

# Community evolution in Greater Antillean *Anolis* lizards: phylogenetic patterns and experimental tests

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## SUMMARY

Phylogenies can be useful not only as a means of examining evolutionary hypotheses, but also as a source of hypotheses that can be tested using extant taxa. I illustrate this approach with examples from the study of community evolution in Caribbean *Anolis* lizards. Phylogenetic analyses indicate that not only are *Anolis* communities on Jamaica and Puerto Rico convergent in structure, but they have attained their similarity by evolving through a nearly identical sequence of ancestral communities. Examination of the pattern of community evolution suggests that interspecific competition is the driving force behind anole adaptive radiation. This hypothesis can be tested by investigating whether anoles shift their habitat use in the presence of competitors and, if so, whether such shifts lead to morphological adaptation to the new habitat. These hypotheses have been tested experimentally by introducing lizards onto small islands. Preliminary results indicate the existence of ecological interactions among sympatric anoles and that shifts in habitat use are accompanied by microevolutionary changes in morphology.

## 1. INTRODUCTION

The use of phylogenies in all manner of comparative studies has increased remarkably in recent years. Five years ago, few would have predicted the integral role that phylogenetic approaches today play in fields as disparate as epidemiology, population genetics and macroevolution, as this volume attests. The goal of this essay is twofold: first, to illustrate the importance of a phylogenetic approach to another field, community ecology, and, secondly, to discuss an important new use to which phylogenies have been put recently – rather than being used to test previously derived hypotheses, phylogenies are now being used to derive hypotheses that can be tested subsequently by using data from extant taxa.

### (a) *Phylogenetic approaches to community ecology*

Two traditions exist in the study of species diversity. Biogeographers and palaeontologists have long been cognisant of historical influences on the structure of communities. By contrast, ecologists have been more concerned with the role that present-day processes play in shaping community composition. Of course, rather than being antagonistic, these approaches are complementary and should be integrated (see, for example, MacArthur 1972; Ricklefs 1987). A phylogenetic context provides the appropriate setting for such integration (see, for example, Gorman 1992).

### (b) *Hypotheses derived from phylogenies*

Phylogenetic comparative methods were developed to permit appropriate and statistically valid means of testing hypotheses (Gittleman 1982; Ridley 1983;

Felsenstein 1985). A large body of literature has developed to elaborate on these methods (reviewed in Maddison & Maddison 1992; Miles & Dunham 1993; Losos & Miles 1994), but these methods all have one feature in common: they are methods for using phylogenies to evaluate previously established hypotheses. By contrast, several workers recently have used phylogenies as the *source* of hypotheses, which can then be tested in the laboratory or in the field (Lauder 1989; Futuyma & McCafferty 1990; McLennan 1991).

In this paper, I shall use my studies of Caribbean *Anolis* communities to illustrate, first, the important role that phylogenetic approaches can play in studies of the causes of similarities and differences among communities and, secondly, the manner in which phylogenetic studies can suggest testable hypotheses. To accomplish these goals, I shall review previously published work and provide preliminary conclusions from unpublished studies and work in progress.

## 2. BACKGROUND ON GREATER ANTILLEAN *ANOLIS* COMMUNITIES

*Anolis* is one of the most speciose vertebrate genera, with well in excess of 300 described species. Approximately 150 of these species occur on Caribbean islands, with most being found in the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico). Two patterns characterize the anole communities on these islands. First, on any of the islands, species within a community occupy different microhabitats. These ecological types, termed 'ecomorphs,' display morphological and behavioural adaptations to their different microhabitats. For example, 'trunk-ground' anoles (ecomorphs are named for the microhabitats they most

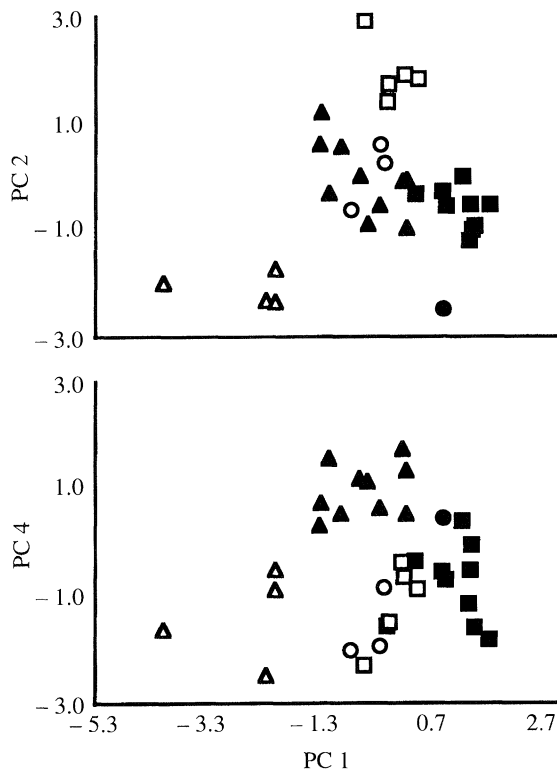


Figure 1. Position of species in a morphological space determined by a principal components analysis. Ecomorphs: filled triangles, trunk-crown; filled squares, trunk-ground; open circles, crown-giant; open squares, grass-bush; open triangles, twig; filled circles, trunk. Effects of size were removed from the variables; a variable representing overall size was also included in the analysis. PC 3 is not shown because it loads only for size and serves only to distinguish the crown-giants from the other ecomorphs. Species include at least one representative of each ecomorph type on each of the Greater Antilles, except that data are not available for several Cuban ecomorphs (from J. Losos & K. de Queiroz, unpublished).

frequently occupy) have long legs and run and jump frequently on broad surfaces, whereas 'twig' anoles have short legs and move slowly on narrow surfaces.

Most remarkably, when one compares communities across islands, one finds essentially the same set of ecomorphs represented on each island. Despite uncertainty about higher-level anole phylogeny (Guyer & Savage 1986, 1992; Cannatella & de Queiroz 1989; Williams 1989; Hass *et al.* 1993), we can conclude confidently that each of the ecomorphs has evolved independently on different islands a minimum of three times (the extent to which the Cuban and Hispaniolan radiations are independent of each other is not clear). Of the six ecomorph types, four occur on all islands (trunk-ground, trunk-crown, crown-giant, and twig), one occurs on all islands except Jamaica (grass-bush ecomorph), and one occurs only on Cuba and Hispaniola (trunk ecomorph).

To determine whether the ecomorph concept is valid, I measured morphology and ecology of adult males of a large number of species. Examination of the position of the species in a multi-dimensional morphological space indicates that species group by ecomorph type, rather than by phylogeny (figure 1).

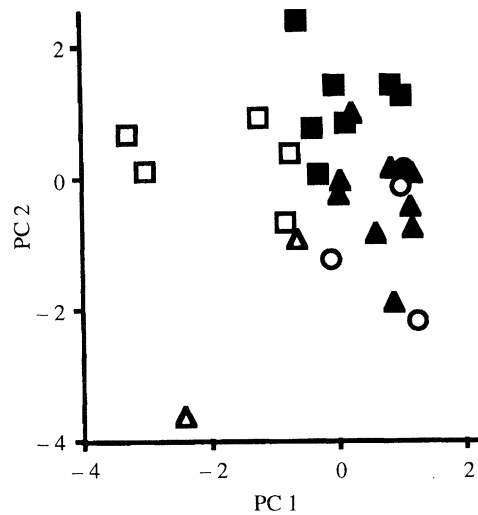


Figure 2. Habitat use by the ecomorphs.

Similarly, the ecomorphs differ in habitat use, although there is some overlap between the crown-giant 'trunk' and trunk-crown ecomorphs (figure 2). Thus, the ecomorph concept is valid; the same ecomorph types have evolved convergently multiple times.

### 3. EVOLUTION OF COMMUNITY STRUCTURE

Two models – the character displacement and micro-habitat specialization hypotheses – have been put forth to explain patterns of community evolution in Greater Antillean anoles (Williams 1972; Losos 1992). Both models invoke interspecific competition as the driving force behind community evolution. The implication of interspecific competition is reasonable because a large body of evidence affirms its importance in extant anole communities. This evidence comes from a variety of sources, including behavioural studies, geographic and temporal comparisons, analyses of the effects of introduced species on native species, and experimental studies (reviewed in Losos 1994).

In a study well ahead of its time, Williams (1972) mapped ecological and morphological characters onto a phylogeny of Puerto Rican *Anolis*. Based on this exercise, Williams concluded that early diversification within the Puerto Rican radiation was a result of two instances of character displacement in body size producing a community composed of three species divergent in size but all living high in the tree. Subsequent evolutionary events then led to species moving out of the crown and occupying other habitats.

Re-examination of this analysis using parsimony techniques to reconstruct the evolution of body size indicates that Williams's analysis was correct: the first two divergence events in Puerto Rico were accompanied by substantial divergence in body size (Losos 1992; see figure 3). However, since Williams's analysis, a phylogeny for the anoles of Jamaica has become available (Hedges & Burnell 1990; Losos 1992). Reconstruction of character evolution on this island provides no evidence of character displacement in early stages of the Jamaican radiation (figure 3).

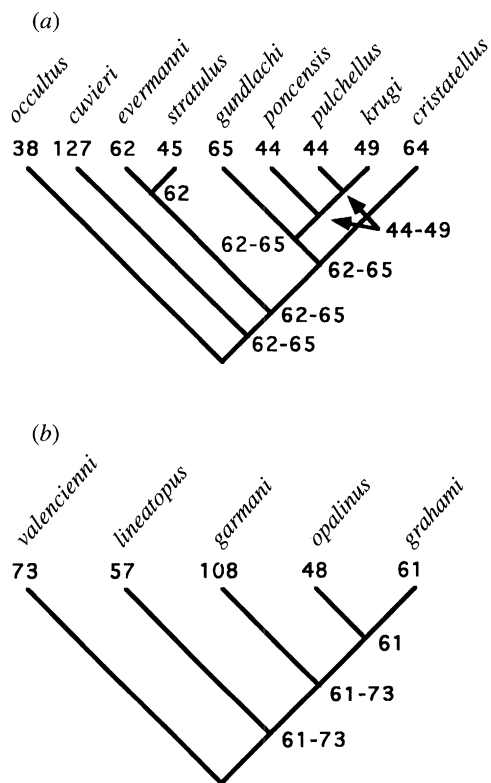


Figure 3. Size evolution (as represented by snout-vent length) in (a) Puerto Rico and (b) Jamaica. Parsimony was used to reconstruct the size of ancestral taxa. In some cases there was a range of equally parsimonious possibilities for an ancestral taxon; this ambiguity does not affect interpretation of general patterns of size evolution. The first two divergence events in Puerto Rico produced communities with small (38) and medium (62–65) and small, medium, and large (127) species, in agreement with the character displacement hypothesis. By contrast, substantial change in size did not occur in Jamaica in early divergence events. From Losos (1992), with permission.

An alternative hypothesis is that the addition of new species to an expanding anole community forces the species to alter their habitat use to minimize competitive pressures. Substantial evidence exists for such habitat resource partitioning among extant anole species (Losos 1994). Over evolutionary time, one would expect these species to evolve adaptations to their altered habitat use.

Note that this hypothesis does not specify how speciation occurs in anoles. Rather, it requires only that once speciation has occurred, the result is two ecologically similar species that compete for resources when they come into sympatry. Little is known about how speciation in anoles occurs, although most discussion has invoked scenarios of allopatric speciation (Losos 1994).

To test the hypothesis that the addition of species to a community leads to shifts in habitat use, I employed parsimony to reconstruct the evolution of the ecomorphs in the Jamaican and Puerto Rican anole radiations (Losos 1992; see figure 4). I based this analysis on morphology, but because morphology and ecology are intimately linked in anoles (Moermond 1979; Pounds 1988; Losos 1990a), this analysis also indicates the evolution of habitat use.

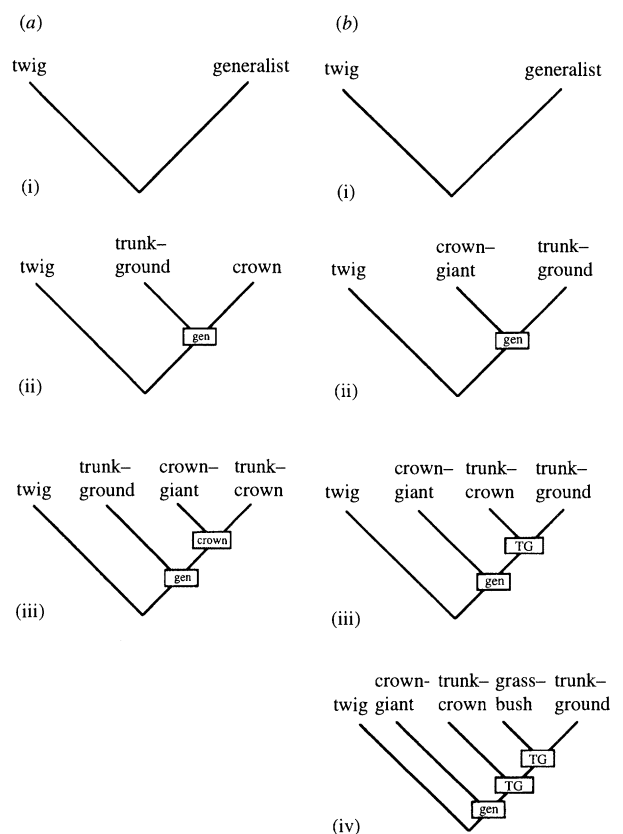


Figure 4. Ecomorph evolution in (a) Jamaica and (b) Puerto Rico. Parsimony was used to reconstruct the ecomorph type of ancestral data. From Losos (1992), with permission.

In Jamaica, the analysis indicates that the initial divergence event led to a species clearly identifiable as a twig anole and another that occurs in a central position in morphological space that does not correspond to the location of any of the ecomorph types. Owing to its central position, I refer to this taxon as a generalist (figure 5). The next divergence event produces a three-species community comprising a twig anole, a trunk-ground anole, and a species occurring in the crown of the tree, but not clearly identifiable as either a trunk-crown or a crown-giant anole. Finally, the four-ecomorph community contains the four ecomorphs present in Jamaica today.

In Puerto Rico, community evolution has followed an almost identical trajectory. The first divergence event again produces a twig anole and a generalist. The three-ecomorph stage comprises a twig anole, a trunk-ground anole, and again a species in the canopy, but in Puerto Rico this taxon is clearly identifiable as a crown-giant. The four-ecomorph community is identical to that in Jamaica, and the fifth ecomorph to evolve in Puerto Rico is the one absent in Jamaica, the grass-bush anole.

Thus, this analysis indicates that anole communities in Puerto Rico and Jamaica have evolved by sequential occupation of new habitats, as predicted by the habitat specialization hypothesis. Further, not only are communities convergent in structure today, but they have achieved this convergence by evolving through a nearly identical sequence of intermediate communities. This is a finding that would not necessarily be predicted

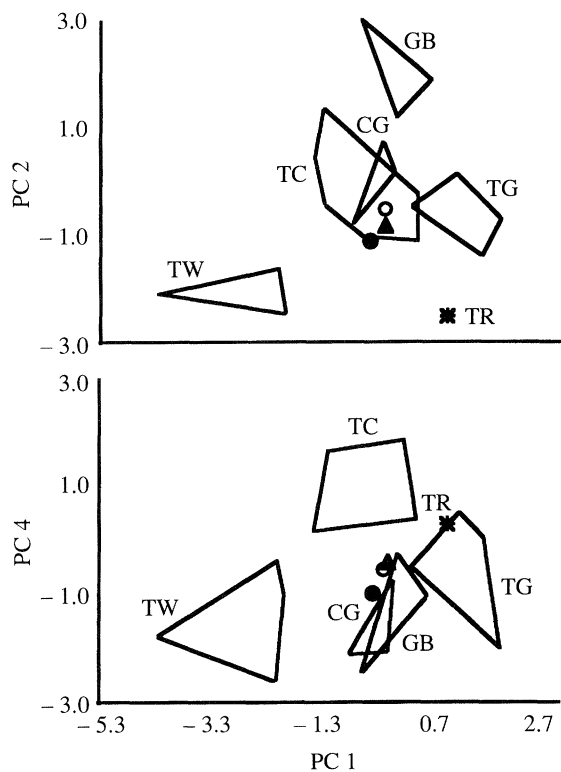


Figure 5. Position of hypothetical ancestral taxa in morphological space. The outlines refer to the position of the ecomorphs in figure 1. The filled symbols are the inferred morphological positions of the generalized ancestral taxa at the two-species stage of community evolution (figure 4) (filled triangles, Jamaica; filled circles, Puerto Rico). Open circles represent the hypothetical position of a generalist species, which was determined by taking the mean position of the centroids for each of the ecomorphs. The hypothetical generalist and the inferred ancestral taxa are similar on PC 3 (which is not shown) and all are greatly different from crown-giant anoles on this axis. Consequently, the two inferred ancestral taxa are more similar to the generalist than they are to any of the ecomorphs (J. Losos and K. de Queiroz, unpublished).

by community ecological theory and that could not be made except in the context of a historical approach to community structure. Further, this similarity in community evolution trajectory suggests the hypothesis that there is a deterministic pathway by which anole communities evolve. This hypothesis, if correct, holds interesting implications concerning adaptive radiation and the anole adaptive landscape (Losos 1992).

One might question to what extent these results might be an artefactual consequence of the use of parsimony to reconstruct the sequence of evolution of ecomorphs. Certainly, the reconstruction of ancestral states by parsimony is prone to error, particularly when the assumptions underlying parsimony (e.g. rates of change relatively slow and constant among lineages) are not met (see Maddison & Maddison 1992). Consequently, I would not be unduly confident that the reconstructed ecomorph type of any particular ancestor is correct. However, the most important finding of this study is not the ecomorph state of any particular ancestor, but instead the conclusion that the sequence of ecomorph evolution has been virtually identical on the two islands. Although uncertainty may

exist in parsimony reconstructions, there is no reason to suspect that parsimony would artefactually reconstruct the same sequence of ecomorph evolution in two independent radiations. Indeed, a randomization analysis indicated that reconstructing two sequences of community evolution as similar as those reconstructed for Puerto Rico and Jamaica is significantly unlikely to have resulted by chance (Losos 1992).

The historical approach provides another insight into anole communities that would not be apparent without recourse to a phylogeny. A number of hypotheses based on current conditions could be proffered to explain why Jamaica lacks the grass-bush ecomorph found on the other three islands. For example, perhaps Jamaica does not have appropriate habitats (unlikely because grass is, in fact, readily available in Jamaica) or perhaps these habitats have been usurped by other taxa. However, the historical perspective indicates that the wrong question is being asked (Williams 1972; Losos 1992). The grass-bush anole is the fifth ecomorph to evolve in the ecomorph sequence, but Jamaica has only advanced to the four-ecomorph stage. Hence, the appropriate question is not 'Why is there no grass-bush anole in Jamaica?' but 'Why has Jamaica only progressed to the four-ecomorph stage?' Rather than focusing on the grass-bush anole *per se*, this approach would concentrate on why Jamaica has not developed as many ecomorphs as the other islands. Possibilities include the age of Jamaica (and how long it has been above seawater) and whether Jamaican anoles are more tightly packed in ecological space than other Greater Antillean anole communities.

The hypotheses developed in this analysis are testable in two ways. First, the evolution of community structure has been examined in only two of the four Greater Antillean islands. As our understanding of anole phylogeny progresses, we shall be able to examine whether communities have evolved in the same sequence among all islands. In particular, we should expect the grass-bush anole to evolve fifth on all islands and the trunk ecomorph, absent from Jamaica and Puerto Rico, to be the last to evolve on the other two islands. Secondly, we can test predictions stemming from this analysis about the role of interspecific competition in driving anole adaptive radiation.

#### 4. THE USE OF PHYLOGENETIC APPROACHES TO DERIVE TESTABLE HYPOTHESES

The phylogenetic analysis suggests that the driving force behind the anole adaptive radiation is interspecific competition, which forces species to use new habitats to which they subsequently adapt. This model of community evolution suggests two predictions that can be tested among extant anole populations:

- (1) the presence of competing anole species should lead to shifts in habitat use, and
- (2) anole populations using new habitats should adapt morphologically.

Several colleagues and I have conducted experimental studies to address these questions. I shall begin

with the second prediction, for which the experiments are complete, and then discuss preliminary results from an experiment in progress that examines both predictions.

**(a) Populations using new habitats should adapt morphologically**

In the late 1970s and early 1980s, Thomas Schoener introduced small propagules of *A. sagrei* to tiny islands ('rocks') in the vicinity of Staniel Cay, Exuma Cays, Bahamas (Schoener & Schoener 1983). These islands do not naturally support anoles; assuming that the islands were thus too small to maintain viable populations, Schoener conducted the introductions to study the process of extinction. In fact, most of the populations have survived and several have exploded in population size (Schoener & Schoener 1983). In retrospect, occasional hurricanes, rather than small island size, probably account for the lack of lizards on these islands (Schoener & Schoener 1983).

The scrubby small-diameter vegetation covering the experimental islands differs considerably from the large trees found at the locality of the source population on Staniel Cay. Further, the experimental islands differ among themselves in vegetational characteristics. Based on the relationship between limb length and mean perch diameter among Greater Antillean anoles (Losos 1990a; Losos *et al.* 1995), we made two predictions: first, that the experimental populations should have shorter limbs than the source population and, secondly, that among the experimental islands, a relation should exist between limb length and perch diameter.

Examination of the populations in 1991 supported both predictions (J. Losos, K. Warheit, and T. Schoener, unpublished). The experimental populations have evolved non-randomly with regard to limb length; 12 of 14 experimental populations have shorter limbs than the source population. Further, among populations, a significant positive relation exists between limb length and perch diameter. At present, laboratory rearing experiments are under way to determine whether such results could be the result of phenotypic plasticity.

Thus, these results indicate that over a period of approximately 20 years (40 lizard generations at most), these populations have evolved adaptively in response to their new environmental setting. Although statistically significant, these morphological differences are relatively minor in absolute terms. However, comparisons among Bahamian populations of *A. sagrei* and *A. carolinensis*, which have been diverging for periods from 10 000 to hundreds of thousands of years, reveal the same trend in both species, but at a greater scale (Losos *et al.* 1995). This congruent relationship between limb length and perch diameter, manifested at different scales among species diverging for millions of years, populations for tens or hundreds of thousands of years, and experimental populations for 20 years, provides strong evidence for the adaptive nature of the relationship.

**(b) The presence of competing species leads to shifts in habitat use and subsequent adaptation**

The experiment just discussed indicates that anole populations will adapt rapidly to new environmental circumstances. However, the study does not indicate that interspecific competition can drive this evolution by causing shifts in habitat use. Habitat shifts in response to the presence of competitors have been noted repeatedly for anoles (reviewed in Losos 1994), including Bahamian populations of *A. sagrei* and *A. carolinensis*. None the less, few studies have documented that these shifts result in adaptive evolution (but see Lister 1976).

To examine this hypothesis, David Spiller and I have introduced populations of *A. sagrei* and *A. carolinensis* to small islands in the Exuma Cays, Bahamas. Some islands only received one species, whereas both species were placed on other islands. One year after the introduction, both species had achieved higher population densities on islands on which they were allopatric compared with islands on which they co-occurred. These results indicate the existence of interspecific interactions, but do not reveal the mechanism; possibilities include exploitative competition, interference competition, and intra-guild predation. We shall continue monitoring these populations to determine whether interspecific effects are apparent in subsequent years and whether the populations show evolutionary responses to these effects.

**(c) Is evolutionary specialization a one-way street?**

The phylogenetic analysis of community evolution suggests another testable hypothesis. If specialization to specific microhabitats is driven by increases in the number of sympatric congeners, as the phylogenetic analysis suggests, then if these competitors are removed, one might expect a species to reverse evolutionary direction and become less specialized. A number of small islands in the northern Caribbean contain one or two species that have clearly descended from a trunk-ground or trunk-crown anole. These species provide an appropriate test of the hypothesis that in the absence of competitors, specialized species should evolve a more generalized condition. The null hypothesis would be that these species have remained specialized and are still identifiable as a member of their ancestral ecomorph type.

An initial test of this hypothesis focused on the anoles of the Bahamas, which exhibit islands containing 1–4 species of anoles (Losos *et al.* 1995). We focused on *A. carolinensis* and *A. sagrei*, which both occur allopatrically on some islands. Of the 8 populations of *A. carolinensis* and 13 of *A. sagrei*, none provided evidence of evolutionary generalization; all were clearly identifiable as trunk-crown (*A. carolinensis*) or trunk-ground (*A. sagrei*) anoles.

A subsequent analysis (Losos and de Queiroz, submitted) examined 10 species, 5 descended from trunk-crown anoles and 5 from trunk-ground anoles, on islands elsewhere in the Caribbean (Cayman Islands, Descho, Inagua, Mona, Navassa, St Croix,

and Swan Island). Whereas most of the trunk-crown anoles had diverged relatively little from their ancestral mould, several of the trunk-ground anoles had diverged substantially. Consequently, these data suggest that some ecomorph types are more capable than others of reversing evolutionary direction and becoming less specialized when environmental conditions change. Thus, we conclude that evolutionary specialization is a two-way thoroughfare for some ecomorphs, but only a one-way avenue for others.

#### (d) *Anolis* radiation in the Lesser Antilles

The Lesser Antilles are considerably smaller than the Greater Antilles and are occupied by only 1 or 2 species of *Anolis*. Williams (1972) suggested that the simple faunas of the Lesser Antilles might be comparable with early stages in the Greater Antillean radiation. If this were so, then Lesser Antillean anoles should be similar to inferred early stages in Greater Antillean community evolution.

Examination of Lesser Antillean anoles does not offer much support to this hypothesis (J. Losos and K. de Queiroz, unpublished). Many Lesser Antillean species, including all species on one-species islands (the species for whom selective pressure to become a generalist might be strongest), are identifiable as trunk-crown ecomorphs. The phylogenetic analysis, however, suggests that generalists occurred in the early stages of Greater Antillean community evolution and that trunk-crown ecomorphs did not evolve until the four ecomorph stage.

Hence, we conclude that the Lesser Antilles are not analogous to early stages in the evolution of Greater Antillean communities, as Roughgarden & Pacala (1989) have argued. Why community evolution should differ between the Greater and Lesser Antilles is not immediately obvious. Possible explanations include differences in the non-anole faunas of the two islands (the Lesser Antilles are relatively depauperate faunistically) or differences in the initial starting conditions of the respective radiations. A better phylogeny for *Anolis* will allow evaluation of this latter hypothesis.

Another possibility is that the phylogenetic analysis has reconstructed incorrectly the early stages of Greater Antillean community evolution. This explanation is unlikely because the most basal lineage in both Jamaica and Puerto Rico is a twig anole, but nothing at all similar to a twig anole occurs in the Lesser Antilles. Evolution in the Greater Antilles would have to be both remarkably non-parsimonious and parallel if the early stages of the Greater Antillean radiation were actually similar to communities seen today in the Lesser Antilles.

## 5. CONCLUSIONS

For years, many ecologists ignored history in their studies of community structure. Implicitly, such studies assume that present-day processes are sufficiently powerful to lead to the same result regardless of

historically determined initial conditions. Recent years, however, have seen a widespread appreciation of the importance of historical effects; consequently, studies of community organization are increasingly incorporating phylogenetic information (see, for example, Losos 1990b, 1992; Richman & Price 1992; Gorman 1992; Grandcolas 1993).

None the less, a distinction must be made between questions that can be addressed by historical studies and those that cannot. In particular, historical studies investigate patterns of evolutionary change through time, but cannot directly examine whether a particular process operated historically. Of course, one can make predictions about what patterns should be observed if a process has been important over time and then compare such predictions with observed patterns. But such studies can only demonstrate consistency of results with predictions, rather than directly demonstrating the operation of a particular process over evolutionary time.

The most effective way to test whether a particular process has been important in community evolution is to show that: (1) the process is important in extant communities; (2) over microevolutionary time, the process leads to evolutionary change in the predicted direction; and (3) historical analyses are consistent with the process's being the driving force behind evolutionary change (Losos 1994). I suggest that these conditions have been met for the hypothesis that interspecific competition is the driving force behind adaptive radiation in Caribbean *Anolis* lizards.

More generally, these studies highlight the important role that phylogenetic approaches can play in the study of ecological phenomena. Such approaches are important not only for testing hypotheses, but also as the source of hypotheses that are ecologically testable. Indeed, without considering historical information, ecologists risk not only getting the wrong answers, but not even asking the correct questions.

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