senior researchers wanting a more in-depth picture of anole ecology and evolution but lacking the time to synthesize the primary literature, college instructors desiring an extremely readable source for teaching “fresh” topics in evolution, and members of the general public interested in knowing more about the processes responsible for generating the amazing biodiversity that surrounds us. Losos intentionally tried to strike a balance between breadth and depth and, in my opinion, succeeded admirably.

In sum, research on the anole radiation has been in full swing since the late 60s. This book is a celebration of the people working in this incredible system and insights they have produced over that span, by one of its foremost researchers.

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