

## THE EVOLUTION OF CONVERGENT STRUCTURE IN CARIBBEAN *ANOLIS* COMMUNITIES

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*Abstract.*—Just as the factors responsible for the origin of an adaptation may not be responsible for its maintenance, the processes currently operating in a community may not have been important in assembling the community. Consequently, historical and ecological studies must be integrated to understand why communities are structured as they are. Examples from Caribbean *Anolis* assemblages indicate the unique ecological insight a historical perspective can provide. In the Lesser Antilles, phylogenetic analysis indicates that character displacement probably has occurred, but perhaps only once, and that patterns of size dissimilarity across islands result from ecological size assortment subsequent to the evolutionary change in size. In the Greater Antilles, not only are communities composed of a suite of convergent "ecomorphs," but the buildup of multispecies communities has followed a very similar trajectory, a finding not demonstrable by nonhistorical analyses. Further, phylogenetic analyses suggest the appropriate direction for ecological research concerning the occurrence of "empty niches." [*Anolis*; character displacement; community assembly; ecomorphology; niche; null model; phylogeny.]

In the study of adaptation, an important distinction exists between the factors responsible for the origin and for the maintenance of a given feature (Gould and Vrba, 1982). A feature may evolve for one reason, but selection may currently maintain it for a different reason. A classic, if still controversial, example concerns the evolution of feathers, which may have evolved first to enhance thermoregulation but then been elaborated to promote flying ability (Gauthier and Padian, 1985; Padian, 1986; Rayner, 1991; and references therein). Consequently, studies on extant populations do not, in themselves, provide information on macroevolutionary events, although they may be informative about ongoing within-population processes. Only when such data are considered in an explicitly historical context can evolutionary inferences be drawn (Greene, 1986; Donoghue, 1989; Baum and Larson, 1991; Losos and Miles, 1993).

A similar distinction can be made in studies of community structure. Investigations of extant communities may indicate what processes are currently operating, but these data may reveal little about the historical path by which the community came to its present state (Ricklefs, 1987; Drake, 1990, 1991; Brooks and McLennan,

1991; Gorman, 1992). A historical perspective is important in community ecology because current conditions may not be indicative of those operating in earlier stages of community buildup and because evolutionary coadjustments of community members may play an important role in community assembly. For example, in a laboratory study, Drake (1991) found that communities with similar compositions could result from radically different sequences of ecological events.

In this paper, I argue that a historical perspective can provide insight on community structure that could not be gained by ecological studies alone. My examples come from assemblages of *Anolis* lizards on islands in the Caribbean. On these islands, which contain from 1 to >40 species, anoles are the predominant diurnal, arboreal, and insectivorous lizards and are often spectacularly abundant. I begin with consideration of the simple anole assemblages of the Lesser Antilles and then move to the more complex faunas of the Greater Antilles.

### LESSER ANTILLES

A remarkable pattern exists on islands in the northern Lesser Antilles, which are occupied by either one or two species of

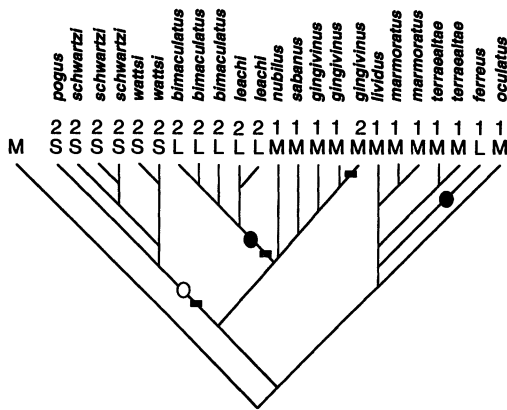


FIGURE 1. Phylogeny for the anoles of the northern Lesser Antilles (modified from Losos, 1990c; based on Roughgarden et al., 1987). Numbers indicate the number of *Anolis* species on the island occupied by each taxon. Letters indicate body size (small, medium, or large). Circles represent major evolutionary change in body size (solid = increase; open = decrease); bars represent the transition from an ancestor on a one-species island to the descendant on a two-species island. The statistical analysis in Losos (1990c) used actual values for body size rather than categorical variables.

anolis (Schoener, 1970). Ten of the 11 one-species islands contain an intermediate-sized species, and 5 of the 6 two-species islands contain a large and a small species. This pattern is decidedly nonrandom (Schoener, 1988; Losos, 1990c) but could result from two quite distinct processes. Size assortment (*sensu* Case and Sidell, 1983) is an ecological process that takes place when species too similar in size cannot coexist because they compete too strongly for food (a tight relationship between body size and prey size has been documented for anoles [Rand, 1967; Schoener, 1967, 1968; Schoener and Gorman, 1968; Roughgarden, 1974]). A stable two-species fauna might only result when an island is colonized by two species dissimilar enough in size that competition did not cause competitive exclusion. The observation that one-species islands generally harbor an intermediate-sized species suggests that these species are able to exclude larger and smaller species, which accords with the results of foraging models that indicate that intermediate size is optimal for the prey base found on these islands (Naganuma and Roughgarden, 1990).

Alternatively, patterns of size dissimilarity could result from the evolutionary process of character displacement (Brown and Wilson, 1956; Schoener, 1970; Lazell, 1972; Williams, 1972)—two initially intermediate-sized species come into sympatry, perhaps because one colonizes an island occupied by the second, and subsequently diverge in body size, thus minimizing competition and allowing coexistence (Roughgarden and colleagues have proposed an alternative coevolutionary hypothesis, the taxon-loop model, which is discussed at length elsewhere [Roughgarden and Pacala, 1989; Losos, 1992; Roughgarden, 1992; and references therein]).

These processes can produce identical biogeographical patterns and are difficult to distinguish with population-level analyses (witness the theoretical and empirical debate about how frequently character displacement occurs [e.g., Slatkin, 1980; Taper and Case, 1985, 1992; Schoener, 1986; Taper, 1988; Dayan et al., 1989; Vadas, 1990]). The two processes do differ, however, in their historical pattern. The character-displacement hypothesis predicts that ancestrally, intermediate-sized taxa occurred on one-species islands. The evolution of larger and smaller size should occur coincident with the transition from a one-species island to a two-species island. By contrast, the size assortment hypothesis does not specify why changes in body size occur but does predict that only lineages that have previously evolved to larger and smaller sizes can stably come into coexistence (see figures in Losos, 1990c).

These differing hypotheses can be tested in the context of a phylogeny for the anoles of the northern Lesser Antilles, which form a monophyletic group (Fig. 1; Losos, 1990c). Inspection of the phylogeny reveals that all of the small species are members of a monophyletic clade and, similarly, the large species on the two-species islands form a second monophyletic clade (although support for the sister-group status of *A. bimaculatus* and *A. leachi* is not strong [see Lazell, 1972; Gorman and Kim, 1976; Roughgarden and Pacala, 1989]). Consequently, the most parsimonious interpretation is that large and small size evolved

only once in these clades. Whether ancestral taxa occupied one- or two-species islands can also be inferred via parsimony (probably the weakest link in this analysis; see Losos [1990c] for justification). Based on this reasoning, the transition from one- to two-species islands occurred simultaneously with the evolution of large and small size (Fig. 1)—exactly the prediction of the character displacement hypothesis. However, the data only provide evidence for one instance of character displacement, which suggests that the widespread pattern of size dissimilarity has resulted from size assortment subsequent to the evolution of size differences.

One frequent objection to the reasoning presented here is that it assumes that size changes occur infrequently, despite the copious literature attesting to the evolutionary lability of body size (e.g., Falconer, 1981). The use of parsimony necessitates no such assumption, but it does identify the minimum number of evolutionary events consistent with the data. Applying this reasoning to the *Anolis* example seems reasonable. If size changes had occurred numerous times, one would expect them to have occurred in numerous lineages. Explaining why changes in size should have occurred in parallel in all members of two lineages but not in members of other lineages (with one aberrant exception, *A. ferreus*) requires further ad hoc arguments (it is possible, of course, that lineages differ in the likelihood of evolutionary changes in body size in the presence of competitors). Smaller size could have evolved independently six times in the *A. wattsi* lineage, for example; still, no evidence supports this interpretation. The parsimony interpretation provides the only evidence of which we can be reasonably sure, i.e., that smaller size has evolved at least once in the *wattsi* lineage and larger size at least once in the *bimaculatus-leachi* lineage.

In summary, the historical approach allows demonstration that both character displacement and size assortment have been operating in the anole faunas of the northern Lesser Antilles and allows an assessment of the relative importance of these

two processes in generating observed patterns. Neither of these conclusions is possible without recourse to the information provided by a phylogenetic perspective.

#### GREATER ANTILLES

The more complex faunas of the Greater Antilles provide a greater challenge. Species numbers on these islands range from 7 on Jamaica to 40+ on Cuba and Hispaniola, with as many as 10 species sympatric in some locations (Williams, 1983). Although anole phylogeny is still highly controversial (e.g., Guyer and Savage, 1986, 1992; Cannatella and de Queiroz, 1989; Williams, 1989; Burnell and Hedges, 1990), it is clear that evolutionary radiations have occurred more or less independently on the four islands (relationships between Cuban and Hispaniolan anoles are particularly unclear, however). On each island, diversification has produced a suite of "ecomorphs" distinct in morphology, ecology, and behavior (Williams, 1972, 1983). Further, the relationship between morphology, ecology, and behavior makes sense in functional terms. For example, the robust and long-legged "trunk-ground" ecomorph occurs on the lower portions of tree trunks and uses its jumping and running abilities to forage on the ground, whereas the short-legged "twig" ecomorph crawls slowly on narrow supports on the periphery of trees. In all, there are six ecomorph types (Table 1; Williams [1983] divides several of the types more finely). Most strikingly, the same "ecomorph" types have evolved on all four islands, producing apparently convergent assemblages. The assemblages are not identical, however, because one ecomorph type, the "grass-bush" ecomorph, is absent on Jamaica and the "trunk" ecomorph occurs on neither Jamaica nor Puerto Rico.

#### *Models for Anole Radiation*

Because the faunas on each island are primarily the result of in situ differentiation, a historical analysis is crucial to understanding how and why the communities have converged, as well as understanding the differences among islands. Fortunately, reliable phylogenies exist for

TABLE 1. Characteristics of anole ecomorph types.

Ecormorph	SVL <sup>a</sup> (mm)	Shape	Hind limb <sup>b</sup>	FL/HL <sup>c</sup>	Tail	Color	No. sub- digital lamel- lae
Trunk-ground	55-75	stocky	long	short	long	brown or gray	17-20
Grass-bush	45-50	slender	long	short	very long	brown, yellow stripe	17-20
Trunk	45-60	intermediate	mod. long	mod. long	mod. short	gray	17-18
Trunk-crown	45-80	intermediate	intermediate	intermediate	intermediate	green	19-28
Crown-giant	>120	intermediate	intermediate	intermediate	intermediate	green or brown	28-35
Twig	40-85	very thin	very short	long	short	white	18-23

<sup>a</sup> Snout-vent length.

<sup>b</sup> Hind limb length relative to body size.

<sup>c</sup> Forelimb length relative to hind limb length.

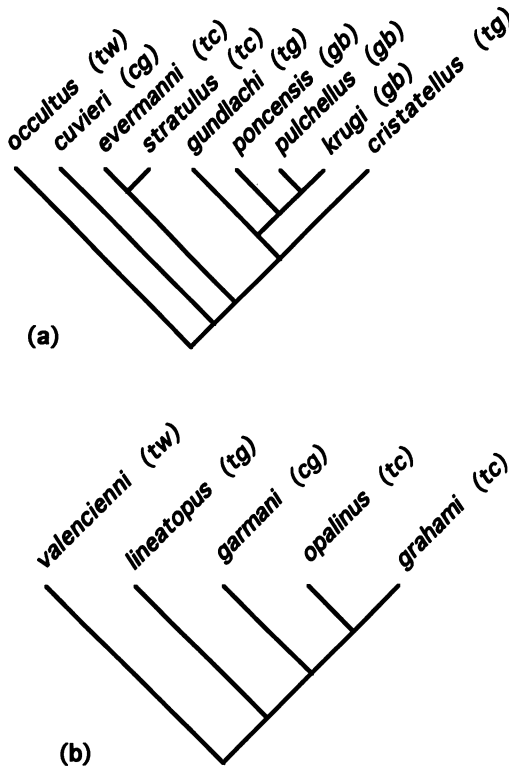


FIGURE 2. (a) Phylogeny for anoles of Puerto Rico. (b) Phylogeny for anoles of Jamaica. *Anolis reconditus*, *A. cooki*, and *A. sagrei* are omitted because (1) data were not available for *A. reconditus* and *A. cooki* and (2) *A. sagrei* is a very recent colonist and not a member of the Jamaican radiation. The *garmani-grahami-opalinus* trichotomy of Hedges and Burnell (1990) is resolved with *grahami* and *opalinus* as sister taxa because of their shared morphological similarities, which were not included in the analysis of Hedges and Burnell (1990; see their discussion). Ecomorph designations: tw = twig; cg = crown-giant; tc = trunk-crown; tg = trunk-ground; gb = grass-bush.

the faunas of Puerto Rico (Fig. 2a; Williams, 1972; Gorman et al., 1983) and Jamaica (Fig. 2b; Hedges and Burnell, 1990).

Two hypotheses could explain the evolutionary assembly of anole faunas. Williams (1972), in a study well ahead of its time, mapped ecological and morphological characters onto a phylogeny for Puerto Rican *Anolis* and concluded that the processes governing faunal buildup in the Greater Antilles were an extension of those operating in the Lesser Antilles. In particular, he suggested that repeated episodes of character displacement led to two and then three species occupying the crown of the tree but diverging in body size. To maintain the same degree of separation in size seen in the Lesser Antilles, however, three species would span the entire range in size demonstrated by extant *Anolis*; it seemed unlikely that a fourth species could fit in by further divergence in size. Consequently, Williams hypothesized that additional species could only be added to the assemblage by moving into additional habitats lower on the tree. The fourth species to be added, the trunk-ground ecomorph, thus was suggested to have moved down to the base of the tree, and the fifth, the grass-bush ecomorph, deserted the tree entirely.

This scenario makes clear phylogenetic predictions: faunal buildup should first be accomplished by evolution in size and subsequently by change in microhabitat. These predictions can be tested by examining the evolution of body size (represented by snout-vent length) in the context of phylogenies for Puerto Rico and Jamaica. According to the character displacement hy-

pothesis, change in body size should be inferred to have occurred early in the radiation—primarily in the initial diversification events—with habitat specialization evolving more recently.

An alternative hypothesis for the assembly of anole communities can be derived by an extension of the niche compression hypothesis (MacArthur and Pianka, 1966; MacArthur and Wilson, 1967; Schoener, 1974; Schoener et al., 1979) to evolutionary time. If search costs are high relative to handling and capture costs, the niche compression hypothesis suggests that sympatric competing species should utilize different microhabitats but continue to capture all suitable prey rather than continuing to search all habitats but partitioning which prey they utilize. Consequently, over evolutionary time, the species should evolve specializations for these microhabitats. Only after all microhabitats have been occupied should species partition food resources within habitats (see Fox [1987] for a similar hypothesis concerning the evolution of small-mammal communities).

Thus, in direct contradiction to the character displacement hypothesis, the niche compression scenario predicts that the evolution of community structure should primarily occur via divergence in microhabitat use, with the partitioning of food resources (perhaps via size differences) evolving secondarily. This hypothesis can be tested phylogenetically by inferring the structure and composition of intermediate communities (i.e., communities composed of one, two, and three species). The niche compression hypothesis predicts that specialization to distinctive microhabitats (which characterize the extant ecomorphs) should occur during each of the first few diversification events. The hypothesis can be rejected if specialization did not occur until relatively late in the radiation.

## MATERIALS AND METHODS

### *Existence of Ecomorphs*

Before undertaking such an evolutionary analysis, however, it is important to verify that the suggested patterns exist and require explanation. If the ecomorph types

are real entities, then members of each type should be more similar to each other than they are to other species from their own island. The ecomorph types are most clearly and easily defined in terms of morphological differences, and morphological data are used in the following analyses. Nonetheless, the ecomorph types can also be distinguished by differences in both ecology and behavior, to which morphology is strongly correlated (Rand and Williams, 1969; Moermond, 1979a, 1979b; Pounds, 1988; Losos, 1990a, 1990b).

The ecomorphs traditionally have been differentiated morphologically on the basis of snout-vent length (SVL), hind limb and forelimb length, tail length, mass, and subdigital lamellae number (Mayer, 1989; Losos, 1990b). Morphological data for 15 Puerto Rican and Jamaican species were presented by Losos (1990b), which should be consulted for further details on character measurements. Table 2 presents data for 13 species of Hispaniolan *Anolis* (it has not yet been possible to conduct field work in Cuba). Values represent means of, ideally, 15 adult males, although for a number of species fewer individuals were procured. Values for each of the variables increase with SVL among species of *Anolis* (Losos, 1990d, unpubl.); in addition, all but lamellae number increase with SVL within species (Losos, unpubl. data).

To compare shape among taxa, it is thus necessary to account for morphological variation that results from differences in body size. For these data, the first axis of a principal components analysis is not interpretable as a size axis; other methods for size correction (e.g., Burnaby's [1966] method) are no more successful (Losos, unpubl.). Consequently, I followed herpetological convention and chose SVL as a measure of size (SVL is highly correlated with all other variables), regressed each variable on SVL (using mean values for each species; all variables ln transformed), and used the residuals of these regressions in subsequent analyses. To reduce the dimensionality of the data, a principal components (PC) analysis was then conducted, based on a correlation matrix of the five residual variables and ln(SVL).

TABLE 2. Morphological data<sup>a</sup> for Hispaniolan *Anolis* species.

Species	Ecomorph <sup>b</sup>	n <sup>c</sup>	SVL <sup>d</sup> (mm)	Mass (g)	Tail (mm)	Forelimb (mm)	Hind limb (mm)	No. subdigital lamellae <sup>e</sup>
<i>aliniger</i>	TC	10	55.9 (0.99)	4.7 (0.25)	92.3 (2.14)	23.7 (0.27)	34.8 (0.34)	22.5
<i>bahorucoensis</i>	GB	15	43.9 (0.45)	1.7 (0.05)	111.4 (3.52)	17.9 (0.28)	36.2 (0.42)	19.5
<i>baleatus</i>	CG	3	156.3 (7.15)	80.8 (5.13)	275	67.7 (2.68)	105.3 (1.08)	31.0
<i>chlorocyanus</i>	TC	9	68.7 (1.60)	6.9 (0.41)	133.8 (5.46)	28.2 (0.61)	43.9 (0.93)	27.0
<i>christopheii</i>	? <sup>f</sup>	13	46.6 (1.02)	2.2 (0.25)	84.6 (4.62)	24.8 (0.36)	38.8 (0.54)	17.7
<i>coelestinus</i>	TC	3	71.7 (4.71)	9.3 (1.51)	128.0 (9.27)	30.3 (2.16)	47.7 (2.48)	27.9
<i>cybotes</i>	TG	15	66.9 (0.93)	9.3 (0.34)	124.4 (2.98)	32.2 (0.55)	54.8 (0.63)	17.7
<i>distichus</i>	TR	15	51.3 (0.65)	3.9 (0.09)	71.5 (3.25)	25.9 (0.26)	38.3 (0.50)	17.6
<i>insolitus</i>	TW	5	41.8 (0.55)	1.0 (0.07)	53.2 (0.96)	13.2 (0.42)	23.4 (0.50)	15.0
<i>longitibialis</i>	TG	15	69.8 (0.60)	9.1 (0.30)	146.6 (3.14)	37.2 (0.36)	61.0 (0.69)	17.6
<i>olssoni</i>	GB	13	46.5 (0.45)	1.6 (0.06)	141.4 (1.85)	16.5 (0.22)	35.8 (0.29)	18.8
<i>semilineatus</i>	GB	2	41.8 (1.77)	1.5 (0.14)	129.0 (9.90)	16.0 (0.00)	34.5 (0.71)	20.5
<i>singularis</i>	TC	1	46	2.2	77	18	27	23.0

<sup>a</sup> Mean (SE).

<sup>b</sup> CG = crown-giant; GB = grass-bush; TC = trunk-crown; TG = trunk-ground; TR = trunk; TW = twig.

<sup>c</sup> Sample sizes for tail measurements are smaller because regenerated tails are not included.

<sup>d</sup> Snout-vent length.

<sup>e</sup> Data from Mayer (1989), except for *longitibialis* and *semilineatus*.

<sup>f</sup> *christopheii* is a member of the distinctive montane fauna of Hispaniola (Williams, 1983) and is ecologically and behaviorally intermediate between a trunk and a trunk-ground ecomorph (Losos, unpubl.).

Two attributes characterize the ecomorph phenomenon: (1) the same set of ecomorph types occurs repeatedly in the Greater Antilles and (2) the occurrence of ecomorph types is nested among islands such that no island contains an ecomorph type absent from an island that contains a greater number of ecomorph types. I devised null models to test how likely such patterns are to occur by chance alone.

If the same ecomorph types occur on different islands, then members of each ecomorph type should cluster together in morphological space regardless of geographic origin or lineage. This hypothesis was examined in two ways. First, multivariate analysis of variance (MANOVA) was used to confirm that the ecomorph centroids differ in their position in a four-dimensional morphospace defined by spec-

ies' scores on the first four PC axes. Second, a UPGMA phenogram was constructed based on the PC scores (using NTSYS, version 1.60 [Rohlf, 1990]). To test whether species clustered by ecomorph type to a greater extent than would be expected by chance, the ecomorph type of each species in the UPGMA phenogram was randomly reassigned with the constraint that the frequency of each ecomorph type remained unchanged (see Manly, 1991). For each arrangement (one real plus 249 randomizations), the test score ( $T$ ) was calculated as the number of taxa that would need to be moved to another location on the phenogram to make the species cluster perfectly by ecomorph (i.e., based on the phenogram, all members of each ecomorph type are closer in morphological space, as indicated by the phenogram, to all other

members of that ecomorph type than to any member of another ecomorph type). For the purposes of this statistic, *A. christophei* (ecomorph = ?) did not need to be moved if it clustered with either the trunk or trunk-ground anoles (see Table 2 footnote). Because the ecomorph types were initially defined on the basis of behavior and ecology as well as morphology (Rand and Williams, 1969), it is legitimate to ask how often species cluster according to pre-conceived groups.

In a similar vein, one can ask whether the distribution of ecomorph types across islands is nonrandom. To test this question, the island occupied by each species in the observed phenogram was reassigned randomly with the constraint that the appropriate number of species on each island was maintained. Again, 249 simulation phenograms were analyzed. The test statistic concerned whether a hypothetical phenogram was as nested as the real phenogram. The real phenogram has four clusters (=ecomorph types) containing species from all three islands, one cluster containing species from two islands, and one cluster containing species from only one island, and that island is one of the islands in the two-island cluster. For a hypothetical phenogram to be considered as or more nested than the real phenogram, it must contain (1) one or more clusters containing species from only one island (if there is more than one such cluster, all clusters must have members from the same island), (2) one or more clusters with species from two islands, one of which is the island represented in the one-island cluster (if there is more than one such cluster, all clusters must have members from the same two islands), and (3) four or more clusters with species from all three islands. All species must belong to one and only one cluster. A cluster was defined as that grouping on the phenogram in which all species were indicated to be more similar to each other than any was to a species not within the group (i.e., analogous to the definition of monophyly on a cladogram).

A more restrictive null model would limit clusters to the more highly differ-

entiated groups (the lower on the phenogram a cluster diverges from its nearest neighbor, the more distinct that cluster is). In this null model, the only clusters examined in the randomization phenograms were those as distinctive as the least differentiated ecomorphs in the observed phenogram (the trunk and trunk-ground clusters). These clusters in the randomizations were then examined by the criteria outlined above to determine whether they were as nested as the clusters in the real phenogram.

For these null models, the null hypothesis can be rejected if fewer than 5% of the hypothetical phenograms are as or more nested than the real phenogram.

#### *Community Evolution*

The morphology of ancestral taxa was inferred using parsimony methods (=character optimization; Maddison and Maddison, 1987) based on existing molecular phylogenies of the anoles of Jamaica and Puerto Rico. Parsimony algorithms considered only members of the ingroup because appropriate outgroups for both island radiations are unclear. As a result, the morphology of the ancestral taxon in each radiation cannot be determined. The results were generally unchanged by the selection of different ecomorphs or Lesser Antillean taxa as the outgroup, except that the reconstruction of size evolution was affected when extreme morphologies (which ecologically are unlikely colonists [Williams, 1969; Schoener, 1988]) were used (Losos, unpubl.). The evolution of size was investigated by reconstructing the SVL of ancestral taxa using the parsimony algorithm of Swofford and Maddison (1987), which minimizes the absolute amount of character evolution summed over the entire tree.

To compare the sequence by which the ecomorphs had evolved on the two islands, it was necessary to reconstruct the morphology of ancestral taxa. The position of ancestral taxa in morphological space was inferred by independently reconstructing the scores for each of the four PC axes, based on the cladogram and the scores of

extant taxa and using the Swofford and Maddison parsimony algorithm. The position of each ancestral taxon in morphological space was then compared with the position of the extant ecomorphs. If the position of a hypothetical ancestor in morphological space lay within or adjacent to the boundaries defined by the extant members of an ecomorph type, then that ancestor was considered to have been a member of that ecomorph. If a hypothetical ancestor was reconstructed as occurring in a position in morphological space on any of the four PC axes not occupied by any extant ecomorphs, then it was considered to be morphologically—and presumably ecologically—different from the extant ecomorphs. These ancestors are henceforth termed “generalists” because their position invariably was intermediate between extant ecomorph types.

To assess the similarity in the sequence of morphotype evolution in the two communities, I compared the positions in morphological space of hypothetical taxa at the two-, three-, and four-species stages of community development (i.e., after the first, second, and third speciation events). At each stage, I compared each hypothetical species on one island to the nearest species in morphological space on the other island to determine whether they were the same ecomorph type. If the faunas of the two communities were identical (i.e., a one-to-one match in ecomorph types), then a score of 0 was awarded. Otherwise, one point was awarded for each pair of nearest neighbors that were not of the same ecomorph type (or were not both generalists). The test statistic ( $Q$ ) for each randomization was the sum of points awarded at each stage.

To determine the statistical significance of the observed similarity in evolutionary sequence between the two islands, it is necessary to generate a null distribution of  $Q$ . A null model to investigate whether two communities evolved in similar ways requires (1) reconstruction of the evolution of hypothetical communities and (2) measurement of how similar the sequence of morphotype evolution is between these

communities. To create hypothetical communities, the position of the species on the cladogram for each island was randomly rearranged, with the constraint that each species still occurred only once and on its native island. Then, the evolution of the two hypothetical communities (one randomized from Puerto Rico, the other from Jamaica) was reconstructed using parsimony methods as above.  $Q$  was calculated as above, with the exception that five-species communities were also compared when the same set of ecomorphs did not occur in both communities at the four-species stage. The null hypothesis, that the observed similarity in evolutionary sequence between Jamaica and Puerto Rico is the result of chance, can be rejected if the similarity between the evolutionary pathways for Puerto Rico and Jamaica (the value for  $Q$ ) is in the bottom 5% of the 199 randomizations.

As a conservative measure, only one of the three Puerto Rican grass-bush anoles (*A. pulchellus*) was used in the randomization because they are very similar morphologically, form a monophyletic group, and do not occur on Jamaica. The inclusion of all three taxa in the randomization would decrease the probability that the two islands would demonstrate similar evolutionary paths in the null model.

Two caveats to the reconstruction of ecomorph types must be stated. First, the *Anolis* of Puerto Rico are not actually monophyletic; they probably represent three separate lineages: the ancestors of *occultus*, *cuvieri*, and the other seven taxa (the *crisatellus* series). Although the phylogenetic affinities of the first two groups are uncertain, it is likely that they are the result of relatively early divergence events in anole radiation. Consequently, the temporal patterns inferred below are probably not greatly mistaken. Until their close relatives are identified, it will not be possible to determine to what extent their morphology reflects their ancestry and to what extent it reflects coevolutionary change subsequent to their arrival on Puerto Rico. For the purposes of this analysis, Puerto Rican anoles are treated as a monophyletic group,



TABLE 3. Factor loadings for principal components analysis. Variables are ln(SVL) and residuals from regressions against ln SVL.

Variable	Axis			
	1	2	3	4
SVL <sup>a</sup>	0.027	0.147	0.984	-0.096
Mass	0.829	0.176	0.014	0.414
Forelimb	0.893	0.222	-0.006	0.278
Hind limb	0.953	-0.161	-0.014	-0.181
Tail	0.533	-0.743	0.059	-0.382
No. lamellae	-0.314	-0.639	0.163	0.678
Eigenvalue	2.78	1.09	1.00	0.21
% variance	46.3	18.1	16.6	14.9

<sup>a</sup> Snout-vent length.

with the understanding that a reanalysis may be warranted when anole phylogeny is more fully understood.

Second, parsimony methods cannot specify where on a branch anagenetic change occurs. For example, twig anoles may have evolved to their extreme morphology via a series of intermediate morphologies, but because no representatives of these putative intermediaries still exist, parsimony cannot identify this possibility. Thus, when the parsimony reconstructions indicate that the twig ecomorph was the first to evolve, the twig morphology may actually have evolved in a series of lesser steps, each step possibly representing the specialization resulting from the addition of another species to the community.

RESULTS

Existence of Ecomorphs

Four principal components account for 95.9% of the variation (Table 3). The ecomorphs differ in their position in morphological space defined by the first four PC axes (MANOVA, Wilks Lambda = 0.001,  $F_{20,63} = 22.9, P < 0.001$ ). Univariate analyses of variance indicate that the ecomorphs differ on all four axes ( $F_{5,22} \geq 16.0, P < 0.001$ ). The significance of these results is not due to the extreme position of the twig anoles; their exclusion does not qualitatively alter the results (all pairwise combinations of ecomorphs are significantly different except those involving the single trunk anole [Losos, unpubl.]).

In the UPGMA phenogram (Fig. 3), each ecomorph type forms a distinct cluster; T

(the number of branches moved to make the clusters perfect) = 0. None of the 249 randomized phenograms displayed a clustering of ecomorphs as perfect as that observed among extant taxa ( $P < 0.005$ ).

In the more restrictive null model of ecomorph nesting by island, seven phenograms exhibited a pattern as nested as that observed among extant taxa ( $P \leq 0.032$ ). In the less restrictive null model, in which less differentiated clusters are also considered, 21 phenograms are as nested as the real phenogram ( $P \leq 0.088$ ).

Community Evolution

As Williams (1972) surmised, the early evolution of Puerto Rican communities is characterized by divergent evolution in

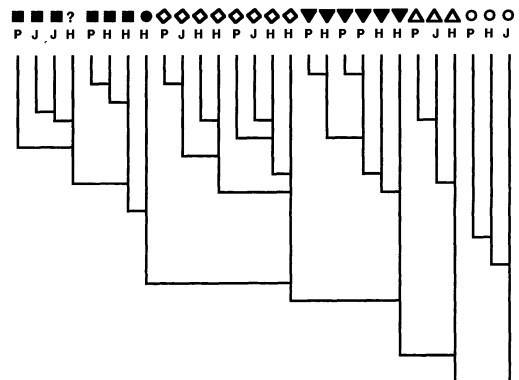


FIGURE 3. UPGMA phenogram of West Indian anoles based on scores on four principal components axes. Symbols represent ecomorph type (■ = trunk-ground; ● = trunk; ◆ = trunk-crown; ▼ = grass-bush; ▲ = crown-giant; ○ = twig; ? = *A. christophei* [see Table 2 footnote]). Letters represent island (Hispaniola, Jamaica, Puerto Rico).

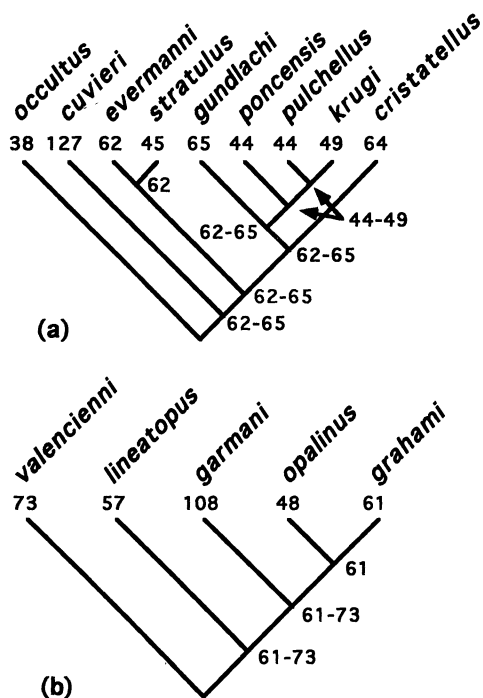


FIGURE 4. Evolution of body size of *Anolis* on Puerto Rico (a) and Jamaica (b). Numbers represent the snout-vent length of hypothetical ancestral taxa inferred using the parsimony algorithm of Swofford and Maddison (1987). A range is indicated for some taxa because of the existence of multiple equally parsimonious reconstructions.

body size (Fig. 4a). The two-species stage was composed of species approximately 38 and 64 mm SVL (*occultus* and the ancestor of all remaining taxa); the sizes at the three-species stage were 38, 64, and 127 mm SVL. In Jamaica (for which a phylogeny was not available to Williams [1972]), however, no such pattern is observed; the two- and three-species communities were composed of species of similar size (Fig. 4b). Consequently, character displacement does not appear to have played an important role in the early stages of diversification in Jamaica.

Position of ancestral taxa in morphological space is displayed in Figure 5 (PC axis III, which is not shown, loads primarily for SVL and separates the crown-giants from the rest of the ecomorphs). The outlines correspond to the boundaries defined by the positions of extant members of each ecomorph type.

The evolution of community structure followed a remarkably similar pattern on the two islands (Figs. 6, 7). On both islands, two-species communities were composed of a twig anole and a generalist species not corresponding to any ecomorph type (Fig. 5a). At the three-species stage (Fig. 5b), Puerto Rico contained a twig anole (*occultus*), a crown anole (*cuvieri*), and a trunk-ground anole. Jamaica contained a twig anole (*valencienni*), a trunk-ground anole (*lineatopus*), and a crown anole intermediate in morphology between a trunk-crown and crown-giant. The four-species stage in Puerto Rico was composed of the same two extant taxa (*occultus* and *cuvieri*) and two ancestral taxa, one clearly a trunk-crown anole and the other a trunk-ground anole. Jamaica exhibited the same four ecomorphs (Fig. 5c). The grass-bush anole, absent from Jamaica, was the last ecomorph to evolve in Puerto Rico. On both islands, the trunk-crown ecomorph differentiated into a large and a small species subsequent to the evolution of the first four ecomorph types (data not shown).

The evolution of the communities in Jamaica and Puerto Rico only differed once ( $Q = 1$ ), i.e., in the composition of the three-species stage (trunk-crown vs. crown generalist). This degree of similarity was significantly unlikely relative to the comparison of the evolution of randomized communities, only seven of which had a score of  $Q \leq 1$  ( $P < 0.04$ ).

## DISCUSSION

Whether assemblages in similar environments converge in structure has long been debated (Orians and Paine, 1983; Schluter, 1986; Wiens, 1989). Convergence among assemblages could occur at two hierarchical levels—either from convergence in emergent properties of the assemblages (e.g., number of species, mean euclidean distance among species in ecological space) or as an incidental consequence of one-for-one convergence (species matching sensu Schluter [1991]) between pairs of species in both assemblages (Orians and Paine, 1983). The analyses reported here confirm that *Anolis* as-

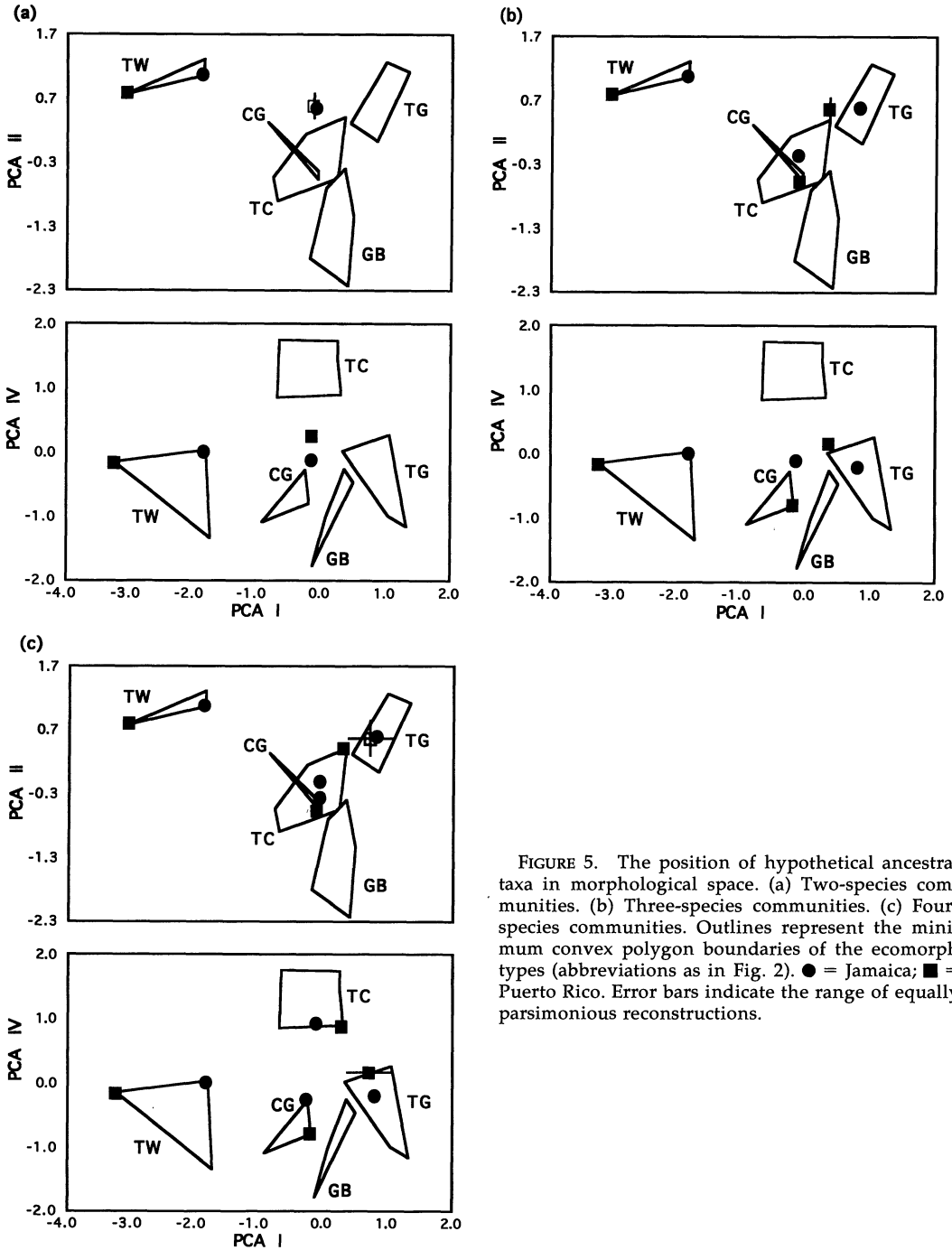


FIGURE 5. The position of hypothetical ancestral taxa in morphological space. (a) Two-species communities. (b) Three-species communities. (c) Four-species communities. Outlines represent the minimum convex polygon boundaries of the ecomorph types (abbreviations as in Fig. 2). ● = Jamaica; ■ = Puerto Rico. Error bars indicate the range of equally parsimonious reconstructions.

semblages in the West Indies are convergent and result from the one-to-one convergence of the same set of "ecomorph" types on each island. A further

twist is the nested pattern of ecomorph occurrence among the islands: four ecomorph types are common to all islands, a fifth type is found on all islands except

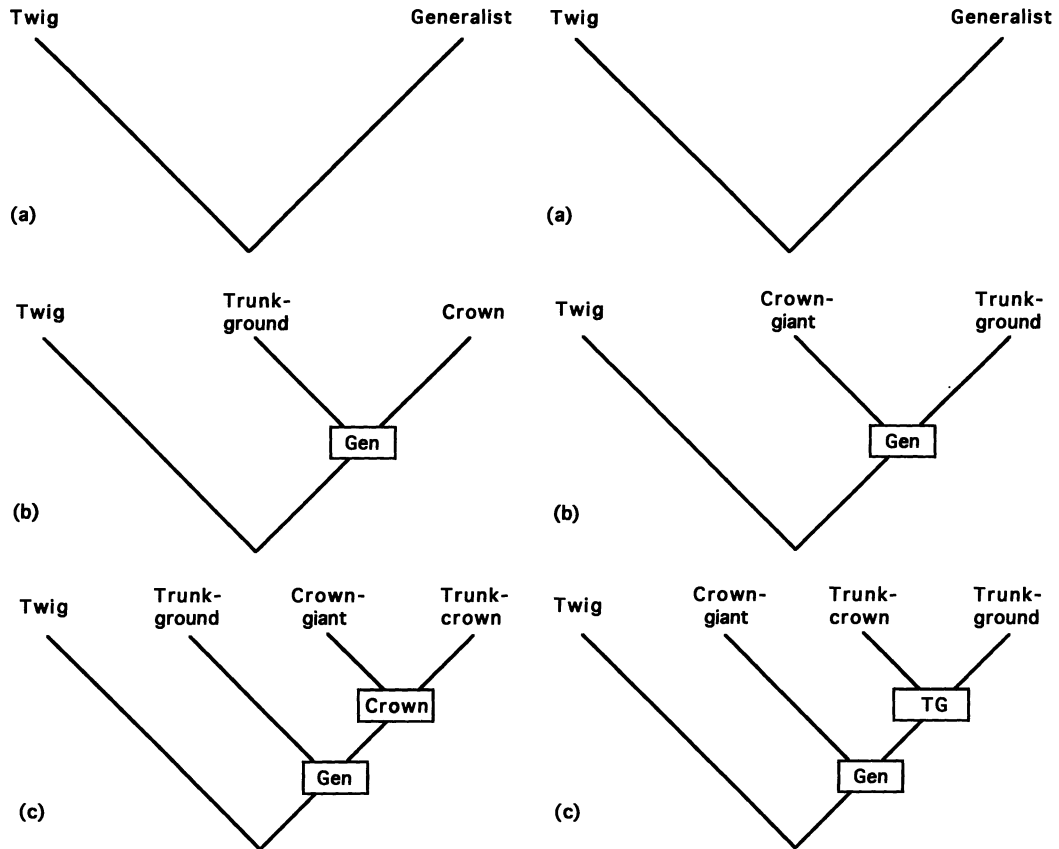


FIGURE 6. The evolution of *Anolis* community structure in Jamaica. (a) Two-species community. (b) Three-species community. (c) Four-species community.

Jamaica, and the sixth type occurs only on Hispaniola and Cuba.

Integration of studies of community ecology into a historical context provides a rich basis for formulating and evaluating hypotheses about the origin of community structure. The phylogenetic analysis supports the predictions of the niche compression hypothesis that faunal assembly on both Jamaica and Puerto Rico has occurred via sequential microhabitat partitioning. Implicit in this hypothesis are two propositions: that competition occurs among *Anolis* species and that morphological differences are related to differences in microhabitat utilization. A wealth of data, mostly observational (e.g., Schoener and Gorman, 1968; Schoener and Schoener,

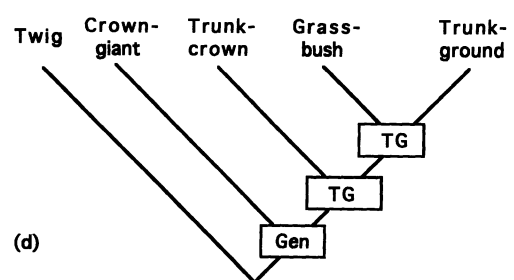


FIGURE 7. The evolution of *Anolis* community structure in Puerto Rico. (a) Two-species community. (b) Three-species community. (c) Four-species community. (d) Five-species community.

1971a, 1971b; Jenssen, 1973; Schoener, 1974; Jenssen et al., 1984; Marcellini et al., 1985) but some experimental (Pacala and Roughgarden, 1982, 1985; Roughgarden et al., 1984; Rummel and Roughgarden, 1985), indicates that competition is a potent force among sympatric anoles. Functional studies, although still in their infancy, indicate

that the morphological differences among the ecomorphs imbue them with different capabilities appropriate for the distinctive microhabitats they utilize (Losos and Sivero, 1989; Losos, 1990b, 1990d).

#### *Community Assembly and Evolution*

Not only does the phylogenetic analysis distinguish between the niche compression and character displacement hypotheses, which are equally plausible when only ahistorical data are considered, but it also reveals a pattern not predicted by current ecological theory: the assembly of anole faunas on Puerto Rico and Jamaica followed a highly similar evolutionary sequence. Considering that anoles use a wide variety of microhabitats, it is striking that diversification on the two islands followed the same sequence of microhabitat partitioning (Figs. 6, 7). Although coincidence in this pattern is highly unlikely by chance, as the randomization analysis confirms, the hypothesis that anole communities evolve in the same sequence can be tested when phylogenies are recovered for Hispaniola and Cuba.

The observation that community evolution has occurred in the same manner on both islands suggests that the assembly of communities is channeled or constrained to occur in a predictable sequence. This directing or constraining force could operate in a number of ways.

1. *Forbidden combinations.*—Some community ecologists (e.g., Diamond, 1975; Gilpin et al., 1986) have argued that certain combinations of species cannot coexist because of competitive pressures, even though these species sometimes are found together in communities containing additional species. The anoles of the northern Lesser Antilles present one example of forbidden body-size combinations. On two-species islands, there are six possible combinations of body sizes of the two resident species (large-large, large-intermediate, large-small, etc.), yet only one combination, large-small, is observed (the one exception is St. Maarten, on which the intermediate *A. gingivinus* may be pushing

the small *A. pogus* to extinction [Roughgarden et al., 1984]). The other five combinations apparently do not represent stable communities.

If the forbidden combinations hypothesis were to explain the similar pattern of diversification observed in Jamaica and Puerto Rico, then it follows that the only stable two-species community would consist of the two ecomorph types inferred to have coexisted at the two-species stage of community development: an arboreal generalist and a twig anole. A priori, this hypothesis seems unlikely—one would not expect other combinations, such as a trunk-ground and a twig anole, to be unable to coexist. Further, two-species communities comprised of anoles other than twig ecomorphs and generalists exist in the Bahamas, Virgin Islands, and satellite islands of the Greater Antilles (Schoener, 1988). Consequently, the similarity in the early stages of diversification in Jamaica and Puerto Rico did not result because no other combinations of ecomorph types can coexist.

2. *Adaptive peaks: global optimization.*—Following Simpson's (1944) adaptation of Wright's (1982 and references therein) metaphor, one can imagine that resources are nonrandomly distributed such that certain ways of making a living (niches, sensu Grinnell [see Schoener, 1989]) confer greater fitness than others (i.e., the adaptive peak for that niche is higher). Consequently, if evolutionary potential is unconstrained, then one would expect a population to evolve to occupy the highest peak. If one species is already present and competition is strong, then one might expect that the second species to join a community (whether via invasion or speciation) would occupy the second-highest peak, and so on. Of course, the presence of a second species may alter the distribution and availability of resources such that the highest peak moves from its position in a one-species community.

If the distribution of resources (e.g., food, perch positions, microclimate space, etc.) is very similar in two environments and if evolutionary change is unconstrained, one might expect the same sequence of com-

munities as species evolve to occupy the highest available peaks. This scenario could explain the patterns apparent in anole communities in both the Lesser and Greater Antilles.

3. *Adaptive peaks: local optimization.*—Populations may not be free to evolve in all directions. When crossing an adaptive landscape, a population may move to the nearest peak rather than to the highest peak, for example when two ecologically similar populations come into sympatry. Rather than moving to the highest available peak, they may only move to the nearest peak that sufficiently minimizes competitive pressures. Further, some directions of evolutionary movement may be easier than others. In this view, environmental heterogeneity, represented by the position of adaptive peaks, is still the underlying determinant of fitness, but the phenotype and genotype of colonizing species also affect evolutionary trajectories. The possibility that in the Greater Antilles the first species on all islands may have been an arboreal generalist (Williams, 1972) could have played an essential role in generating the observed parallel patterns. When the original species speciated, the resultant two species may have evolved along the easiest route to diminish competition by simply partitioning the arboreal habitat rather than taking the perhaps larger evolutionary step of moving toward the ground. In contrast to the "global" adaptive peak hypothesis above, this model predicts that a community originally colonized by a grass-bush ecomorph, for example, would exhibit a quite different trajectory of community assembly.

These phylogenetically inspired hypotheses suggest several lines of ecological research. Of particular interest is mapping the *Anolis* adaptive landscape and understanding to what extent transitions from one state to another are possible. When a species is added to a preexisting community, in which way will selection direct its evolution? Although this experiment could not be conducted ethically, several approaches can get at it indirectly. First, many anoles have been accidentally or in-

tentionally introduced throughout the Caribbean and elsewhere (summarized in Williams, 1977). Study of the microevolutionary outcome of such inadvertent experiments may provide considerable insight into what happens when a new species is added to a community. Similarly, many small islands in the Caribbean (e.g., the Bahamas, Virgin Islands) contain derivative subsets of the anole faunas of nearby Greater Antillean islands and contain various combinations of two to four ecomorphs (Schoener, 1988). To what extent, if at all, the evolutionary sequence reverses when ecomorph types are absent may also be informative. Functional and experimental studies can also indicate what happens when a particular ecomorph has access to and utilizes new microhabitats (see Rummel and Roughgarden, 1985; Malhotra and Thorpe, 1991).

#### *Empty Niches*

Whether the concept of an empty niche is meaningful has long been debated. There are countless theoretically possible ways of making a living (why are there no grass-eating snakes or winged molluscs? [Levontin, 1978]). Speculation on why such organisms do not exist will rarely provide insight into the ecological realm. However, in some cases the relationship between selective demands of the environment and organismal responses is well-enough understood to identify particular environmental features that routinely elicit specific evolutionary solutions. The *Anolis* ecomorphs are one such case. For example, grassy areas are utilized in similar ways by morphologically very similar taxa in Puerto Rico, Hispaniola, and Cuba and in Central and South America. Grass exists in Jamaica, and yet the grass-bush ecomorph has not evolved. Further, other taxa have not usurped the ecological position of grass-bush anoles. Thus, in this instance, it is meaningful to ask why the grass-bush ecomorph has not evolved in Jamaica, and, similarly, why the trunk ecomorph does not occur in Jamaica or Puerto Rico.

Phylogenetic analysis makes one otherwise-overlooked hypothesis obvious. The

grass-bush anole was the last ecomorph to evolve in Puerto Rico. Its absence from Jamaica may have resulted not because suitable habitat is unavailable but rather because Jamaica has not continued along the trajectory and added the fifth ecomorph type. This hypothesis is easily testable phylogenetically because it predicts that when phylogenies for Hispaniola and Cuba are available, not only will the grass-bush ecomorph evolve fifth, but the trunk ecomorph will be the last to evolve.

This perspective switches the focus of investigation from why a particular ecomorph type is absent to why the islands differ in the number of ecomorph types they contain. Why the fifth ecomorph has failed to evolve in Jamaica is not obvious. Perhaps Jamaica has not been above water long enough for five ecomorphs to evolve. However, Jamaica has been emergent for at least 20–30 million years (Buskirk, 1985; Hass and Hedges, 1991), which would seem an adequate amount of time. Alternatively, perhaps the species already compete too strongly (i.e., niche packing is high), so that there is not enough ecological space to add another type even if it is produced via speciation events. The Jamaican ecomorphs are generally not as distinctive as those on the other islands (Williams, 1983) and hence may compete more strongly, precluding the addition of a fifth ecomorph to the anole community. Other alternatives are possible, and distinguishing among them will not be easy. Nonetheless, the phylogenetic analysis has indicated where fruitful lines of ecological inquiry lie.

### Conclusions

The importance of integrating phylogenetic approaches into investigations of historical processes such as community assembly can be seen in the study of the communities of Caribbean *Anolis* lizards. A thorough study requires both present and historical data. Ecological studies may indicate what processes are currently operative, but these factors may have had little relevance in the evolution of community structure. Phylogenetic patterns are just

that; without an understanding of the biology of the organisms, usually gained by study of extant forms, little more can be said. The phylogenetic approach to *Anolis* community structure is only fruitful because the biology of these lizards has been so thoroughly studied. When ecological and historical studies are properly integrated, phylogenetic information can reveal patterns not apparent from investigations of ongoing interactions and can direct ecological studies toward particularly promising and informative areas.

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