ADAPTATION, SPECIATION, AND CONVERGENCE: A HIERARCHICAL ANALYSIS OF ADAPTIVE RADIATION IN CARIBBEAN *ANOLIS* LIZARDS[1]

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ABSTRACT

Caribbean *Anolis* lizards are a classic case of adaptive radiation, repeated four times across islands of the Greater Antilles. On each island, very similar patterns of evolutionary divergence have occurred, resulting in the evolution of the same set of ecological specialists—termed ecomorphs—on each island. However, this is only part of the story of the Caribbean anole radiations. Indeed, much of the species diversity of Caribbean *Anolis* occurs within clades of ecomorphs, which contain as many as 14 ecologically-similar species on a single island. We ask to what extent the classic model of ecological interactions as the driving force in adaptive radiation can account for this aspect of anole evolutionary diversity. Our answer is that it can in part, but not entirely. More generally, the most complete understanding of evolutionary diversification and radiation is achieved by studying multiple hierarchical evolutionary levels from clades to populations.

Key words: adaptive radiation, *Anolis*, Caribbean, ecomorphs, lizard, speciation.

Adaptive radiation is "evolutionary divergence of members of a single phylogenetic line into a variety of different adaptive forms" (Futuyma, 1998). Models of adaptive radiation (Simpson, 1953; Schluter, 2000) begin with a species in an environment in which resources are plentiful, but few, if any, other species are present to use them. Such a situation could occur in a number of ways, such as colonization of a new area, evolution of a trait that allows the species to use resources previously inaccessible to all species, or surviving a mass extinction. Through time, two things happen: species proliferate and resources become limiting. In some scenarios, speciation occurs first and only later do resources become limiting—this seems to be the model Simpson (1953) had in mind. Alternatively, in other models, resource limitation occurs first, thus driving speciation (e.g., Orr & Smith, 1998; Dieckmann & Doebeli, 1999). In either case, however, the main point is clear: species (or subpopulations of one initial species) alter their behavior and habitat use to partition resources, minimizing competitive interactions. Over time, the species (or subpopulations) evolve features to increase their adaptation to their new niches (i.e., character displacement occurs). In this scenario, multiple, possibly simultaneous, instances of character displacement ensue. The end-result is that a single species has given rise to a number of species each adapted to a different part of the environment—i.e., an adaptive radiation.

Both the definition of adaptive radiation and these models say nothing about the species richness of an adaptively-radiating clade. Indeed, such clades may not be rich in species, despite their ecological and phenotypic disparity. Examples of adaptive radiations with unexceptional species richness include Darwin's finches (Grant, 1986), pygopodid lizards (Webb & Shine, 1994; Jennings et al., 2003), and postglacial lake fish (Schluter, 1996). Nonetheless, many other adaptive radiations—e.g., Rift Lake cichlids (Verheyen et al., 2003), passerine birds (Lovette & Bermingham, 1999), Hawaiian silverswords (Baldwin, 1997)—exhibit not only great ecological and phenotypic disparity, but also exceptional species richness. This species richness is generally not obtained by adaptation to an extraordinary variety of different environments, but rather by the existence of sets of species that are ecologically similar, with each set adapted to a different part of the environment. Understanding the genesis and maintenance of this diversity obviously requires a more complicated model than the simple model of speciation and character displacement just discussed.

The goal of this paper is to examine one species-rich adaptive radiation, Caribbean lizards in the genus *Anolis* Daudin, 1802. By doing so, we hope, first, to

explore whether the classic model of adaptive radiation can adequately explain the ecological diversification of Caribbean anoles and, second, to examine the determinants of the great species richness of this radiation and investigate whether these determinants are related to the patterns of adaptive differentiation.

THE EVOLUTIONARY RADIATION OF CARIBBEAN ANOLES

The lizard genus *Anolis* is one of the largest genera of vertebrates (and the largest of amniotes), with well over 300 described species, 154 of which occur on islands in the Caribbean (Nicholson et al., 2005). Of particular interest are the anole faunas of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). On each of these islands, typical communities contain a number of species, each of which is morphologically distinct, behaves differently, and uses a different part of the structural habitat (e.g., on broad surfaces near the ground, on twigs, in grassy areas). Detailed functional and behavioral analyses support the hypothesis that the morphological differences between the species—in traits such as hindlimb length and toepad size—are adaptations to the functional demands imposed by living in different parts of the environment (e.g., Irschick et al., 1996; Larson & Losos, 1996; Elstrott & Irschick, 2004).

The most striking aspect of this diversity, however, is its repeated occurrence across all four Greater Antillean islands. For the most part, the same set of habitat specialists—termed "ecomorphs" and named for the part of the habitat in which they are usually found (Williams, 1972, 1983)—recurs on each island. In all, there are six ecomorphs: trunk, trunk-crown, trunk-ground, grass-bush, twig, and crown-giant. Four are found on all four islands, whereas grass-bush anoles are absent from Jamaica and trunk anoles are only found on Cuba and Hispaniola. Phylogenetic analysis of morphological and molecular data confirms Williams's pre-cladistic conclusion (1972, 1983) that the ecomorphs are independently derived on each island (Losos et al., 1998; Poe, 2004).

Two aspects of the ecomorph story have received relatively little attention in the years since Williams (1983) classic review. First, the ecomorphs are represented on each island, not necessarily by a single species, but sometimes by many. At the extreme, there are 14 trunk-ground and 15 grass-bush species on Cuba. All ecomorph types are represented by more than one species on at least one island, and at least two trunk-ground and trunk-crown species are present on all islands (Table 1).

Second, in addition to the ecomorphs that have evolved repeatedly on different islands, a number of

Table 1. Numbers of *Anolis* species of each ecomorph type on each island in the Greater Antilles.

	Cuba	Hispaniola	Jamaica	Puerto Rico
Crown-giant	6	3	1	1
Grass-bush	15	7	0	3
Trunk	1	6	0	0
Trunk-crown	5	4	2	2
Trunk-ground	14	9	2	3
Twig	5	4	1	1
Other/unique	12	8	1	0
Total	58	41	7	10

habitat specialists have evolved on only one island. These "unique" types include the semi-aquatic streamside *Anolis vermiculatus* Duméril & Bibron, 1837 on Cuba, the rock wall specialist *A. bartschi* Cochran, 1928 on Cuba, and the leaf-litter specialist *A.* (*Chamaelinorops*) *barbouri* Schmidt, 1919 on Hispaniola, among others. In some cases radiation has occurred subsequent to the evolution of such specialists; for example, four large species on Cuba (formerly comprising the genus *Chamaeleolis* Cocteau, 1838) are particularly slow-moving species specialized for narrow perches high in the canopy, and may prefer to feed on molluscan prey (Leal & Losos, 2000). All told, 21 such unique specialist species exist, 12 on Cuba, 8 on Hispaniola, 1 on Jamaica, and none on Puerto Rico (Table 1).

MOLECULAR PHYLOGENETIC PERSPECTIVE

Recent molecular studies have provided a phylogeny for most of the species in the entire Caribbean radiation (Jackman et al., 1999, 2002; Creer et al., 2001; Schneider et al., 2001; Glor et al., 2003, 2005; Harmon et al., 2003; Brandley & de Queiroz, 2004; Poe, 2004). The most recent phylogeny (Nicholson et al., 2005), based on sequence from a 1.8 kb region of mitochondrial DNA for 132 of the 154 Caribbean species, provides the ability to thoroughly examine the Caribbean anole radiation, including both ancient events deep in the tree and many of the more recent divergences. This examination reveals three patterns of interest that characterize anole evolutionary diversification in the Greater Antilles (Fig. 1):

(1) Ecomorphs have generally evolved only once on each island. Given that each ecomorph has evolved on multiple islands and that multiple representatives of each ecomorph type are present on most islands, one might predict that ecomorph types have evolved more than once within islands. The phylogeny, however, reveals this not to be the case. Most ecomorphs have
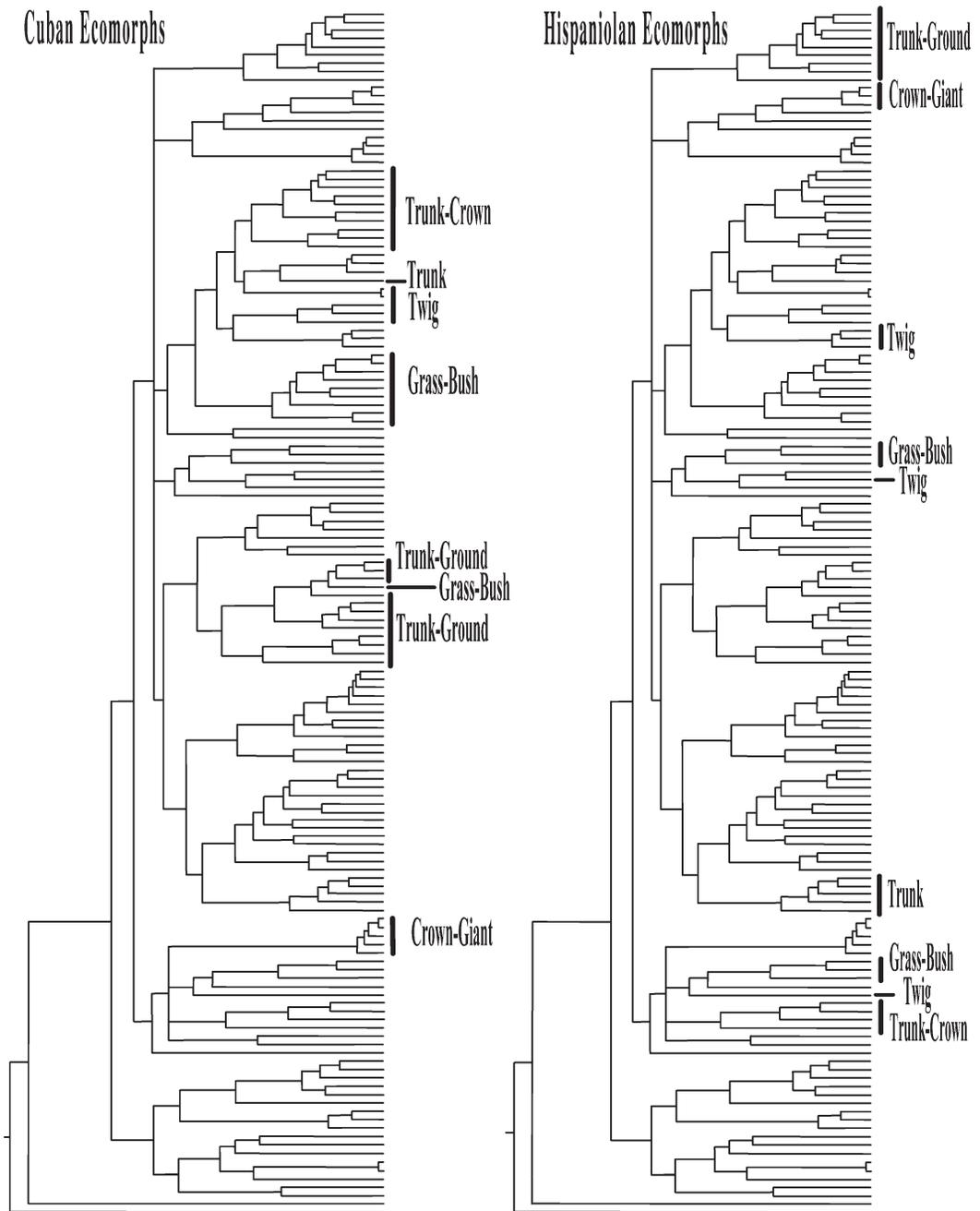
Figure 1. Island-by-island examination of the evolution of habitat specialization in the Greater Antilles. Anole phylogeny from Nicholson et al. (2005); branch lengths made ultrametric using penalized likelihood (Sanderson, 2002). Penalized likelihood was implemented using the program r8s (Sanderson, 2003). The smoothing parameter was 0.90, and branch lengths were scaled to relative time by assigning the root node an arbitrary age = 100. All Central and South American branches were subsequently pruned out using the program TreeEdit (Rambaut & Charleston, 2001). Terminal taxon names were removed for conciseness, but may be viewed, along with the tree file, online at <http://biology4.wustl.edu/~lososlab/anolis_mbg_2005/>. Ecomorph designation is based on previous analyses or, for some newly described species, represents new interpretations based on the species' description. In a few cases (Losos & de Queiroz, 1997; Glor et al., 2005), ecomorph species occur on nearby islands (e.g., the trunk-crown *carolinensis* group in Cuba also contains ecomorphologically similar species in the Bahamas, Little Cayman, Navassa, and Florida). In the figure, these species are included with their Greater Antillean relatives (i.e., all *carolinensis* group species are indicated as Cuban trunk-crown anoles).
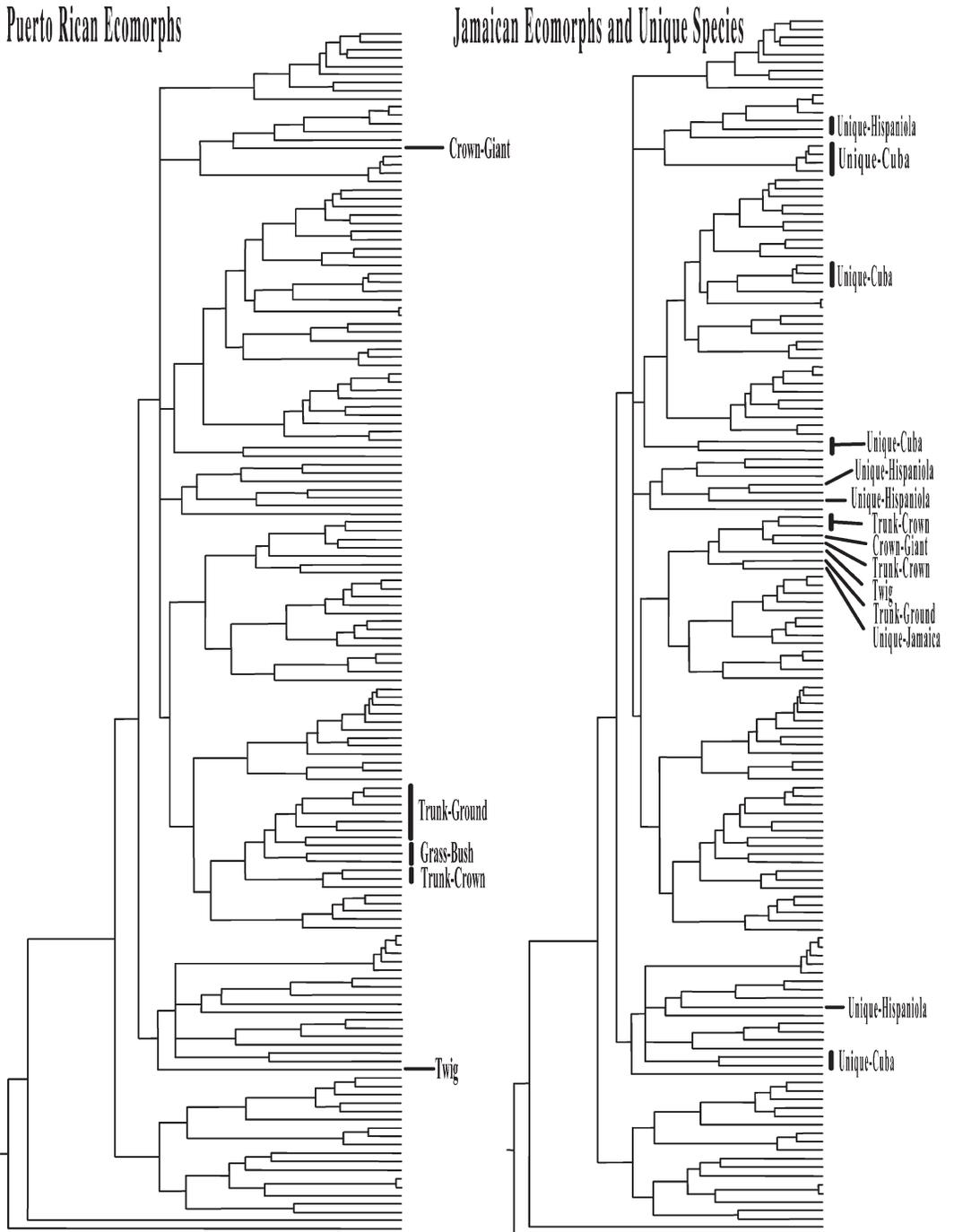
Figure 1.   Continued.

evolved only a single time on an island, though evidence exists for two instances of evolution of twig and grass-bush anoles on both Cuba and Hispaniola (however, a phylogeny in which the two twig lineages in Cuba are sister taxa, implying a single origin, is almost as well-supported as the phylogeny in Fig. 1).

In addition, either trunk-ground or grass-bush anoles have evolved twice on Puerto Rico (the nested position of the trunk-ground *Anolis gundlachi* Peters, 1876 within a clade of grass-bush anoles makes distinguishing between the two possibilities difficult; see Brandley & de Queiroz, 2004) and trunk-crown anoles

may have evolved twice on Jamaica (alternatively the crown giant *A. garmani* Stejneger, 1899 may have evolved from an ancestral trunk-crown anole).

(2) Ecomorphs are generally not phylogenetically nested within other ecomorphs. With few exceptions (e.g., the grass-bush anole, *Anolis ophiolepis* Cope, 1862, which arose from within a clade of Cuban trunk-ground anoles [Fig. 1] and the two other cases mentioned above), most ecomorph clades are monophyletic and do not give rise to other ecomorphs. The "unique" habitat specialists also rarely, if ever, arise from within a clade of one of the ecomorphs (Fig. 1; one possible exception is ambiguous: two Hispaniolan unique anoles, *A. eugenegrahami* Schwartz, 1978 and *A. christophei* Williams, 1960, form a clade with the clade of Hispaniolan crown-giants; in turn, the sister taxon to this clade is the Puerto Rican crown-giant *A. cuvieri* Merrem, 1820).

(3) Ecomorph and "unique" habitat specialist clades are old. Examination of Figure 1 indicates that almost all ecomorph clades arose in the first half of anole evolutionary history on most islands (the exception is Jamaica, the short branches of which support suggestions that Jamaica was underwater until well into the Miocene; but see Hedges, 2001). But how old does that make them in absolute terms? Very old, according to several lines of evidence. First, if one accepts clock-like evolution of the mtDNA region examined, the maximum pairwise difference among species exceeds 40% (after correction for multiple substitutions), which suggests evolutionary divergence more than 30 million years ago (based on calibration from Macey et al., 1998). Second, microcomplement fixation, an independent molecular clock estimation based on divergence in albumin proteins, provides a very similar estimate for the earliest divergence within *Anolis*, 35–40 million years (Shochat & Dessauer, 1981). Third, three fossil amber anoles from the Dominican Republic date to the Miocene or possibly older (Rieppel, 1980; de Queiroz et al., 1998; Polcyn et al., 2002). Two of these specimens are whole animals (the third, described by Polcyn et al. (2002) comprises little more than the head) and are morphometrically indistinguishable from extant trunk-crown anoles, indicating that at least one ecomorph clade was present > 20 million years ago (de Queiroz et al., 1998). Moreover, the trunk-crown anoles from Hispaniola, the *chlorocyanus* group, comprise an ancient clade (Fig. 1), and the amber specimens cannot be osteologically distinguished from extant members of this group.

The Role of Ecological Interactions in Driving Anole Diversification

The classic model of adaptive radiation posits that ecological interactions, primarily interspecific competition, drive ecological divergence and adaptation to different parts of the environment (Simpson, 1953; Schluter, 2000). A corollary of this hypothesis, however, would be the prediction that once one species specializes for a particular aspect of the environment, other lineages should have difficulty occupying this niche. This prediction could explain the paradox of ecomorph evolution: repeated evolution across islands, but few instances of multiple evolution within an island. Thus, it would appear that once an ecomorph evolves on an island, it achieves ecological incumbency and prevents other lineages from entering that niche. The inability of introduced species to become invasive when ecologically similar species already occur in an area, in contrast to their invasiveness in areas lacking such species, further supports this prediction (Losos et al., 1993).

The adaptive radiation scenario hinges on the assumption that anoles interact strongly. Indeed, a wealth of data (reviewed in Losos, 1994; Roughgarden, 1995; more recent examples include Leal et al., 1998; Losos & Spiller, 1999; Campbell, 2000) attests to the strength of interspecific interactions among anole species. These studies come in a variety of forms, including experimental manipulations, natural experiments, and comparative ecology. Studies document effects in terms of differences in growth rates, habitat use, reproductive rates, and density. Despite the great variety of study systems and approaches taken, one result is readily apparent: sympatric anole species tend to interact strongly. Review of these studies leads to several conclusions (Losos, 1994): first, the more similar species are ecologically, the stronger are the interactions between them; second, anole species alter their habitat use in the presence of ecologically similar species; and, third, anoles evolve phenotypically in response to shifts in habitat use.

Evolution within Ecomorphs

The evolutionary divergence and stasis of ecomorph types can reasonably be interpreted as the result of interspecific interactions. These interactions, however, also have likely played a role in within-ecomorph differentiation.

When examining diversity within ecomorph clades, several patterns are apparent. First, many species are allopatrically or parapatrically distributed. At least some of these allopatric forms are located in different mountain ranges. The most parsimonious explanation of these distributions is that they reflect the early stages of allopatric speciation: populations that have become isolated and diverged to the point that they are likely to be reproductively isolated. In this context, the use by anoles of their dewlap (an extensible flap of skin located on the throat; Fig. 2) in communication is fortuitous. Sympatric anole species invariably differ in some aspect of dewlap "design" (color, pattern, size); these differences appear to be used as species recognition signals (reviewed in Fleishman, 2000; Losos, 2004). As
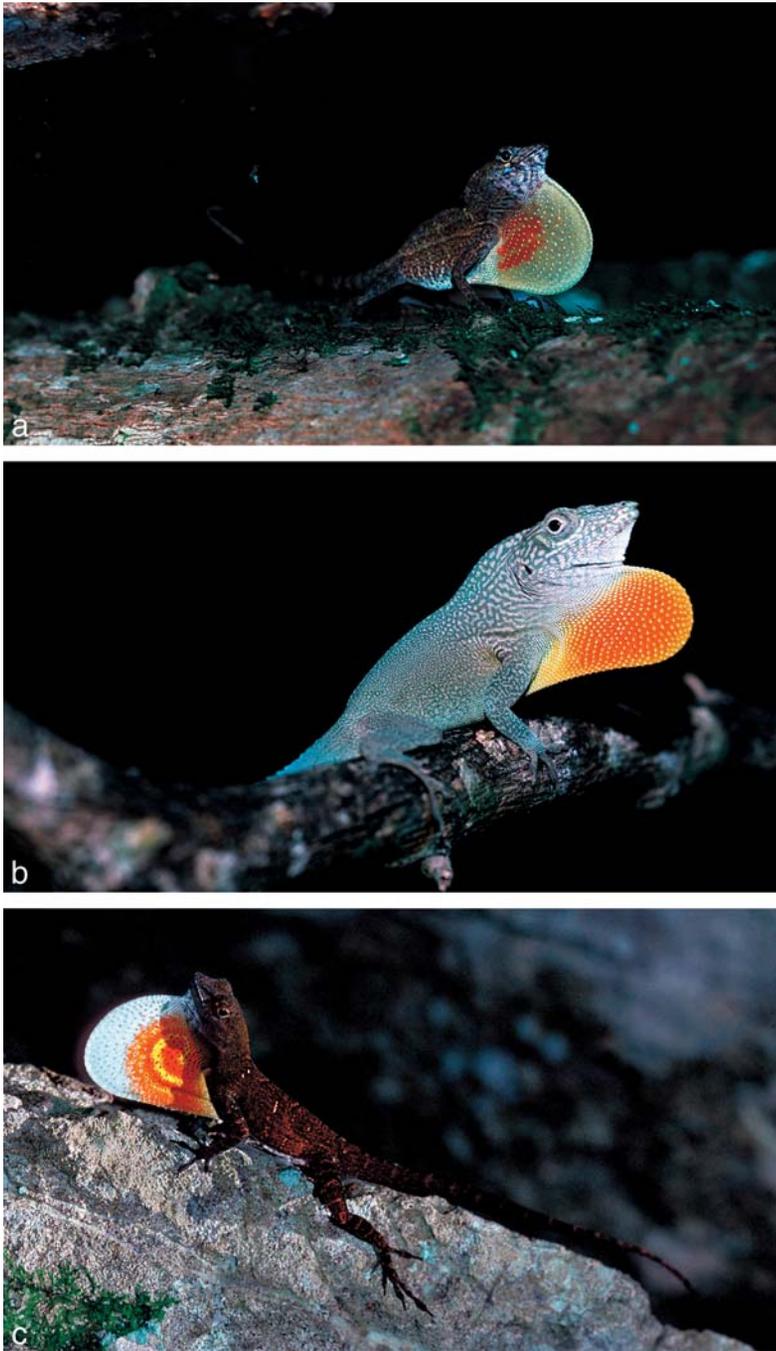
Figure 2.   Dewlap diversity in Caribbean anoles. —a. *Anolis allogus* (Barbour & Ramsden, 1919), Cuba. —b. *A. grahami* (Garman, 1888), Jamaica. —c. *A. mestrei*, Cuba.

a result, it is possible to identify allopatrically distributed taxa that are likely to be reproductively isolated in a non-arbitrary way.

Many of these allopatrically and parapatrically distributed taxa (which correspond to the concept of "allospecies" or "semi-species"; Mayr, 1963) appear to be ecologically very similar; that is, they are ecologically equivalent, but occur in different places. Of course, because the ranges of these species are often small and in out-of-the-way places, the ecology of many of these species is poorly known, so this statement must be considered tentative.

Not all of these species are ecologically similar, however. In some cases closely related species have differentiated to adapt to local conditions. For example, members of the *Anolis cybotes* Cope, 1862 group in Hispaniola are adapted to use a variety of different habitat types, such as pine forest, rocky terrains, and semi-deserts (Glor et al., 2003). Moreover, these ecological differences are so great as to permit sympatry in some cases, the extreme of which is the trunk-ground anoles of Soroa, in western Cuba, where four members of the *sagrei* group coexist. All four of these species can be distinguished ecologically by a combination of their thermal and structural microhabitats (one species occurs in hot, open habitats at the forest edge, a second in relatively open areas within the forest, and two in deep forest; the latter two, in turn, differ in their use of boulders within the forest, with one species, *A. mestrei* Barbour & Ramsden, 1916, always found on or near boulders or rock walls; Losos et al., 2003; see also Ruibal, 1961).

More generally, a pattern exists in the ecological means by which closely-related members of the same ecomorph type are able to coexist. In the ecomorphs that occur on or near the ground, the trunk-ground and grass-bush ecomorphs, sympatric species usually differ in thermal microhabitats, as just discussed for Soroa (sympatry of grass-bush anoles in eastern Cuba requires further study; at this point, ecological differences are not known, but few data are available). By contrast, sympatry in the more arboreal ecomorph types (trunk-crown and crown-giant) is correlated with differences in body size, which correlates with prey size (references in Losos, 1994). Thus, sympatric trunk-ground and grass-bush anoles tend to be approximately the same size, but occur in different microclimates, whereas sympatric trunk-crown, twig, and crown-giant anoles tend to be more similar in microhabitat, but differ in body size.

These patterns of ecological divergence in members of an ecomorph class lead to the following scenario: first, speciation occurs in allopatry. The mechanisms contributing to allopatric speciation within islands are poorly understood, but one recent study suggests that fluctuating sea levels and tectonic events have contributed to population fragmentation and allopatric divergence in Cuban trunk-crown anoles (Glor et al., 2004). Most allopatric populations remain ecologically similar (the concept of "niche conservatism"; Webb et al., 2002). This ecological similarity precludes sympatry when allopatric species come into contact, leading in some cases to parapatry. Second, in some instances, allospecies diverge to adapt to their local environments. Third, such divergence sometimes permits sympatry, leading to the coexistence of

members of the same ecomorph class, which partition resources along axes other than the structural habitat axis (which is the axis that is partitioned between ecomorphs). An alternative possibility, of course, is that the differences permitting coexistence arise after sympatry (the classic model of character displacement). Although detailed examination of particular cases is required to distinguish these two scenarios, the existence of ecological divergence in allospecies indicates that sympatry is not required to drive divergence.

WITHIN-SPECIES DIVERGENCE

Recent studies have added an unexpected new twist to the scenario detailed above. Studies beginning in the mid-1990s on several Lesser Antillean anole species revealed high levels of inter-populational genetic differentiation in mitochondrial DNA (Malhotra & Thorpe, 1994; Thorpe & Malhotra, 1996; Schneider, 1996). Although a number of subspecies had previously been described for some of these species (as many as 12 for *Anolis marmoratus* Duméril & Bibron, 1837 on Guadeloupe; Lazell, 1972), levels of genetic differentiation exceeding 9% uncorrected sequence divergence between geographic haplotype clades were unexpected, particularly for densely populated, mobile organisms such as Caribbean anoles.

Further research, however, reveals that the same pattern is found in Greater Antillean (Jackman et al., 2002; Glor et al., 2003, 2004; Kolbe et al., 2004) and Amazonian anoles (Glor et al., 2001). Ongoing research indicates that extremely high levels of geographic differentiation in mitochondrial DNA may be the norm (R. Glor, unpublished).

These results are exciting for several reasons. First, and most generally, they indicate that, despite 40 years of intensive work on anole evolutionary ecology, one aspect of anole diversity has been overlooked. Second, the results suggest the existence of unrecognized evolutionary units, perhaps worthy of recognition as species. As a result, the species diversity of anoles may, possibly, be much greater than previously recognized. Of course, robust diagnoses of morphologically cryptic species will require more than mitochondrial DNA data (Moritz, 1994; Sites & Crandall, 1997). Analyses of variation at a nuclear locus in one Cuban group supports the major intraspecific differentiation identified by mtDNA (Glor et al., 2004), but the same is not true of at least one Lesser Antillean species where the pattern of gene flow inferred from microsatellite data disagrees with that of mtDNA (Stenson et al., 2002). Further work examining other loci is necessary to test

the hypothesis that these forms are genetically distinct.

If these forms are genetically distinct, then what are currently recognized as single, island-wide species in the Greater Antilles may, in fact, be complexes of parapatrically-distributed species. Such parapatry would suggest that the forms are ecologically identical and thus unable to coexist in sympatry. Certainly, ecological differences had not previously been identified for most of these populations, so the hypothesis is reasonable, though requiring further, detailed investigation. Nonetheless, to the extent that the hypothesis is correct, then these recent findings on intraspecific differentiation extend the scenario for differentiation proposed above for semispecies: the first step in differentiation may be the evolution of ecologically similar forms that occur in allo- or parapatry; evidence of these forms comes not only from allopatrically distributed populations recognized as different species, but also by the existence of genetically differentiated populations that are parapatrically-distributed and may be reproductively isolated.

CONCLUSIONS

Evolutionary diversification of *Anolis* lizards in the Greater Antilles conforms to our ideas about adaptive radiation. On each island, species have diversified, producing a set of species adapted to different ecological niches. Studies on extant species indicate that sympatric species routinely experience strong ecological interactions, the strength of which is a function of how similar ecologically two species are. Moreover, species alter their resource use in the presence of ecologically similar congeners and, over evolutionary time, evolve adaptations to their altered regime of resource use. In sum, the evidence for ecological interactions as the driving force in adaptive radiation is probably as strong for Caribbean anoles as it is for any other group.

However, this is not the whole story for the Caribbean anole radiation. Many closely-related species are ecologically similar, but not sympatric. Ecological divergence appears to play little role in the speciation process of these species (at least ecological divergence that relates to resource partitioning among sympatric species; see Losos, 2004). Moreover, some of these semispecies have diverged ecologically to adapt to the particular environment in which they occur. Thus, not all speciation is related to ecological divergence, and not all ecological divergence is related to resource partitioning among sympatric species.

Nonetheless, when these closely related species—which occupy the same structural habitat niche and are members of the same ecomorph class—are found sympatrically, they do partition resources. Whether the differences among these species arise prior to sympatry and are a necessary prerequisite for co-existence, or whether they arise after sympatry in the same sort of character displacement process presumably responsible for ecological divergence between the ecomorphs, is not yet clear.

Regardless, these closely related sympatric species indicate that adaptive radiation has occurred within, as well as between, ecomorph classes. At least some, but certainly not all, of the diversity within ecomorphs is the result of the same sort of evolutionary ecological processes responsible, at a deeper phylogenetic level, for evolution of the ecomorphs themselves.

A second message to be taken from the anole story is that adaptive radiations often must be studied at multiple levels: at the level of clades, species, and populations. Only by studying all of these levels can we get the most complete picture of the patterns and processes responsible for evolutionary diversification in Caribbean anoles.

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