

EVOLUTIONARY BIOLOGY AS A HISTORICAL SCIENCE

When we regard every production of nature as one which has had a long history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, in the same way as any great mechanical invention is the summing up of the labor, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting...does the study of natural history become!

CHARLES DARWIN, *ON THE ORIGIN OF SPECIES*, 1859, PP. 485–486

One of the great goals of modern science is to understand biological diversity: where it comes from, how it evolves, and what maintains it. It has fallen to the field of evolutionary biology to try to answer these questions. In attempting to do so, evolutionary biology does not fit the everyday view of science in which hypotheses are put forward and subjected to experimental test.

The reason is obvious. The scale in space and time is simply too large. It would be wonderful to be able to do an experiment on, for example, the role of interspecific competition as a driving force in evolutionary diversification. Just get an island archipelago, seed it with an ancestral finch population, and let nature take its course. Then get another archipelago, seed with the same type of finches, but add an overabundance of resources so that resources are not limiting and competition does not occur. Replicate the treatments a few times (say, four archipelagoes flush with resources, four without), come back in several million years, and, *voilà*, the hypothesis has been tested.

Too bad we can't do this. In trying to understand how and why evolutionary diversification has occurred, we're stuck with studying a phenomenon that has occurred over large spatial scales through the course of thousands to millions of years. For this reason, evolutionary biology is more akin to a social science—history—than it is to laboratory based sciences like chemistry (Cleland, 2002; Mayr, 2004) Lacking time machines, both AQ1

historians and evolutionary biologists must draw inferences from a variety of different sources and approaches in their attempts to understand the past^{2,3}.

I like to compare studying evolutionary diversification to a detective story:⁴ something happened in the past, and it is our job to build the best case to explain whodunit (or, at least, whathappenedtoit). In doing so, there usually is no smoking gun, no decisive experiment or single piece of evidence (Turner, 2005). Rather, we must gather as much data, from as many different sources, as possible. Then we must weave together these data to present the best explanation of what happened.⁵ As in a court case, the more consistent and corroborative the data, the more compelling the case (for a generally congruent, but slightly different, view, see Cleland [2002]; also see Pigliucci [2006]).

Such explanations, of course, are more than mere stories; they are the hypotheses that guide further work. Each time we learn something new, each time we bolster our case a bit more, new hypotheses are suggested that await subsequent testing. The better supported an explanation is, the less likely it will be that a single new piece of data will discredit it. Nonetheless, given that we are trying to explain what happened in the past, we can never know for sure what happened,⁶ and it is always possible that additional data will change our thinking.

SYNTHESIZING DATA FROM THE PRESENT AND FROM THE PAST

Ideally, we would like to know what processes occurred in the past and how these processes shaped the diversity we see today. This is where building the best detective case comes in. We can't directly study the processes operating in the past (Cracraft, 1981). But we can study processes in the present, and we can even observe their outcome over short evolutionary timescales.

What we can study in the past is the pattern: the history of change through time. Depending on the quality of the historical record, we can infer, with a greater or lesser degree of confidence, what happened. The key, then, is to extrapolate from our understanding of the relatively short term outcomes of ongoing processes to explain the patterns of change in the past.

2. Evolutionary biology is not alone among the natural sciences in taking this approach. Astronomy and some branches of geology are two others that attempt to unravel the mysteries of the past.

3. A footnote on footnotes: in an effort to make this book more readable, I will remove many detailed points and parenthetical statements from the main text and place them as footnotes. For those in a hurry or who can't be bothered, the footnotes are not crucial, although readers bypassing these notes risk missing the rare hilarious joke or witticism.

4. An analogy made independently by Grant (1986, p.11), Cleland (2002, p.17), myself (Losos, 2001, 2007), and probably many others.

5. Mayr's (2004) "historical narrative."

6. In fact, most scientists today would hold that science cannot "prove" anything. Rather, hypotheses are repeatedly tested; those that withstand every test, and for which it is inconceivable that future data will overturn current understanding, are elevated to the status of theories, such as the theory of evolution and the theory of gravity. Some would consider these overwhelmingly supported theories to be what we commonly refer to as "facts."

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HISTORICAL PATTERN

The historical record of evolution comes primarily in two forms: fossils and phylogenies. Each has its advantages and disadvantages. The strength of the fossil record is that we have concrete evidence of what extinct species were like and when they occurred. Were the fossil record complete, we would need nothing else to reconstruct the evolutionary history of a group.

But, of course, the fossil record is not complete. In some groups, such as horses (MacFadden, 2005) and trilobites (Fortey, 2000), it's still good enough to tell us a great deal about evolutionary history. In other groups, however, the situation is much less rosy. In *Anolis* lizards, for example, only four fossils⁷—all specimens entombed in amber—have been scientifically described (Figure 1.1; Lazell, 1965; Rieppel, 1980; de Queiroz et al., 1998; Polcyn et al., 2002), with perhaps another dozen or two undescribed (most in the hands of private collectors);⁸ all but one are from the same deposit from the Dominican Republic. Clearly, what we can learn from anole fossils is limited (although valuable).



FIGURE 1.1

One quarter of the fossil record for *Anolis*. This 15–20-million-year-old juvenile lizard from the amber mines of the Dominican Republic is indistinguishable in skeletal anatomy from the green anoles found on Hispaniola today (de Queiroz et al., 1998).

7. This does not include Pleistocene subfossils (e.g., Etheridge, 1964; Pregill et al., 1988; Roughgarden and Pacala, 1989).

8. Interest in amber fossils has greatly increased in recent years, perhaps in part as a result of the movie *Jurassic Park*, in which dinosaur DNA was extracted from mosquitoes entombed in Dominican amber (no matter that the dinosaurs had been extinct for over 40–50 million years by the time Dominican amber was formed!). This interest has driven the price of amber specimens through the ceiling—one anole in amber was initially marketed with an asking price of \$1,000,000 and still hasn't sold despite a 90% price reduction. Unfortunately, such specimens are usually unavailable for scientific study.

The other source of historical information comes from phylogenetic inference. Phylogenies have the advantage that they can provide evolutionary insights even in the absence of fossils (although whatever fossil data are available should be incorporated into such analyses). The disadvantages are twofold: first, many types of data (e.g., DNA sequences) generally cannot be obtained from fossils, limiting analyses only to extant taxa; and, second, the results of phylogenetic analyses are only as good as their underlying assumptions, which must be made both in constructing the phylogeny and in drawing evolutionary interpretations from it.⁹

Potential shortcomings notwithstanding, phylogenies are enormously useful and can provide information on a wide variety of evolutionary patterns, including rates of evolution, extent of convergence and stasis, the order in which particular traits evolve, and the timing of evolutionary events; they can inform biogeographic scenarios; and they can suggest hypotheses such as character displacement, taxon cycles, and cospeciation (those looking for an entrée to this literature might start with Felsenstein [2004] or by picking up a recent issue of a journal such as *Evolution*, *American Naturalist*, *Journal of Evolutionary Biology*, *Systematic Biology* or many others).

PRESENT-DAY PROCESSES

Historical patterns are fascinating and suggestive, but processes can only be studied directly among extant taxa. The processes that are evolutionarily important are those that affect how species interact with each other and with the environment, and how these interactions lead to evolutionary change.

Ecological interactions can be studied in many ways (Diamond, 1986). Recent years have seen an emphasis on manipulative experiments. Such experiments are extremely useful, but by necessity are limited in both length and size. Other useful information can be obtained from detailed observational studies and by following the results of species introductions or other changes to the environment brought on by human activities. By some combination of these approaches, scientists can investigate which processes operate in a given system, and how the operation of such processes may vary in different circumstances.

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The evolutionary outcome of ecological processes also can be studied in a variety of ways (reviewed in Fuller et al., 2005; Reznick and Ghalambor, 2005). Experimental laboratory studies are common, and a few controlled and replicated experimental studies

9. To summarize: you can hold a fossil in your hand and inspect it directly, but usually there aren't enough of them; you can't hold phylogenetic inferences in your hand and are potentially misled by the assumptions you make in deriving them, but they're a lot easier to obtain. Of course, in practice these two approaches are not alternatives because in the absence of a complete fossil record (i.e., always), a phylogenetic framework is required to interpret fossil data.

have been conducted in the field. Studies of the microevolutionary change following from human manipulations and introductions also can document the evolutionary response to processes operating in particular circumstances (e.g., Carroll et al., 1998; Huey et al., 2000; Hendry, 2001).

MUTUAL ILLUMINATION

Given that we have data on both pattern and process, how should these data be integrated? Over the past 2–3 decades, ecologists have pioneered this approach. Starting with an observation from the natural world that suggests a mechanistic hypothesis, ecologists often design a manipulative experiment to test whether the process produces the predicted result. Less frequently, the reverse occurs: an experiment suggests that a process may work in a certain way; field work is then conducted to see if variation among study samples conforms to predictions.

A similar mutual illumination occurs between historical and present-day studies. On one hand, historical studies can identify a pattern. Studies in the present can then examine whether a hypothesized process can produce such a pattern. If, for example, historical analysis (either examination of fossils or phylogenetic inference) reveals that sister taxa have evolved differences in body size whenever they have become sympatric, then the hypothesis that the species have diverged in size to minimize resource competition (a phenomenon termed “character displacement” [Chapter 7]) can be tested in several ways: An experiment can be established to investigate whether species similar in body size compete for resources; if competition does occur, natural selection can be measured to determine whether selection favors divergence in body size, and cross-generational studies can be conducted to see if the species begin to diverge.

This procedure can work equally well in the opposite direction. Studies can reveal that a particular process plays an important role in extant populations. Then historical analyses can investigate whether evolutionary diversification has occurred in the manner predicted if the process in question has played an important role. Reversing the example from the previous paragraph, if data from extant populations suggested that character displacement occurred, a historical test might involve examining whether evolutionary changes in size occurred when similar-sized ancestral taxa came into contact due to colonization or earth history events.

A CAVEAT

A uniformitarian assumption underlies this reasoning. That is, if a given process—say, interspecific competition—leads to microevolutionary change in a predictable direction today, then I assume that interspecific competition would have affected ancestral species in the same way. I take this uniformitarianism one step further by extrapolating from the

relatively small changes that occur over limited evolutionary time scales in the present to the much greater changes that have occurred over longer periods through the past.

But is the present really the key to the past? Not necessarily. Species and environments in the past may be different from those that exist today, and as a result, the ways ancient species interacted with each other and with their environment may have been fundamentally different from the interactions that occur today. For example, a common scenario of adaptive radiation begins with an ancestral species colonizing an island poor in competitors and rich in resources. The processes that affect such a species and the evolutionary outcome of such processes may be very different from what happens today among specialized descendant species in an environment in which resources are much less abundant. Thus, studies of the microevolutionary effects of interspecific competition among species in the Greater Antilles today may not be informative about how the initial stages of anole adaptive radiation proceeded.¹⁰

This is an important problem for any study trying to infer what happened in the past. Certainly, to the extent that what happened in the past is a series of historically unique events operating under rules that do not apply today, scientific study of the past will be difficult, if not impossible. To get around this difficulty, we must distinguish between the basic rules—e.g., those underlying the basic tenets of genetics and population biology—that we assume applied to extinct lizards in the same way that they apply to modern ones from those rules that may be contingent upon the situations in which they occur. Similarly, we must be sensitive to the many ways that past situations may have differed from present situations, and how these differences may have affected the evolutionary outcomes of ecological processes. This approach will not be easy, but is not impossible, either; it is an issue to which I will return periodically throughout the book.

More generally, I must acknowledge that not all scientists subscribe to the “detective story” approach to studying historical phenomena. Some scientists hold that the only way to study a process is to measure it directly, which, of course, is impossible for past events (Cracraft, 1981; Leroi et al., 1994). Others even more strictly restrict their view of science to those questions that can be investigated experimentally.¹¹

These views are understandable, but excessively restrictive. No doubt one would have greater confidence that natural selection had operated if one measured selection directly on an extant population, rather than inferring its action from other sorts of data. But to

10. A related example of the inability to extrapolate from the present to the past is the hypothesis for the amazing diversity of morphological forms in the famous Burgess Shale fauna of the Cambrian Period. Gould (1989) argued that the abundance of resources led to the evolution of a variety of morphological forms and further suggested that the explanation for this great morphological disparity, which has never since been rivaled in magnitude, is that genetic regulatory systems were much more flexible at that time and have since become more canalized, so that the morphological variety that can be produced by mutation today is constrained. As a result, an extant population experiencing comparable ecological opportunities to those that occurred in the Cambrian would be evolutionarily incapable of producing comparable morphological variety (for an alternative view, see Conway Morris [1998]).

11. In fact, some have referred derisively to field-based studies of ecology and evolution as “Boy Scout science.”

suggest that in the absence of direct measurement or experimentation, investigation of the processes that occurred in the past is impossible amounts to throwing the baby out with the bathwater. Taking this view means that some of the most fascinating questions facing humanity—How has life evolved? Did a Big Bang occur, and what happened afterward?—could not be investigated.

Moreover, neither direct measurement nor experimentation is a panacea. For many reasons, from technical to interpretational, the results of contemporary studies may be no more definitive than those obtained from historical studies (Cleland, 2002; Turner, 2005). These problems may tend to be greater for historical studies than for non-historical ones (compare Cleland [2002] to Turner [2005]; also see Pigliucci [2006]); regardless, the fact that the same issues bedevil both indicates that historical and non-historical science differ in degree, not in kind.

The bottom line is that historical hypotheses operate in the same way as non-historical ones. Hypotheses are developed and then tested with further data. Some tests are stronger than others; we must not overstate the confidence we have in particular inferences, and we must acknowledge the limitations and assumptions of any test, as well as alternative interpretations of the data. These caveats apply to all scientific studies, not just historical ones. By taking this approach, we can best understand what happened in the past, and why. That is not to say that we will be able to study all past events, just as we can't study all non-historical phenomena. But we will be able to learn much about how life has evolved through time.

OUTLINE OF THE BOOK

The thesis of this book is simple: interspecific interactions—primarily, but not exclusively, competition—among extant *Anolis* species play a dominant role in shaping their ecology and microevolution, and the historical record is consistent with the hypothesis that interspecific interactions have been the force driving evolution throughout anole history.

While presenting this thesis, I hope to integrate the enormous body of research conducted on anoles over the course of the past four decades. My goal will not be to exhaustively review all of this work. Rather, by synthesizing it, I hope to substantiate my claim in the prologue that the breadth and depth of our knowledge of all aspects of the organismal biology of such an ecologically and phenotypically diverse group makes *Anolis* one of the best subjects for the study of evolutionary diversification.

The book is organized in the following order. First, in Chapters 2–4, I will introduce the ecological and evolutionary diversity of anoles. Although of central significance to the discussion of evolutionary diversification, phylogenetic issues will be postponed so that anole diversity can be fully presented before its evolutionary pathways are analyzed. The subsequent phylogenetically-oriented Chapters (5–7) will serve

a dual purpose, both discussing the advantages and limitations of a phylogenetic perspective, as well as examining patterns of anole diversity in a historical context. Chapters 8–13 will examine anole biology, focusing on behavior, ecology, and life history (Chapters 8–10), community ecology (Chapter 11), microevolutionary change (Chapter 12), and functional capabilities (Chapter 13). Chapters 14–16 will examine speciation and adaptive radiation, and Chapter 17 will conclude by placing discussion of anole evolution in a broader context in comparison to patterns of evolutionary radiation in other taxa.

One theme that permeates this book is the importance of natural history. Only by having a rich and deep understanding of the organisms we study can we have insights into how and why they vary and how they have evolved (Greene and Losos, 1988; Greene, 2005; Dayton and Sala, 2001). For this reason, I have not shied away from providing a wealth of detail about particular species when I feel that information is important. I also hope such descriptions will bring to life the fascinating and diverse nature of these charming creatures and, in so doing, will enliven the book as a whole.

I have two audiences in mind for this book: those deeply interested in anoles and those interested in general questions of biodiversity, evolutionary biology and ecology. I have tried to walk a fine line in keeping the book general enough to be of broad interest, yet specific enough to be useful to those working, or thinking of working, on anoles. Of course, compromises are necessary, and to both audiences, I apologize in advance. To readers with more general interests, I am sorry for what at times might seem excessive details. Some times I just can't help myself! I've tried to move as much of the anole trivia as possible to footnotes, so those not so enamored with all things *Anolis* can zip right by. To anole aficionados, I beg forgiveness for not discussing every paper and every species. Where possible, I have generalized, or used the best example of many, and I have often cited the most recent or most comprehensive paper, rather than every paper on a topic.

Given the extraordinary breadth of work on *Anolis*, my review covers many fields, from phylogenetic analysis to behavior, ecology, functional morphology and beyond. In reviewing this literature, I have tried to explain methods and approaches at a basic level, as well as to provide an entrée to the literature, where possible by way of work done on anoles. Of course, this means that for readers knowledgeable about a particular area, the discussion may seem overly simplistic. In this regard, too, I have tried to walk the fine line between making the work accessible to a broad audience, while providing at least some measure of the detail of interest to the specialist.

Finally, a disclaimer about my review of the literature. Although a goal is to make this book the first place people look when they have a question about anoles, I am not trying to be encyclopedic. The reason is simple: the literature is too vast. For example, a Web of

Science search conducted in December 2007 with the keyword “*Anolis*” retrieved 1,901 papers and a Google Scholar search yielded 13,300 results. For this reason, in many cases I cite only papers which can serve as an entrée into the literature with the hope that readers can follow from those references to other relevant works.

FUTURE DIRECTIONS

I conducted my college honors’ research project on display behavior and species-recognition of a sympatric pair of closely related anoles (Losos, 1985a,b). When I left and went off to graduate school, I vowed to work on anything but *Anolis* because I perceived that we already knew the important stuff, and I wanted to blaze my own trail. It was only after two years of course work and a dozen failed projects that I realized while on an Organization for Tropical Studies summer course what should have been obvious before: the extensive previous work on anoles, rather than leaving few interesting questions, provided the groundwork for synthesis and application to conceptually important ideas.

That should have been enough to teach me a lesson, but I’m not a quick study. After working on anoles for more than 10 years, I decided it was time to work on other groups, where more interesting questions remained. And so I started to do so, conducting studies on other types of lizards (e.g., Losos et al., 2002; Schulte et al., 2004), and even opossums (Harmon et al., 2005)! But again anoles drew me back. The more we learned, the more new interesting and unforeseen questions arose. And, as before, the wealth of knowledge of all things *Anolis* continues to make them an ideal group for testing new ideas. AQ3

I mention these anecdotes to highlight that there is much we do *not* know about anoles. The more we know, the more we discover we don’t know. And surprisingly, even basic aspects of anole biology (e.g., diet, social structure) are not known nearly as well as one might expect. Consequently, many research areas are wide open, begging for more research.

With nearly 400 species in the genus and the possibility of studying almost any aspect of its natural history, *Anolis* welcomes new researchers. For this reason, I will end chapters with a brief discussion of questions that I think would be worth pursuing. Of course, these represent just those questions that occur to me; no doubt many others exist as well. My emphasis will be on what we don’t know about anoles, rather than the broader conceptual framework in which such studies could be conducted. This is not to say that the broader context is not important; quite the contrary, many eminent biologists have made their names by studying *Anolis* to address important questions of the day. Indeed, in many areas, I would argue that *Anolis* is an ideal subject to use in

testing outstanding hypotheses and in developing new ones. My hope is to entice workers—particularly students developing their dissertation ideas—to consider studying anoles both to increase our knowledge of these interesting animals and to investigate topics of wider interest. 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.¹²

12. Anologists? Incidentally, this is probably a good place to point out that honorable, right-thinking people can disagree over whether the correct pronunciation is uh-nole or an-ole. I am less charitably inclined to my ninth grade biology teacher’s uh-no-lee, but, although I have never heard “anole” articulated in that way by anyone else, I am told that it is common in the South, from whence she came (I was surprised to find that this is the preferred pronunciation of the Random House Unabridged Dictionary, according to www.dictionary.com).

As for the origin of the name, Daudin (1802), who named the genus, said that “anolis” was the name the indigenous Caribs used for these lizards. However, there is some possibility that in fact “anolis” may have been their name for lizards in the genus *Ameiva* and that the correct Carib word was “oulléouma” (see discussion in Breuil, 2002). Right or wrong, Daudin clearly chose the more mellifluous name to bestow upon these lizards! A more interesting, though doubtless less accurate, explanation is the Saba Tourist Bureau’s statement (www.sabatourism.com) that “The scientific name of ‘Anolis’ comes from the popular name of “anole” for these lizards. Anole is an ancient African name, meaning “little devil”, that is given to small lizards in western Africa.”