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15 Ecomorphs, Faunas, Island Size, and Diverse End Points in Island Radiations of *Anolis*

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IN 1972 I CHOSE Puerto Rico, because it was relatively well known and had a fauna of moderate complexity, for a test analysis of the evolutionary radiation of anoline lizards within an island. It seemed reasonable to regard the Puerto Rican *Anolis* as a readily analyzable stage in the evolution of faunal complexity in relation to island size and topographic diversity. I expressed the hope that this analysis could be extended to the faunas of the other Antillean islands once sufficient data became available.

Unfortunately more data have not permitted fulfillment of this hope—certainly not in the simple fashion that was then expected. It is now apparent that an increase or decrease in area has effects that are much more than simple additions and subtractions. There are qualitatively differing end points and even—as we shall see for Hispaniola below—differing faunal end points on the same island.

The ecomorph concept that was introduced in the 1972 paper remains crucial to the new analysis. The concept is basically the familiar one of convergent evolution—a set of animals showing correlations among morphology, ecology, and behavior, but not lineage—a concept usually applied to widely divergent taxa (for example, the birds of different continents; Karr and James, 1975) but here seen in the radiations of a single genus within a single archipelago.

The phenomenon that I have called ecomorph is obtrusively evident in the Greater Antillean islands. Anyone who visits more than one of these islands is struck at once not only by the abundance and diversity of the anole faunas and the corresponding diversity of the microhabitats in which they occur but also by the conspicuous presence of highly similar species from one island to another, always occupying very similar habitats. The similarity in each case extends to color, size, body proportions, perch, and foraging and escape behavior. Further information, however,

always makes it quite clear that these are ecological analogues, not closest relatives. On the contrary, the several very distinct types on one island may be much more closely related to one another than any of them is to analogous species on another island.

Figure 15.1 shows the major ecomorph categories found in the Greater Antilles and indicates that both the major structural categories within *Anolis*, alpha and beta of Etheridge (1960), are represented by species in each of these categories.

It is noteworthy that this crossing of phyletic boundaries by ecomorphs does not depend upon any specific classification. Currently, Etheridge's major subdivisions are under attack (Gorman, Buth, and Wyles, 1980; Shochat and Dessauer, 1981), but the proposed rearrangement, while it switches the presumed relationship of whole lineages, still finds the same ecomorph occurring in two or more major groupings.

As in the many other cases, the ecomorph concept began to take shape

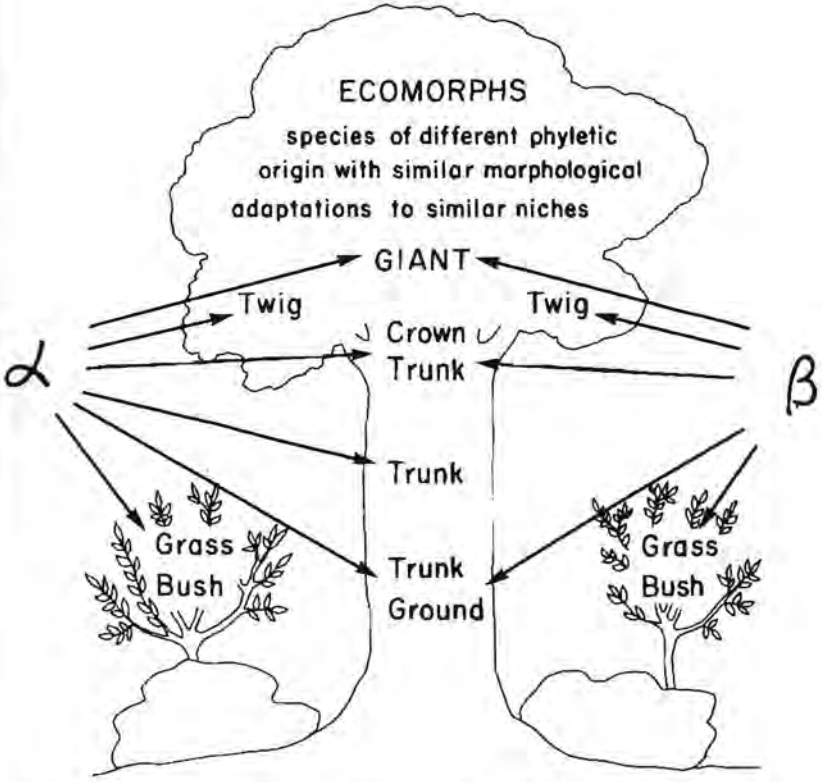

Figure 15.1 Six named ecomorphs with the perch position characteristic of each.

as soon as a close look was taken at the relationships of the compared taxa. The more conspicuous ecological types of Greater Antillean anoles were first recognized by A. S. Rand (1964) in Puerto Rico. It was soon realized that similar types existed on the other Greater Antilles but that not all of these could possibly belong to similar phyletic stocks. In 1969 Rand and I found it useful to define the characters and to provide simple names for these ecological types. Table 15.1 details some of the defining characteristics of the major ecomorphs more fully than has been done before. I coined the term *ecomorph* in 1972 to emphasize the morphological aspect of the similarities between types and to avoid confusion with the significantly different term *ecotype* proposed by Turesson (1922) and much used by botanists.

Unfortunately the ecomorph categories that Rand and I erected have their strict application only for the anoles of the Greater Antilles, not even for the Lesser Antilles, and not consistently for mainland anoles, let alone other lizards. Even for the anoles of the Greater Antilles other than Puerto Rico we have had to make emendations and additions to the concepts that had their origin and primary base in Puerto Rico.

Before I go further, it will provide perspective to look in broad terms at the niche and mode of radiation of *Anolis*. The background facts are that *Anolis* are primarily but not exclusively arboreal, are exclusively diurnal, and include both thermoregulators and thermoconformers, that is, species that bask and those that do not bask. Figure 15.2 describes the niche of *Anolis* in terms of 3 axes: size, perch, and climate, and their attendant morphological and behavioral correlates. These 3 axes seem to have general descriptive utility and validity.

However, the ways in which these axes determine the species characters of *Anolis* are clearly different in different areas (Chapter 16). Size, perch, and climate all differ in the sympatric species pairs that occur in the Lesser Antilles, as Schoener and Gorman (1968) first announced for the 2 species of Grenada, but differences in morphology (other than size) are muted as compared with the stronger specialization that occurs on the Greater Antilles. The Lesser Antillean pairs have clearly not reached the level of differentiation that I called ecomorph in Puerto Rico and of which 5 examples typical in size, perch, and shape are given in Figure 15.2.

In the Greater Antilles size and perch sort out the ecomorphs. These two factors are correlated with foraging and defense behavior (Table 15.1). Position, whether on tree, bush, or grass, determines foraging opportunities and defensive possibilities. Size has an influence on size of prey and mode of defense. Climate subdivides ecomorphs and by permitting some spatial separation provides room for more species. Body form, as a defining feature of ecomorph, relates to the constraints and

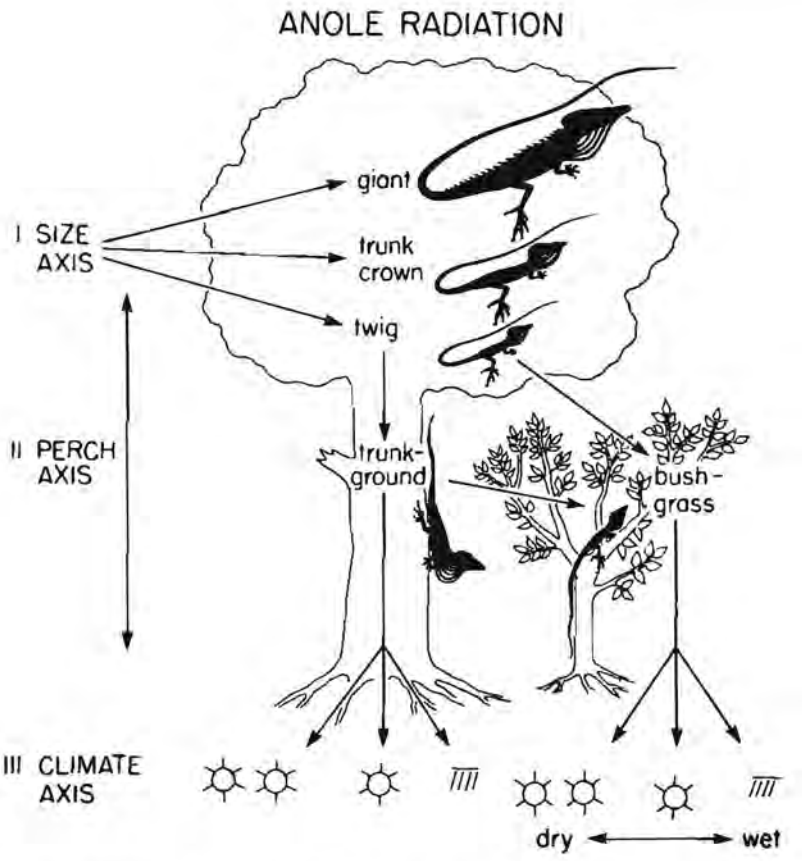

Figure 15.2 Ecological axes that appear to be involved in the evolution of *Anolis*. Five of the 6 ecomorphs of Figure 15.1 are shown in characteristic sizes as well as perches.

opportunities imposed by the vegetational matrix (Moermond, 1979). Color may promote crypsis or may be related primarily to mate choice. Color and particularly changes in color may also be related to thermoregulation. The scale differences cited in Table 15.1 are less obviously adaptive, but they contribute to the very visible sharp distinctions between the ecomorphs. The contrast between this Greater Antillean diversity and the severely limited between-species variation found in the Lesser Antilles is very striking.

Size, perch, and climate are clearly important also in mainland anoles, and one might naively expect the mainland to have anole faunas much more diverse than those of the largest islands. We must confess at once that we know much less about mainland anoles than those of the

Table 15.1 Defining characteristics of major ecomorphs.

Characteristic	Ecomorph					
	Crown giant	Twig dwarf	Trunk-crown	Trunk	Trunk-ground	Grass-bush
Size:	> 100 mm	< 50 mm	> 70 mm	< 50 mm	> 60 mm	Usually < 50 mm
Color:	Green, patterned or not	Gray, lichenate	Green, sometimes grayish	Variable, green, grayish, or brownish	Brown with variable pattern, more rarely green	With distinct lateral or dorsal stripe in both sexes
Modal perch:	Typically high in the crown	Twigs of canopy	Canopy and upper trunk	On trunk between trunk-crown and trunk-ground	On lower trunk	On grasses or bushes
Body proportions:	Head large, massive, often casqued	Long head, short body, short legs	Large head, body tending to be long, short legs	Head and body short	Head relatively short, body short and stocky, limbs long	Head moderately long, body slender, tail long
Scales:	A vertebral crest present	Uniform dorsal scales	Uniform dorsal scales	Dorsal scales usually uniform	Middorsal scales abruptly (in 2 rows) or gradually enlarged	A zone of few to many rows of dorsal scales
Foraging behavior:	Primarily a canopy forager	A *slow* searcher on twigs	A searcher on leaves and branches	Primarily a forager on its trunk perch	Sit-and-wait predator on ground prey	Primarily a grass-bush forager
Defensive behavior:	Primarily aggressive	Primarily crypsis	Flight upward	Squirreling	Flight downward	Flight downward

NOTE: Moermond (1979, 1981) describes twig and trunk-crown ecomorphs as "crawlers," the trunk ecomorph as a "runner," and the trunk-ground and grass-bush ecomorphs as "jumpers." He cites different types of prey attack behavior as associated with these ecomorphs also—that is, "stalk-strike" with the twig ecomorph, "jump-strike" primarily with grass-bush anoles, whereas "stationary-strike" and "approach-pause-strike" were used by all ecomorphs some of the time.

islands, too little even of their taxonomy, less about their ecology, and almost nothing of their evolution. What information we do have, however, does not show them impressively more diverse ecologically or morphologically than those of the islands. There is, in fact, a difficulty in comparability, and it is evident that the Greater Antillean ecomorphs are only imperfectly paralleled on the mainland.

It is facile to explain the special features of mainland anoles by the fact that, in contrast to the island species, they are parts of truly complex faunas of which they are not the most conspicuous or important components. It is, for example, vividly and immediately evident to the observer coming from the islands that mainland anoles have far less dense populations than their island congeners, so much less dense that any competitive interactions must be much more with distantly related taxa (even other classes or phyla) than with congeners.

The high divisibility of the *Anolis* niche is a major feature of the genus; it is the other side of the phenomenon of radiation that is so much an anoline characteristic. My concern in this chapter is with the effects of area on this niche divisibility and hence on faunal complexity, an interaction that was only partly explored in my 1972 paper. But this new look at the phenomenon which is here proposed is necessarily limited by the availability of data. The mainland cases must be put aside for the reasons mentioned just above. Cuba likewise cannot be adequately treated. Although it is far from a terra incognita, it is still relatively poorly studied, even at the alpha taxonomic level, and, unique among the islands, species of *Anolis* have been described for Cuba that I do not know even as preserved specimens. (See Ruibal, 1964, for a useful but outdated review of Cuban *Anolis*. Schwartz and Thomas, 1975, and Schwartz, Thomas, and Ober, 1978, provide a more current list of names.)

Omission of mainland anoles is not a problem: the factors that have impinged upon them seem clearly different from those that have affected the island anoles. The omission of Cuba may also not seriously flaw our analysis. It is now very evident that the Hispaniolan anole fauna may be even more complex than that of Cuba and may therefore quite plausibly serve as the final term in a series of West Indian anole faunas grading upward in size and complexity.

Such a series of West Indian islands and faunas cannot, however, show an even gradation. To speak of emergent islands only, the smallest of the Greater Antilles (the main island of Puerto Rico, 3,421 mi^2) is about 5 times larger than the largest of the small islands (Guadeloupe, 687 mi^2), and Hispaniola is 40 times larger than Guadeloupe. A logical first grouping is into large and small islands, but the small islands must immediately be broken into two categories: the *small old islands*, old

enough and high enough to have been emergent for a long time with the consequence that the evolutionary processes that we are interested in have played their appointed role, and the *small low islands,* which are so recently emergent that they are better studied in terms of ecological rather than evolutionary time. As for the large islands, it will be a major point of this study that they are each quite different and that the substantial differences in area between them may be, in great part, the explanation of their faunal differences.

Where published documentation of the habits and habitat of the anoles discussed below is available, I have cited it. However, much detail is still unpublished or, worse, unknown. Some published data—quantitative though they may be—are based on observations at restricted localities and for limited periods. Most of the species I have seen alive myself, and I have not hesitated to reinterpret the observations or interpretations of others in the light of my own observations.

All determinations about relationship and phylogeny are my own. I crystallized these judgments into a formal system in an earlier paper (1976). Unfortunately not all the reasoning behind those assignments is yet in print. In extenuation I can only report that a series intended to summarize information on all the West Indian anoles is in preparation, of which Williams (1976) was the first paper.

The Small Old Islands

The small old islands of the Caribbean include, in addition to the Lesser Antilles of geographers, 3 islands adjacent to the mainland of Venezuela: Curaçao, Bonaire, and Blanquilla. All of these islands, although 3 distinctive lineages of *Anolis* are represented on them, show only 1 or 2 anoles per island.

In 1972 I used the so-called solitary (named by Schoener, 1970) anoles and species pairs of these islands as models of the first stages in the evolution of the coadaptation of faunas. At that time I emphasized size. Solitary species—so named because they occur without any congener—were found to belong somewhere in the middle range of all sizes exhibited by *Anolis*, whereas pairs of species were usually skewed away from that middle range, one of each species pair being distinctly below the middle range and the other distinctly above it (Schoener, 1970; Williams, 1972).

Grenada (Schoener and Gorman, 1968), as the ecologically first studied of the Lesser Antilles, may serve as an example of all the species pairs (Fig. 15.3).

It must be emphasized that the size difference between members of species pairs is considerable, up to nearly 2 times in snout-vent length. It is an impressive difference, but the point I want to stress is that size is the

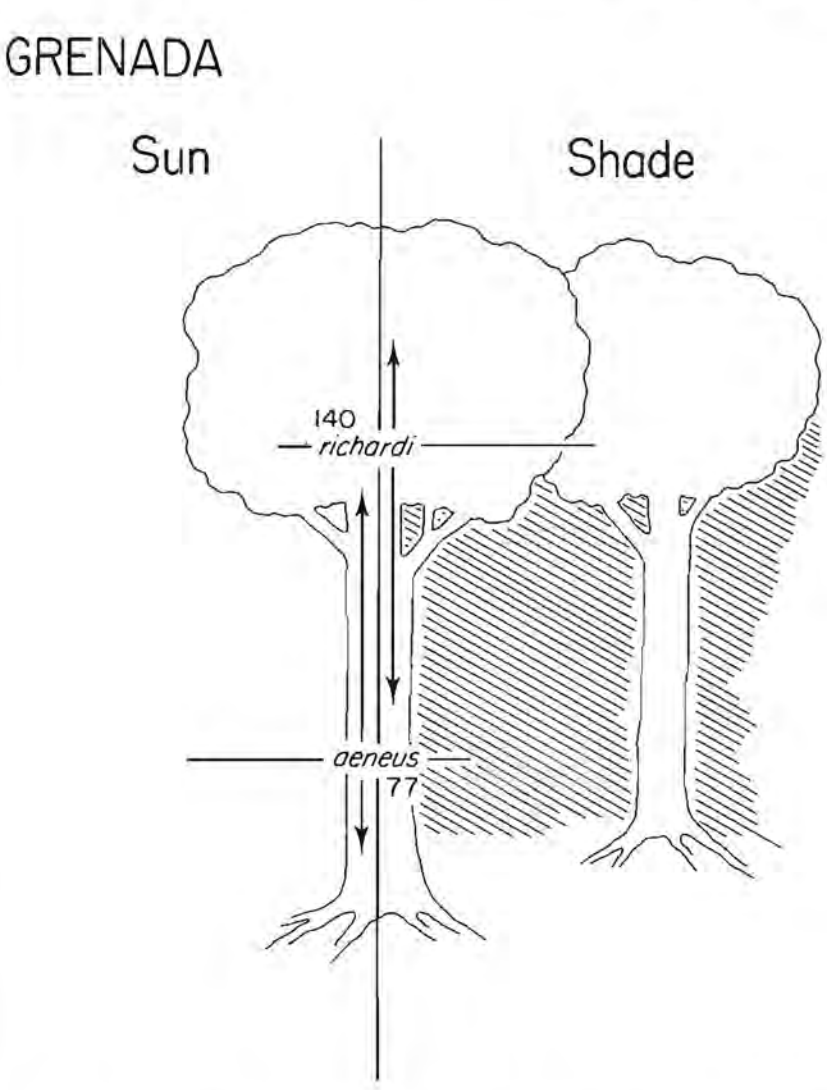

Figure 15.3 Perch and climatic preferences of the 2 anoles of Grenada. Numbers are maximum adult male snout-vent sizes in mm. Horizontal lines indicate preferential positioning of *A. richardi* in the shade, of *A. aeneus* in the sun. Vertical arrows indicate the preference of *A. richardi* for higher perches than those favored by *A. aeneus*.

only impressive difference between these species pairs. The differences in scalation between members of the species pairs are not impressive in terms of the differences between species on the larger islands, and, similarly, the climatic preferences between species, while real, allow major

overlap (Schoener and Gorman, 1968). Perch does differ in that the larger species tend to perch higher and prefer bigger trees. Where the habitat does not permit big trees, the larger species tend not to occur. Within this limitation, species pairs in the Lesser Antilles are almost ubiquitously syntopic, occurring in the same trees, only at different heights. See, however, the species of St. Martin (Williams, 1972; Roughgarden et al., Chapter 16).

The Lesser Antillean pairs thus have some striking features in common: (1) there is always at least partial sympatry and, when there is sympatry, there is often near total syntopy; (2) the major differentiation is in size axes, and there is minimal differentiation as regards other morphology; (3) no species is wholly montane, although one species may extend altitudinally higher than the other; (4) neither member of any species pair shows any geographic variation comparable to that of certain solitary species.

Morphological and ecological differences can be greater within solitary species than between species pairs. The most striking example is *A. marmoratus* within the island of Guadeloupe, where scale size and color change vary radically within the species, and there is one differentiated population that is montane (Lazell, 1964, 1972). There are parallels in *A. oculatus* and *A. roquet* (Lazell, 1962, 1972) that are somewhat less extreme and less clearly differentiated geographically (personal observation). In the species pairs of any island bank, there is nothing quite comparable either within or between the species. Although, as Lazell (1972) has emphasized, there is very striking variation within *A. aeneus,* it is a phenomenon of individuals, not populations. There may be considerable nongeographic or erratically geographic variation. One of the 2 species may climb higher into the mountains than the other, or farther out into scrubby vegetation, but strong modifications are not seen.

The Small Low Islands

The small low islands in the West Indian region may show only 1 or 2 anoles per island or in the exceptional case, the emergent islands of the Great Bahama bank, 4 species.

The 4-anole fauna of the Great Bahama bank, first studied on Bimini by Schoener (1968), might on the basis of numbers be considered one of the terms in a series of more and more complex faunas. In fact, however, it does not fit into a series in complexity, conceived as an evolutionary sequence. The fauna of the Great Bahama bank, like that of the other low West Indian islands, is recent and derivative, compounded from the specialized endemics of adjacent large islands (Williams, 1969). As I have personally observed, 4 strongly marked ecomorphs do exist on Bimini, but they have not evolved there. Instead, they have come as fully differentiated species, preadapted to coexist (see Case, Chapter 14).

The situation is comparable to that occurring on a newly emergent

portion of a large island just opened to colonization. The new area is colonized by that portion of the fauna of the major island that (1) can reach it and (2) is suited to depauperate areas of relatively uniform ecology.

The animals that arrive in such situations are not just fractions of larger faunas but highly selected fractions. Three of the Great Bahaman anoles—*A. carolinensis, A. angusticeps, A. sagrei*—are Cuban in origin and all are edge animals; they have no readjustments to make in order to coadapt ecologically. They were already coadapted on Cuba. The fourth animal—*A. distichus*—is more interesting; it is a Hispaniolan animal that has inserted itself within a set of Cuban animals. Note that it has never invaded Cuba, although the overwater distance to the Great Bahama bank is greater than that to Cuba. It is, however, preadapted; it has the ideal ecology to insinuate itself into the depauperate fauna of the Bahamas because its ecological relationships to the other species parallel its native niche in Hispaniola: between, on the one hand, the trunk-crown ecomorph—in the Bahamas, *A. carolinensis* (in Hispaniola it was *A. chlorocyanus* or *A. coelestinus*)—and, on the other hand, the trunk-ground ecomorph—in the Bahamas, *A. sagrei* (in Hispaniola it was *A. cybotes* or a close relative). The forms on Cuba that are ecologically analogous to *A. distichus* are more mesic than the colonizing populations of *A. distichus* and may have therefore been unable to follow their 3 successful Cuban colonizers of the Bahamas on to these low, relatively dry, and open islands. (On these points see Williams, 1969.)

The Large Old Islands: The Greater Antilles

In 1972 the anole fauna of Puerto Rico was very elaborately described and discussed. It will not be desirable to describe Jamaica and Hispaniola in equivalent detail, nor will it be possible to develop a phylogeny for the anoles of the other 2 islands as well documented and as apparently tidy as that which was presented for Puerto Rico. What I intend here instead is a relatively gross comparison, with emphasis on the distribution of ecomorphs over the 3 islands.

Table 15.2 makes a comparison solely in terms of number of species per ecomorph present on each island. I have ordered the island faunas from left to right in an order of complexity which is the same as the order of size of island banks. (The Puerto Rican bank, which includes the Virgin Islands, is much larger than the Jamaican bank which has very little offshore extent.) Table 15.2 in conjunction with Table 15.3a and b, which adds species names, size, and some other details, allows an analysis in terms of three topics: (1) what is regularly present, (2) what is added, (3) what is left out.

(1) What is *regularly* present in the three islands?

The ecomorphs are, of course, by definition the set of categories that

Table 15.2 Number of species per ecomorph.

	Jamaica	Puerto Rico	Hispaniola
Giant	1	1 + 1[a]	3
Twig I	1	–	1
Twig II	–	1	2
Trunk-crown I	1	1	2
Trunk-crown II	1	1	2 +
Trunk-ground	1 (subspecies) + 1[b]	3 (1 with subspecies)	5 + 1[c]
Grass	–	–	3 + (2)
Bush	–	3	3
Trunk	–	–	5 + (1)
Other	1	–	7
Total	6 + 1[b]	10 + 1[a]	36 + 1[c]

a. Probably extinct.
b. Possible invader (*A. sagrei*, see text).
c. Invader (*A. cristatellus*: Roughgarden, 1974; Williams, 1977).

regularly recur and that in color, habitus, squamation, ecology, and behavior are dramatically similar, in spite of the fact that they may not be at all closely related.

For Puerto Rico I recognized in 1972 only 5 ecomorph categories: crown giant, twig, trunk-crown, trunk-ground, and grass-bush anoles. For the whole set of large islands I now (Tables 15.2 and 15.3) recognize 9; 2 of these are subdivisions of an older category, that is, I now recognize 2 sizes of twig anoles (I, giant, mentioned above, and II, dwarf) and 2 of trunk-crown anoles (similarly I, large and II, small). I recognize also a trunk ecomorph which does not occur in Puerto Rico and I subdivide the grass-bush category. (The last is the weakest of my new decisions, since the subdivision occurs only in Hispaniola.) I shall call these standard-sequence ecomorphs.

In Tables 15.2 and 15.3 there is a category "Other," in which I list animals that in one way or another do not fit the ecomorph concept, the essence of which is convergence and stereotypy. In the table I have accommodated some species that I would formerly have listed as other by subdividing the twig and the trunk-crown ecomorphs into 2 sizes of categories.

Discrepant taxa aside, however, the morphological, ecological, and behavioral congruence of the species that are listed in any one ecomorphic category is amazing, the more so since (a) closest relatives may belong to different ecomorphs, for example, *A. gundlachi* and *A. krugi* on Puerto Rico (see discussion in Williams, 1972), and, especially, all the native Jamaican anoles which, despite their rather full roster of ecomorphs, are closer phyletically to each other than to other anoles anywhere (Underwood and Williams, 1959; Williams, 1976), and since (b)

Table 15.3a Anole ecomorphs on three Greater Antillean islands.

Island	Crown giant	Twig I	Twig II	Trunk-crown I	Trunk-crown II
Jamaica N = 6 (7) (1 invader)	*A. garmani*[124] FW	*A. valencienni*[86]		*A. grahami*[72]	*A. opalinus*[56]
Hispaniola N = 36 (37) (1 invader)	[*A. ricordii*[160] FW *A. baleatus*[180] FW *A. barahonae*[158] FW]	*A. darlingtoni*[72] FW–M *A. fowleri*[77] FW–M	*A. insolitus*[47] FW–M *A. sheplani*[41] M	[*A. chlorocyanus*[80] *A. coelestinus*[84]]	[*A. aliniger*[60] M *A. singularis*[52]]
Puerto Rico N = 10 (11) (1 extinct?)	[*A. cuvieri*[137] FW *A. roosevelti*[157]]		*A. occultus*[40] FW	*A. evermanni*[78]	*A. stratulus*[50]

NOTES:
N = species number per island or island bank.
FW = forest/wet habitat.
M = montane.
Superior number = reported maximum male size, snout-vent, mm.
Allospecies are bracketed.

Table 15.3b Additional anole ecomorphs on three Greater Antillean islands.

Island	Trunk-ground	Grass	Bush	Trunk	Other
Jamaica	*A. lineatopus*[73] FW/OA (*A. sagrei*)[56]				*A. reconditus*[88] FW
Hispaniola	*A. cybotes*[81] *A. marcanoi*[65] *A. longitibialis*[72] *A. strahmi*[79] *A. whitemani*[72] OA (*A. cristatellus*)	*A. olssoni*[48] OA *A. semilineatus*[47] *A. alumina*[40] *A. etheridgei*[43] FW–M *A. koopmani*[39] FW–M	*A. hendersoni*[49] FW–M *A. bahorucoensis*[51] FW–M *A. dolichocephalus*[51] FW–M	*A. distichus*[58] *A. brevirostris*[51] *A. marron*[47] *A. websteri*[47] *A. caudalis*[48] *A. christophei*[49] FW–M	*A. armouri*[59] M *A. shrevei*[56] M *A. rimarum*[45] FW–M *A. monticola*[48] FW–M *A. rupinae*[56] FW–M *A. eugenegrahami*[72] FW
Puerto Rico	*A. gundlachi*[72] FW *A. cristatellus*[74] *A. cooki*[62] OA		*A. krugi*[55] FW *A. pulchellus*[51] *A. poncensis*[48] OA		

NOTES:
FW = forest/wet habitat.
OA = open/arid habitat.
M = montane; in Hispaniola there is also a montane genus, *Chamaelinorops*.
Superior number = reported maximum male size, snout-vent, mm.
Allospecies are bracketed; invader species are enclosed in parentheses.
All doubly underlined species are in the *monticola* species group.

very similar ecomorphs may be phyletically quite distant, for instance, *A. cybotes* on Hispaniola and *A. lineatopus* on Jamaica.

Clearly, selective pressures on the several islands have been powerful enough and similar enough to call into existence on 4 islands (Cuba also has the standard-sequence ecomorphs) strongly convergent ecological types, so strongly convergent that the cross matches are ecologically nearly perfect.

(2) What is differentially added on each of the islands?

Within the series Jamaica to Puerto Rico to Hispaniola there are both (a) additions within the standard sequence, that is, climatic vicariants and allospecies, and (b) additions outside the standard sequence, such as montane faunas and specialist species using some niche unknown in the standard sequence. Table 15.4 lists examples of these additions.

Both climatic vicariants and allospecies multiply the species count within ecomorphs but they do so in differing and interesting ways. *Allospecies* by definition are closely related species with allopatric or parapatric distributions. However, though they may achieve parapatry, they are characteristically ecologically close enough to exclude one an-

Table 15.4 Examples of additions to the standard ecomorphs.

Within the standard sequence
Climatic vicariants (closely related species with strongly differing modal climatic associations *and* marked morphological differences)
Among Hispaniolan trunk-ground ecomorphs (Williams, 1963b)
A. cybotes (mesic, large, ventrals smooth)
A. whitemani (arid, smaller, ventrals keeled)
Among bush ecomorphs of Puerto Rico (Williams, 1972)
A. krugi (mesic, few dorsal rows enlarged)
A. pulchellus (less mesic, several dorsal rows enlarged)
A. poncensis (arid, many dorsal rows enlarged)
Allospecies (closely related species, parapatric or allopatric, differing little in climatic preference or in morphology)
Among Hispaniolan trunk-ground ecomorphs
A. cybotes/marcanoi (Williams, 1975)
Among Hispaniolan grass ecomorphs
A. semilineatus/alumina (Hertz, 1976)
Outside the standard sequence (morphologically and behaviorally distinct)
Montane
In Jamaica
A. reconditus, a montane generalist
Specialist
In Hispaniola
A. eugenegrahami, a semiaquatic species

other and are not even locally syntopic except in very narrow zones or occasionally (apparently by accidental transport) very temporarily, even in terms of ecological time.

Climatic vicariants, on the other hand, while they may be in large measure allopatric, if climatic conditions are different over wide areas, are often in broad sympatry and may in intermediate or edge situations be locally syntopic, even exhibiting the phenomenon that Schoener (1970) called "nonsynchronous spatial overlap"—literal occurrence in identical places but at different times of day.

Anolis cristatellus and *A. cooki* are such climatic vicariants. In southwest Puerto Rico, they do co-occur and are even intimately interspersed, but there is good evidence that they utilize slightly different climatic microhabitats within the same general habitat (Huey and Webster, 1976; Lister, 1976; personal observation).

Climatic vicariants commonly show significant differences in scale characters, for example, scale size, degree of keeling, as well as in thermal behavior. They may have overlapping temperature tolerances but with different maxima and minima.

It can be inferred that all climatic vicariants were once allospecies but have become further differentiated. What is implied here is a spectrum of climatic specialization; it follows that the distinction between allospecies and climatic vicariants will sometimes be subtle or equivocal. Probably all allospecies differ somewhat in climatic preference.

Montane faunas, at least in the examples before us, are to the species of the classic ecomorph sequence as allospecies to climatic vicariants. Some montane species (for example, *A. koopmani* on the mountains of southwest Haiti is a parallel to the lowland grass-bush species) approach the morphological and behavioral characters of the lowland ecomorphs, but they do so incompletely. They are certainly quite independent of their lowland parallels and they are also more or less divergent. I shall regard them below as representing different end points alternative to the classic sequence.

Specialist species: I have in mind here especially the aquatic species—*A. eugenegrahami* in Hispaniola with its parallel in Cuba, *A. vermiculatus*—phyletically quite distant, morphologically dissimilar, analogous only in their semiaquatic habits. The species pair in Cuba, *A. lucius* and *A. argenteolus,* restricted to the trunks of huge complex trees with special hiding places, also qualify as specialists—in this case without known parallels on other islands. *A. bartschi,* a cliff species replacing the *A. lucius-argenteolus* species pair in western Cuba is another specialist.

(3) What is differentially absent in the three islands?

An absence is invisible unless it has left a trace or unless it is suggested by a presence elsewhere (Williams, 1969).

If, as I argued in 1972, there is a natural ecological sequence in eco-

logical radiation, then some absences can be accounted for by the stage in any sequence reached in any island or subfauna. The absence of a grass-bush ecomorph in Jamaica might be accounted for in this fashion. Similarly, the absence of a trunk ecomorph in both Jamaica and Puerto Rico, while this ecomorph occurs in both Hispaniola and Cuba, could be accounted for as an earlier stage in the sequence. Both trunk and grass-bush ecomorphs in my 1972 scheme are late in the ecological sequence and might never have evolved on the smaller islands.

But another possible explanation for the absence of ecomorphs is extinction. This would seem unlikely for the major ecomorphs in the standard sequence, since the niches that they occupy are present nearly everywhere. However, there are cases in front of us that point to the real possibility of extinction for certain categories. One of the 2 large-twig anoles of Hispaniola, *A. darlingtoni,* is known from a single specimen. It is certainly local; it might already be extinct or on the verge of extinction. The apparently demonstrated rarity of *A. fowleri,* known from only 7 specimens, which I interpret as the north island representative of *A. darlingtoni,* may be a stronger case. (The exact habitat of *A. darlingtoni* has not been penetrated since its discovery.) *A. fowleri* occurred in a region of Hispaniola which has been devastated by the recent hurricanes. The absence of a large-twig anole in Puerto Rico or the absence of a small-twig anole in Jamaica might be explained by an analogy with these examples.

The second giant anole of Puerto Rico, *A. roosevelti,* is known from 2 specimens. It has been vigorously looked for and is probably extinct. *Anolis eugenegrahami,* the semiaquatic anole very recently discovered in Haiti, is known from a single locality. It may or may not be genuinely rare, but its habitat requirements appear to be such that its extinction is not unlikely. I mentioned in 1972 *A. poncensis* and *A. cooki,* confined to the most arid areas of southwest Puerto Rico, as species that might be threatened by climatic change and that *A. cooki* may also be threatened by competition with the more eurytopic *A. cristatellus.*

The species confined to the broadleaf forests of montane Hispaniola—*A. christophei, A. etheridgei, A. insolitus*—although they have been abundant, will surely suffer the fate of those forests, if they do not disappear before the forests do.

Note also the restricted range of the *monticola* group on the south island, the Massif de la Hotte in farthest western Haiti. Clearly, the *monticola* group, if it is a natural unit as it appears to be, must have had a distribution well to the east, up to and across the Cul de Sac plain. There must at some time have been a very severe contraction of range. This area (cf. *A. darlingtoni* above) has not been well explored and new taxa and new localities for those already known are to be expected. The rarity or commonness of individual taxa cannot be assessed until the region is better canvassed.

From these cases of apparently or genuinely vulnerable species, it is necessary to extrapolate to the possibility of unobserved species that went extinct before collections were ever made, perhaps normally as part of the fauna-building process, perhaps as a result of secular climatic change, perhaps as a result of post-Columbian, particularly recent, destruction of habitats.

Extinction is clearly an undefined—worse, indefinable—term in our assessment of possible anole communities. The anole communities we see are very possibly a residue only. On the worst view we see only the animals commensal with or tolerant of man; on the best view we see climax communities, the end result of a long history of species-species, species-environment interactions in which many nascent and perhaps also many fully evolved species have gone to extinction. On this point, the discovery in 1977 of an animal so distinct as the semiaquatic *A. eugenegrahami* should give skeptics pause. There are still unknown areas and unknown animals in the West Indies.

Components of the anole faunas of the 3 large islands and the individual species were categorized above. Differences between the 3 islands and especially the relationship of fauna to area will, however, be better appreciated if the faunas are compared as assemblages.

Jamaica

The 7-anole fauna of Jamaica (of which I have seen all species alive and in the field many times) is the simplest of the Greater Antilles. We can be sure that 6 of the 7 evolved in place; the seventh, *A. sagrei,* is conspicuously a late, perhaps human assisted, invader from Cuba that is still confined to the western half of the island. The native Jamaican anoles are all clearly their own closest relatives, an unquestioned intra-island radiation.

This may be our only example of a complex anole fauna evolved within an island. I formerly (1972) tried to portray Puerto Rico as such an island. Since the discovery of *A. sheplani,* more primitive than its relative, Puerto Rican *A. occultus,* (Schwartz, 1974a), on Hispaniola, there is good reason to reject that hypothesis and to assume that Puerto Rico has had at least 3 invasions, one ancestral to *A. occultus,* one ancestral to *A. cuvieri,* and a third for the stock ancestral to all the remaining Puerto Rican anoles. Cuba certainly has had 2, while Hispaniola has been invaded and back-invaded (Williams, 1969, also Table 15.5 and Figure 15.4).

Ecomorphs are clearly present on Jamaica: (1) the active and aggressive *A. garmani* is the crown giant, tending to occur high; (2) a somewhat smaller species, *A. valencienni,* a slow searcher, tending also to be high but preferring smaller perches, even twigs, represents what I now call the twig-giant ecomorph; (3) *A. grahami* is the larger of the 2 trunk-crown

Table 15.5 Invasions into and within the West Indies, and the resulting faunas.

Target	Invasion number	Faunal number
Cuba (43,036 mi^2)	2	> 35[a]
Hispaniola (28,242 mi^2)	4	> 35[a]
Puerto Rico (3,421 mi^2)	3	11
Northern Lesser Antilles	1	1 or 2 per island bank
Southern Lesser Antilles	1	1 or 2 per island bank
Jamaica (4,450 mi^2)	1 + 1[b]	7

NOTE: Island area according to Rand, 1969.

a. Species numbers for Cuba and Hispaniola are already 2 to 3 species greater than 35, with more species to be described.

b. *Anolis sagrei* remains equivocal—probably imported by man, but not demonstrated to be so.

ecomorphs that I now recognize, foraging in the crown and on the upper trunk; (4) *A. opalinus* I now regard as a second smaller trunk-crown ecomorph, on this island somewhat more shade loving than its larger counterpart; (5) *A. lineatopus,* representing the trunk-ground ecomorph, typically perches head downward, foraging for prey on the ground. Different races of this last species (Fig. 15.5) prefer sun (*A. l. lineatopus*) or shade (*A. l. neckeri*).

Anolis sagrei (separated as a nonnative species in Fig. 15.5) is a second trunk-ground ecomorph. In western Jamaica its perch is lower than that of neighboring *A. lineatopus* and it is sun loving in contrast to western shade-loving *A. lineatopus neckeri.*

The last Jamaican species, *A. reconditus*, is a montane isolate in eastern Jamaica. It is outside the ecomorph series, a solitary generalist of high wet forest.

This is a summary of data reported in Underwood and Williams (1959), Rand (1967b), Schoener and Schoener (1971a) and Hicks (1973) as well as personal observations. One caveat is necessary: the Jamaican ecomorphs are most distinctive in size and color, less so in body proportions or scales, and least so in behavior, which depends substantially on the presence or absence of other species (see Jenssen, 1973).

Modal perch and climatic preferences are diagrammed in Figure 15.5. Maximum snout-vent length in males is indicated opposite each name. An altitudinal profile (Fig. 15.6) is intended to indicate that lowland diversity tends to attenuate (in reality only slightly) until only *A. garmani* and *A. opalinus* are adjacent to the wet montane forest that *A. reconditus* inhabits alone (Hicks, 1973). Note in Figures 15.5 and 15.6 that in Jamaica the bush habitat has no species specifically adapted to it, that there is no dwarf-twig ecomorph, and that the trunk-crown ecomorph is divided by size.

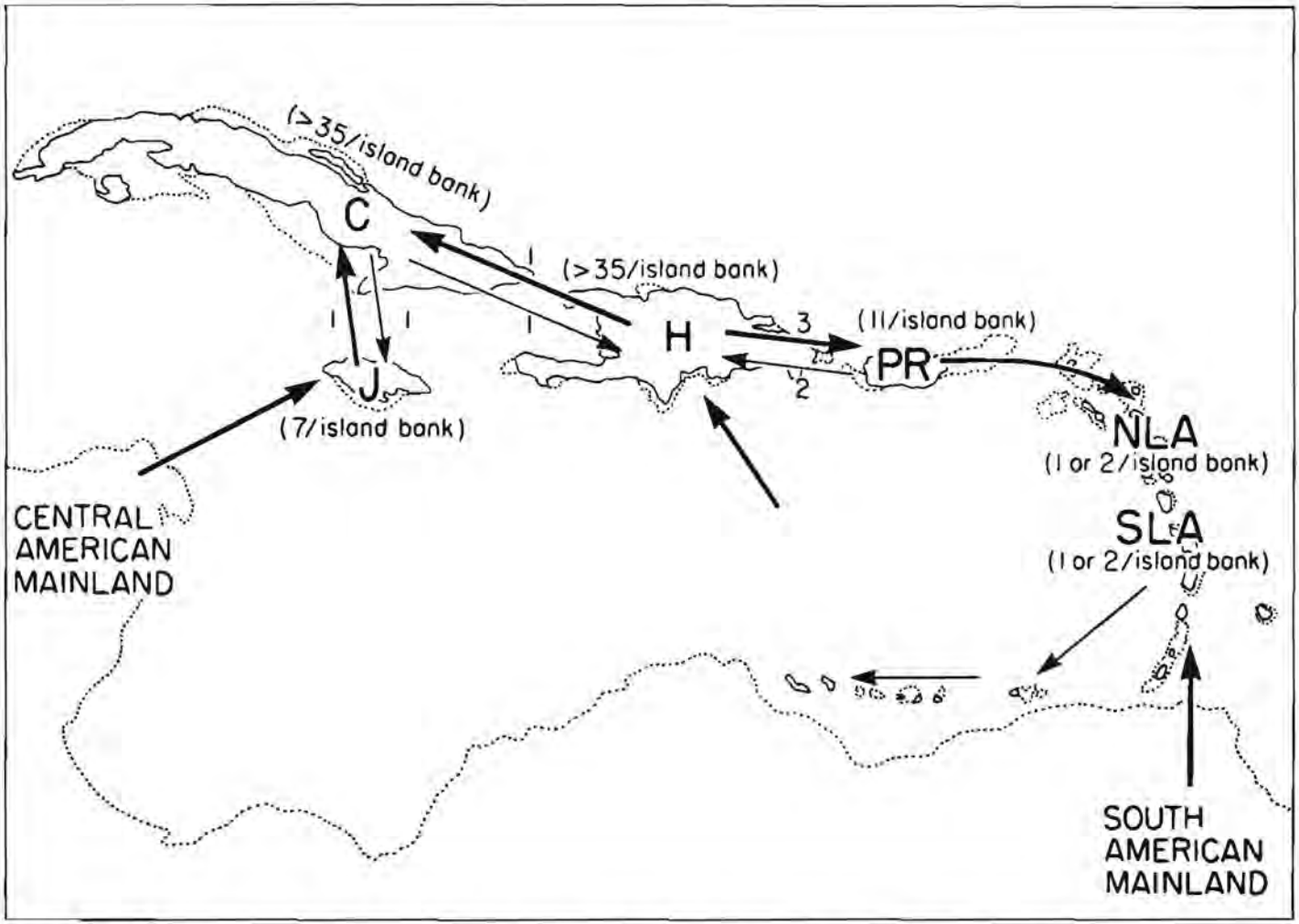

Figure 15.4 Postulated invasions of *Anolis* into and between West Indian islands (modified from fig. 2, Williams, 1969).

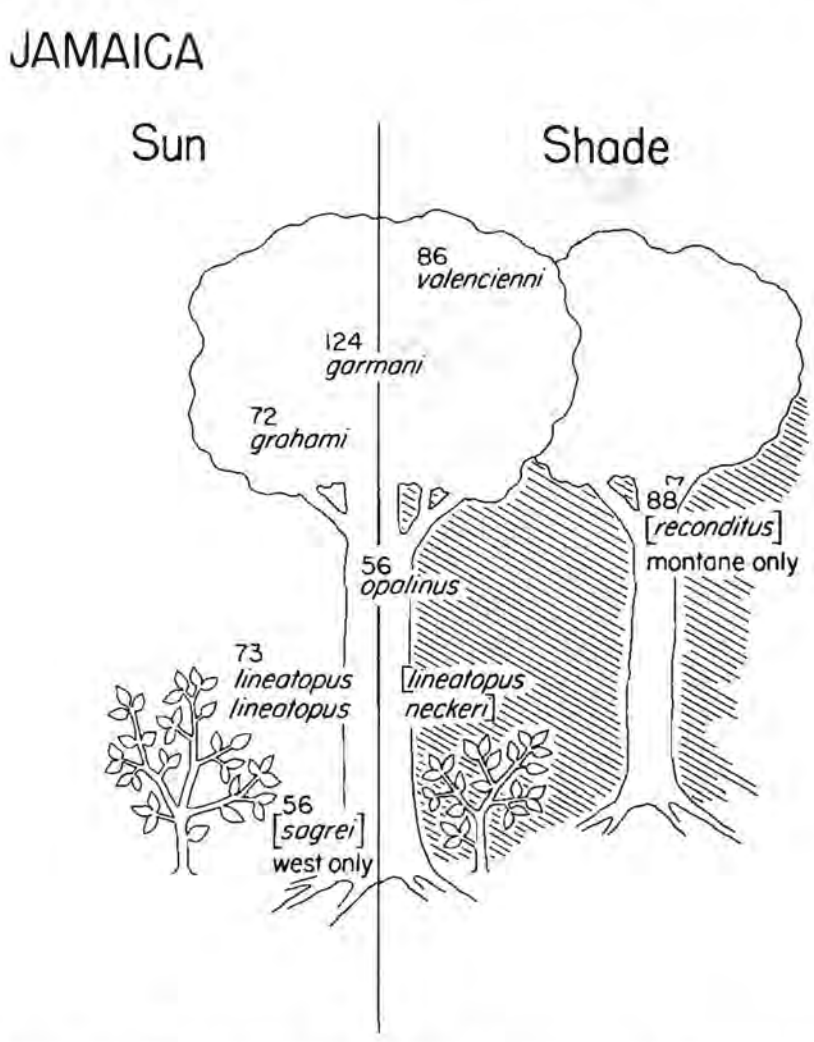

Figure 15.5 Perch and climatic preference of Jamaican species. Numbers are maximum adult male snout-vent size in mm. Note that there are no species specialized to the grass-bush niche. The ecological relationships of the 5 anoles not bracketed are as shown on the campus of the University of the West Indies near Kingston (Rand, 1967).

In Jamaica we have neither climatic vicariants nor allospecies. Climatic adaptation occurs within species—conspicuously within *A. lineatopus* where climatic variants are sharply distinguished by color, including dewlap color, and are recognized as subspecies. A lesser climatic adaptation exists within *A. grahami*, identifiable by color and taxonomically recognized as subspecific.

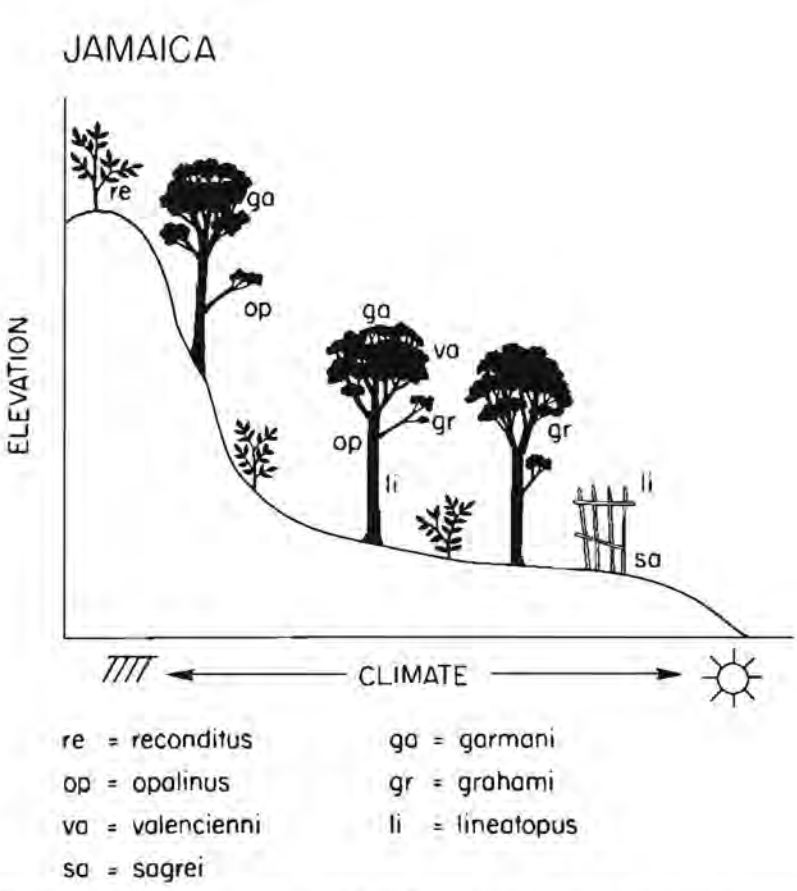

Figure 15.6 Diagrammatic profile of Jamaica showing variation of community structure with elevation and climate. There is considerable behavioral and some morphological variation within species with respect to climate, for example, *A. lineatopus* would not typically be found above *A. sagrei* on fence posts because in western Jamaica, where *A. sagrei* occurs, *A. lineatopus* is a relatively shade-loving species. In the Kingston area, in contrast, *A. lineatopus* is the characteristic lizard of sunny fence posts.

All Jamaican species are sympatric, often syntopic, except *A. reconditus,* which minimally overlaps with *A. garmani* and *A. opalinus. Anolis reconditus* is the only real addition in Jamaica and one, as mentioned above, that is outside the classic sequence.

Puerto Rico

In Puerto Rico there are only standard-sequence ecomorphs (Fig. 15.7): 2 giants, *A. cuvieri* and *A. roosevelti,* a cryptic dwarf-twig *A. occultus,* a large green anole (trunk-crown ecomorph I) *A. evermanni,* and a smaller

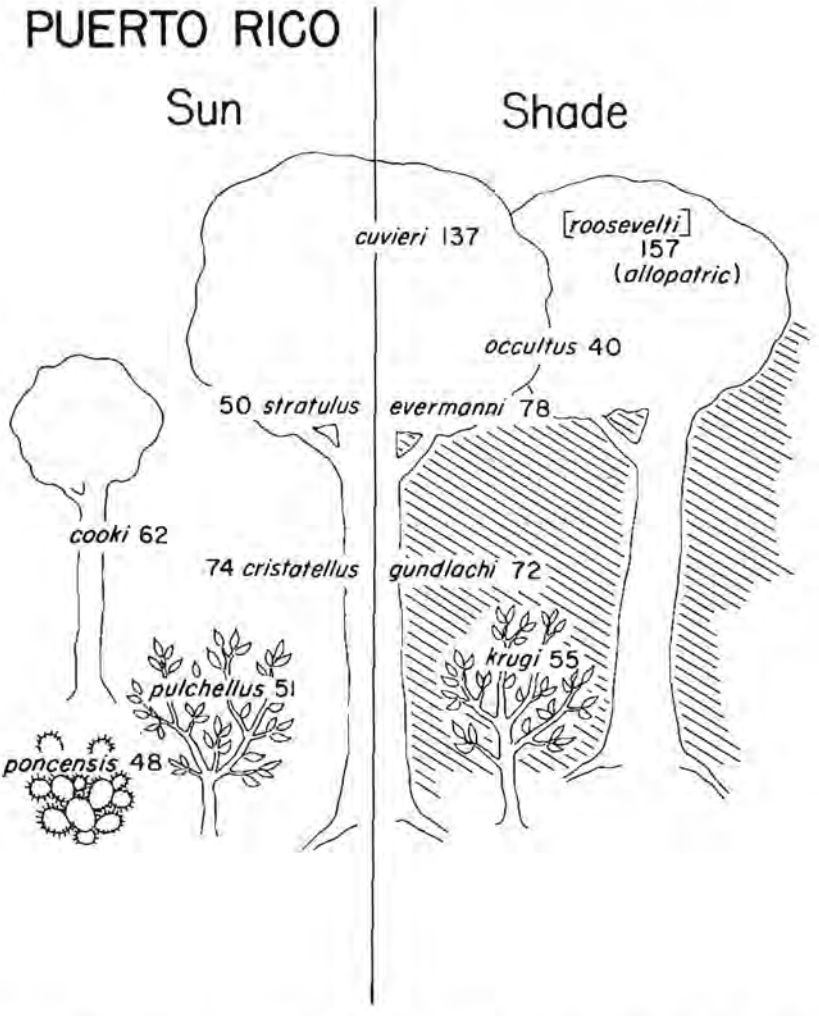

Figure 15.7 Perch and climatic preferences of Puerto Rican anoles. Numbers are maximum adult male snout-vent sizes in mm. *Anolis roosevelti* is bracketed because it is known only from Culebra Island and may be extinct (modified from Williams, 1972).

greyish species (trunk-crown ecomorph II) *A. stratulus,* 3 trunk-ground species, *A. gundlachi, A. cristatellus* and *A. cooki,* and, in addition, a type missing on Jamaica, the grass-bush ecomorph, here represented by 3 species (relatively heavy-bodied for this ecomorph), best called bush ecomorphs, *A. krugi, A. pulchellus* and *A. poncensis.* I have seen all species alive and in the field with the sole exception of *A. roosevelti.* Named from

2 specimens, this species has not been found again in spite of determined search.

Missing in Puerto Rico is the large-twig anole. (There appears to be some complementarity—see below for the Hispaniolan fauna—between giant and dwarf-twig species.) Missing also is the trunk ecomorph. In contrast to Jamaica, also, there is no distinctive montane species. Even the dwarf-twig anole, *A. occultus,* formerly Puerto Rico's last candidate for an exclusively montane species, has been found at elevations of only 200 m in northwestern Puerto Rico (Thomas and Thomas, 1977). (Note that in Puerto Rico the mountains rise only to 4,000 feet, while those in Jamaica go to 7,000.)

The striking new additions in Puerto Rico are by climatic vicariance (Fig. 15.8). In contrast to Jamaica, where climatic divergence is infraspecific, visible in behavior or at the subspecific level, in Puerto Rico climatic divergence shows itself at the specific level. Even the 2 giants appear to be such: *A. cuvieri* on mainland Puerto Rico occurs characteristically in more mesic situations than are (or were) available to *A. roosevelti* in the comparatively dry forest of Culebra.

Quite classic cases of climatic vicariance are the trio of trunk-ground species, *A. gundlachi, A. cristatellus, A. cooki,* which range in that order from habitats that are quite wet to those that are very arid. These are paralleled by the trio of grass-bush species, *A. krugi, A. pulchellus, A. poncensis,* which have the same range of climatic preference and hence quite parallel distributions. The members of neither trio are allospecies. All of these species are quite distinct in many ways and at least interdigitate. *A. cristatellus,* in fact, is sympatric, even syntopic, with *A. cooki* over most of the latter's range.

I emphasize that there are no allospecies in Puerto Rico. This, as we shall see, is in stark contrast to the situation on Hispaniola.

It is an interesting point that the smaller of the two trunk-crown species of Puerto Rico, *A. stratulus,* is believed to represent the exact stock that, when it colonized Hispaniola from Puerto Rico, evolved into the *distichus* complex in Hispaniola, which are the classic trunk ecomorphs.

As might be expected in such an ancestor-descendant relationship there are similarities between *A. stratulus* and the distichoids. They are similar in size and even in shape. In behavior, however, they differ strongly. *Anolis stratulus,* like all trunk-crown anoles, do spend much time on the trunks of the trees on which they are resident, but *A. stratulus* is found with higher frequency in the canopy. Above all, *A. stratulus* is never inserted between the larger trunk-crown species and a trunk-ground species; it is never inserted between *A. gundlachi* and *A. evermanni.* In relation to *A. cristatellus,* it behaves as a trunk-crown species should and there is no species above it. In fact, because it is a less shade-loving species than *A. evermanni,* it is often found at the outer margins of forests

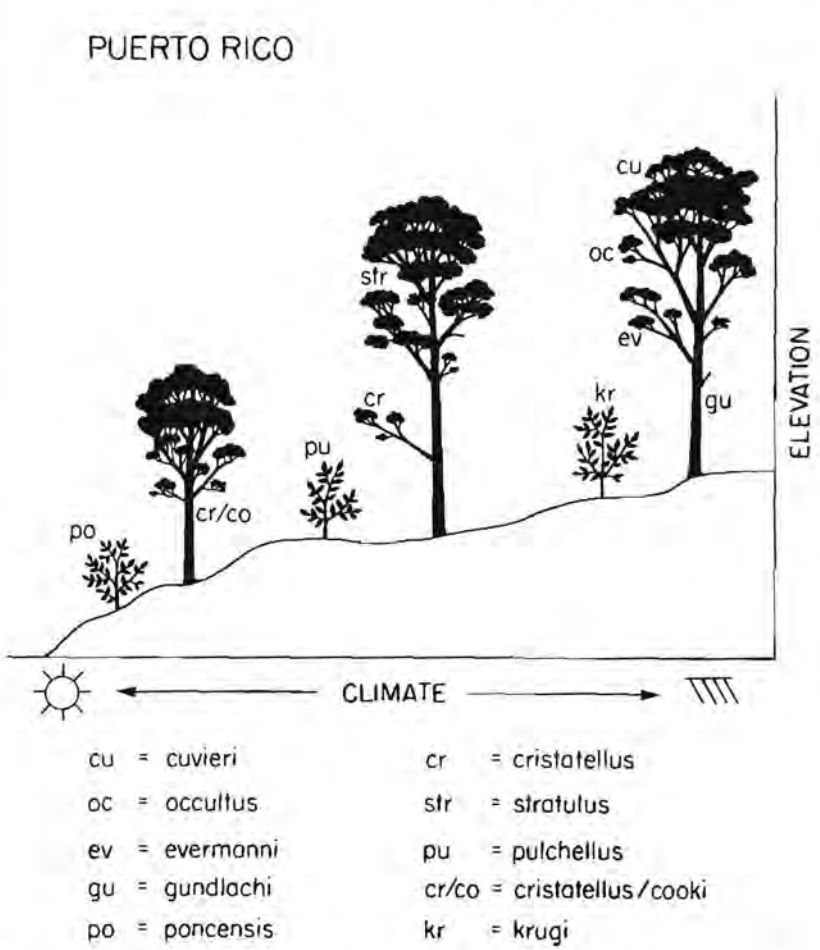

Figure 15.8 Diagrammatic profile showing variation of community structure in Puerto Rico with elevation and climate.

inhabited by *A. evermanni*, including the top of the canopy, thus higher than *A. evermanni*.

Hispaniola

Hispaniola is very different from the 2 smaller islands in much more than mere faunal number. The increased number is achieved in a distinctive way: there is an extraordinary proliferation of allospecies (see Tables 15.3a and b where they are named and marked off in brackets). Each of the standard sequence ecomorphs is represented by two or more allo- or parapatric species. In 2 of the more complex cases—the trunk-ground and grass ecomorphs—there are additionally in each case exam-

ples of the climatic vicariance first found in Puerto Rico: in the trunk-ground series *A. whitemani* is in the very arid lowlands and *A. cybotes* in adjacent more mesic situations, and in the grass series *A. olssoni* is in arid lowland, whereas *A. semilineatus* is typically in more mesic situations in the lowlands and at high elevations. In the trunk ecomorph—this is the first level of complexity at which this ecomorph is found—the situation is still more complicated: there is a series of allospecies, the *brevirostris* complex (Arnold, 1980)—*A. websteri, A. caudalis, A. marron, A. brevirostris*—the members of which are sometimes allopatric to, sometimes parapatric to, sometimes complexly interdigitated with or intervening between subspecies of a sister species that is infraspecifically divided climatically—*A. distichus* (cf. Schwartz, 1968).

In this island, while I have seen most of the 36 described species repeatedly in the field, I have seen *A. eugenegrahami* alive only in captivity and *A. darlingtoni, A. dolichocephalus, A. haitianus, A. koopmani, A. marron, A. monticola, A. rimarum, A. rupinae,* and *A. sheplani* only as preserved specimens.

The allospecies of Hispaniola are only partly correlated with the major physiographic subdivision of the island—a trough, the Cul de Sac–Valle de Neiba plain, partly below sea level—that divides Hispaniola into north and south islands (Williams, 1961). This trough, which was at times in the Pleistocene a real physiographic barrier, must have played a part in the origin of the trunk-crown I allospecies, *A. chlorocyanus* and *A. coelestinus;* it still coincides with the boundary between them. It is astonishing, however, that this is the only instance in which the below-sea-level trough and the consequent north and south islands are a sufficient explanation of Hispaniolan allospecies. In other cases dispersal across the boundary is the minimum explanation required, while in still other cases no obvious explanation of allospecies is currently available. *Anolis marcanoi* (Williams, 1975) is an especially provocative example. It is a close relative of *A. cybotes,* and its range in the south central Dominican Republic is entirely surrounded by that species. Schwartz and Thomas (1977) have pointed to the parallel occurrence of a *Sphaerodactylus* with a distribution entirely coincident with that of *A. marcanoi.* Yet neither for *A. marcanoi* nor for the *Sphaerodactylus* has it been possible to point to any physiographic or vegetational or climatic factor that can in any way isolate these 2 taxa or explain their origin and persistence in the area they occupy.

The proliferation of allospecies in Hispaniola becomes especially interesting when it is realized what it implies: allospecies are sets of populations that have begun the speciation process but have not carried it beyond its first stages; they have been unable to achieve sympatry with their sister populations. Thus, in contrast to Jamaica and Puerto Rico, where all populations were either clearly species in the fullest sense of the term or were as clearly below that level, it is a characteristic of His-

paniola that the majority of named species-level taxa appear to have at best only recently crossed the species threshold. The situation could be described in terms of permissiveness and restraint: Hispaniola, presumably because of its size and physiographic complexity, has been permissive of differentiation but has also, for whatever reason, held most differentiation to a relatively low level.

Extraordinary also in Hispaniola is the existence of not one but several montane faunas. The exclusively montane species are marked by a special symbol "M" in Tables 15.3a and b. There is first a highly distinctive fauna (evolved mostly from a single-species group, the *monticola* species group, doubly underlined in Table 15.3b) in montane broadleaf forest.

In addition, there is a second montane fauna made up of taxa either directly ascending from the lowlands, for example, *A. cybotes, A. chlorocyanus, A. distichus,* the *ricordii* allospecies (*A. ricordii, A. baleatus, A. barahonae*), or the more or less modified descendants of such lowland dispersers, *A. shrevei* and *A. armouri* (Williams, 1963b).

This is a far cry from the single montane species of Jamaica and the absence of distinctively montane species in Puerto Rico. Furthermore, the greater part of the montane faunas either do not fit the classic sequence and are as clearly separately evolved as compared with the lowland members of the standard sequence as if they had evolved on a different island.

Montane *A. cybotes, A. chlorocyanus, A. coelestinus, A. distichus, A. semilineatus,* and the *ricordii* allospecies, it is true, are changed little or not at all from their corresponding lowland populations. But these are not, except perhaps the *ricordii* allospecies, inhabitants of undisturbed montane broadleaf forest and appear to do relatively poorly or fail entirely in montane pine forest. These montane representatives of lowland species appear to be, as Schwartz (1974b) has suggested, very recent immigrants into open areas, especially the areas opened by roads and the disturbance associated with man.

The truly montane species include species closely related to the characteristic lowland species as well as the others that are quite separate lineages. These montane vicariants of lowland species were not seen on the smaller islands. They include the trunk-crown II species, the smaller subdivision of that ecomorph. There are 3 species: *A. aliniger* and *A. singularis* (Williams, 1965) and an undescribed blue-dewlapped taxon known only from the Sierra Martin Garcia. The first 2 have distributions parallel to those of their close lowland relatives, *A. aliniger* primarily on the north island, *A. singularis* solely on the south island, but *A. aliniger* has somehow gained a foothold south of the Cul de Sac on the Massif de la Selle. In scales also they quite parallel their lowland relatives: *A. singularis* is distinguishable only minimally except in size; *A. aliniger* has one unique peculiarity—its partly pigmented but wholly

scaleless axilla. For all 3 Hispaniolan trunk-crown II species, however, their restriction to high elevations is presumably related to a physiological difference from the primarily lowland Hispaniolan trunk-crown I species.

(There is clearly a tendency for differences other than size to distinguish the 2 subdivisions of the trunk-crown ecomorph, but this ecological divergence appears to differ opportunistically on the different islands; thus on Jamaica *A. opalinus* prefers shade or cooler situations than does *A. grahami.* It tends therefore to be found in open situations in the mountains only. In contrast, Puerto Rican *A. stratulus* accepts sun more readily than *A. evermanni.* In Hispaniola the 2 sizes of trunk-crown ecomorphs are separated by still another device, lowland-highland vicariance.)

There are montane vicariants also in the trunk-ground ecomorph. *A. armouri* (Massif de la Selle) and *A. shrevei* (Cordillera Central) are obviously closely related to *A. cybotes.* (In 1963, I considered *A. armouri* a subspecies of *A. cybotes.*) Animals of the montane pine forests, they live primarily on the ground and rarely perch on pine. Smaller than *A. cybotes* (and *A. shrevei,* unlike *A. cybotes,* heavily keeled), they have, however, diverged from their lowland relative more in behavior than in structure.

The bush niche in Hispaniola is montane. It is occupied by the *hendersoni* (Williams, 1963a; Schwartz, 1977) set of allospecies (*A. hendersoni, A. bahorucoensis, A. dolichocephalus*) limited to the mountains of the south island—south central and western Hispaniola. They are in habit and habitat bush anoles but distinctive in morphology: their extraordinarily long heads, reduced dewlaps, and spectacular coloration put them outside the standard set of bush-grass anoles and require that they be recognized as another of the unique montane components of the Hispaniolan fauna, in this case probably rather distantly related to the Hispaniolan trunk-crown anoles and not nearly as closely to the Hispaniolan grass anoles. As bush animals they are inhabitants of the edge rather than the interior of montane broadleaf forest (Moermond, 1979; personal observation).

Montane *A. insolitus* and *A. sheplani* (Williams and Rand, 1969; Schwartz, 1974a) belong in the standard sequence as twig dwarfs and as such closely resemble the twig dwarf of Puerto Rico, *A. occultus,* in both morphology and behavior.

Anolis darlingtoni (Cochran, 1935) is known from a single specimen from the Massif de la Hotte in southwest Haiti; *A. fowleri* (Schwartz, 1973) is known from the Cordillera Central. Nothing at all is known of the habits of the first; of the second nothing is known except where it was found sleeping, "on twigs" and "across branches." On the basis of the same close resemblance that made Cochran (1935) place *A. darlingtoni* in the same genus (*Xiphocercus*) that Jamaican *A. valencienni* was then rele-

gated to, I infer that the habits of *A. darlingtoni,* when known, will be very like those of *A. valencienni,* those of a twig giant. (These 2 species are quite distinct phyletically; the resemblance is clearly ecological convergence.) *Anolis fowleri* has never previously been compared with *A. darlingtoni.* It is clearly a quite distinct species, but I again infer from its morphology that it is a second giant twig species of Hispaniola—a geographic representative of *A. darlingtoni* in the Cordillera Central and phyletically related as well as ecologically equivalent.

It is noteworthy that twig anoles are curiously spotty in their distribution; only Jamaican *A. valencienni* is genuinely widespread within its island. All 4 Hispaniolan species are not only strictly montane, they are local within this restriction. *Anolis insolitus* is locally common (personal observation) and known from several localities but all are in the Cordillera Central. *Anolis sheplani,* while known from fewer localities, does occur on both sides of the Cul-de-Sac–Valle de Neiba plain, south of it on the Sierra de Baoruco, north of it on the Sierra de Neiba. *Anolis fowleri,* known from 7 specimens from 2 localities, in the Cordillera Central, may be genuinely rare. *Anolis darlingtoni,* although nothing can be said about its local abundance in its unvisited type locality in the Massif de la Hotte, appears to be really absent from the relatively well-collected mountains of the eastern portion of the Hispaniolan south island.

Close to the same basal stock as the twig anoles is the *A. monticola* series—the one really distinctive montane radiation in Hispaniola, as diverse as it is distinctive. There are 2 widely disjunct subgroups within it, the more primitive on the 2 northernmost of the 3 mountain ridges that dominate the Hispaniolan north island—the Cordillera Central and the Cordillera Septentrional, the second, highly specialized, again, like *A. darlingtoni,* confined to the Massif de la Hotte in the extreme southwest.

Anolis christophei (northern group) is much the most primitive of these. It has been classified in Table 15.3b as a trunk anole. It fits in size but not very well in any other way. In montane broadleaf forest it has the tree trunks and the branches of adjacent bushes and banks and rock ledges to itself. It has neither a trunk-crown anole above it nor a trunk-ground anole below it. Its habitus is quite unlike that of *A. distichus.* It is something of an analogue but not at all a homologue of a standard trunk anole.

Anolis etheridgei is in the undergrowth under the trees of the northern montane broadleaf forest. In morphology it resembles neither the grass anole of the standard sequence nor the *hendersoni* allospecies that has the same niche in the south island of Hispaniola. It is again an analogue rather than a homologue.

Anolis rimarum (again northern group) is an anole of rocky fields but not in any obvious way specialized for this habitat. It has no parallel in Jamaica or Puerto Rico and does not belong in the standard sequence,

does not in fact make any approach to any of the standard ecomorphs.

Anolis monticola and *A. rupinae* (southern group) are again two rock anoles, the second larger than the first, with which it is syntopic. They are both gaudily colored, obviously closer to each other than to anything else, and not especially similar to *A. rimarum*. They clearly do not belong to the standard sequence. (For a comparison of *A. monticola* with the standard sequence see Moermond, 1979.)

Anolis koopmani is phyletically closest to *A. monticola* and *A. rupinae* (Thomas and Schwartz, 1967; Webster, Hall, and Williams, 1972) but behaviorally and morphologically it is the most similar of any of the *monticola* series to a standard ecomorph, specifically the grass ecomorph (Williams and Webster, 1974; Moermond, 1979). In a disturbed area in southwest Haiti where Moermond observed it, it exists alongside *A. semilineatus* like a climatic vicariant of the latter, although it is conspicuous that the resemblance is not phyletic.

The anole fauna of the Hispaniolan montane broadleaf forest, in fact, looks as though it evolved quite separately from the lowland fauna, as though it were on an island within an island. More interesting than that, however, it may present us with an example of an incomplete or an *alternative sequence* (see below).

The montane faunas contribute most of the ecomorph category "Other" in Hispaniola. There is, however, one *outré* species that is lowland: recently described *A. eugenegrahami* (Schwartz, 1978). Ecologically it fits very well in the semiaquatic niche well known from several species in South and Central America and from one species in Cuba. But this is a niche that apparently does not impose any rigid morphological constraints. *Anolis eugenegrahami* does not closely resemble any other anole, not Cuban *A. vermiculatus*, not the *lionotus* group, nor *A. barkeri* nor *A. aquaticus* of the mainland. On this point see Schwartz (1978), who has made all the necessary comparisons. *Anolis eugenegrahami* is not an ecomorph in my sense; except in its behavior, it is idiosyncratic. If its distribution is as limited as present information might indicate, it would fit, classically, a category of "local survivor"—if, in fact, it has long to survive.

The allospecies and the montane faunas so complicate the distributional/ecological patterns within Hispaniola that figures fully comparable to those for the other islands cannot tell the full story. Figures 15.9–15.12, however, should assist.

It is necessary to treat the lowlands and montane areas separately, and the north and south island faunas must be distinguished also. Figure 15.9 shows size, perch, and climatic preferences for species from the north island lowland faunas, and Figure 15.10 does the same for the north island montane faunas. Figure 15.11 provides an altitudinal/climatic profile for all north island species; arrows indicate the altitudinal

placement but not the perch of two species recently discovered and still poorly known. Figure 15.12 is a south island altitudinal and climatic profile. Comparison with Figure 15.11 will show obvious general parallels despite dissimilarity in the species represented. As in Figure 15.11, species doubly underlined belong to the *monticola* series. The figure is composite in that several of the species are localized even within the south island, for example, *A. armouri* is known only from the central south island range, the Massif de la Selle, *A. sheplani* only from the Sierra de Baoruco, the 3 *monticola* series species only from the western Massif de la Hotte, *A. alumina*, *A. longitibialis*, and *A. strahmi* only from the Barahona Peninsula. *Anolis brevirostris*, although isolated populations or related species occur on other parts of the south island, is itself known only from the Barahona Peninsula and the adjacent Cul-de-Sac–Valle de Neiba plain. The three allopatric species of the *hendersoni* superspecies, spread across the whole of the south island, are represented in Figure 15.12 by the single symbol "h."

As the comment on the last figure implies, these figures understate the complexity, which is at a completely different level from that of the smaller islands.

Discussion

Faunas—Ephemeral or Persistent

In an evolutionary sense no faunas are permanent. At best they are more or less persistent. In this chapter I have treated present faunas as persistent, and even local situations as persistent—not without occasional cautionary phrases about the past, present, and future effect of human action. Roughgarden and his colleagues (Chapter 16) treat even the simplest of my faunas, the Lesser Antillean species pairs, as evanescent, a temporary phase in a dynamic ineluctable process. I do not argue the case, but I take the opportunity here to warn that the details that I have reported here are quite possibly labile and unstable, even if they have been stated with total accuracy—something more to be hoped for than achieved—but I am confident that large patterns here merit attention, whether persistent or dynamic, and whether I have presented them with entire fairness or not. For a critique of generalization from faunal data, see Sih and Dixon (1981) and the immediately following reply by Fretwell (1981).

Syntopy, Interdigitation, and Parapatry

Complex faunas here described are made complex by both spatial overlap and spatial separation of their contained species.

Table 15.6 lists for selected localities in each of the 3 large islands the number of anole species that might be found within a few feet of one

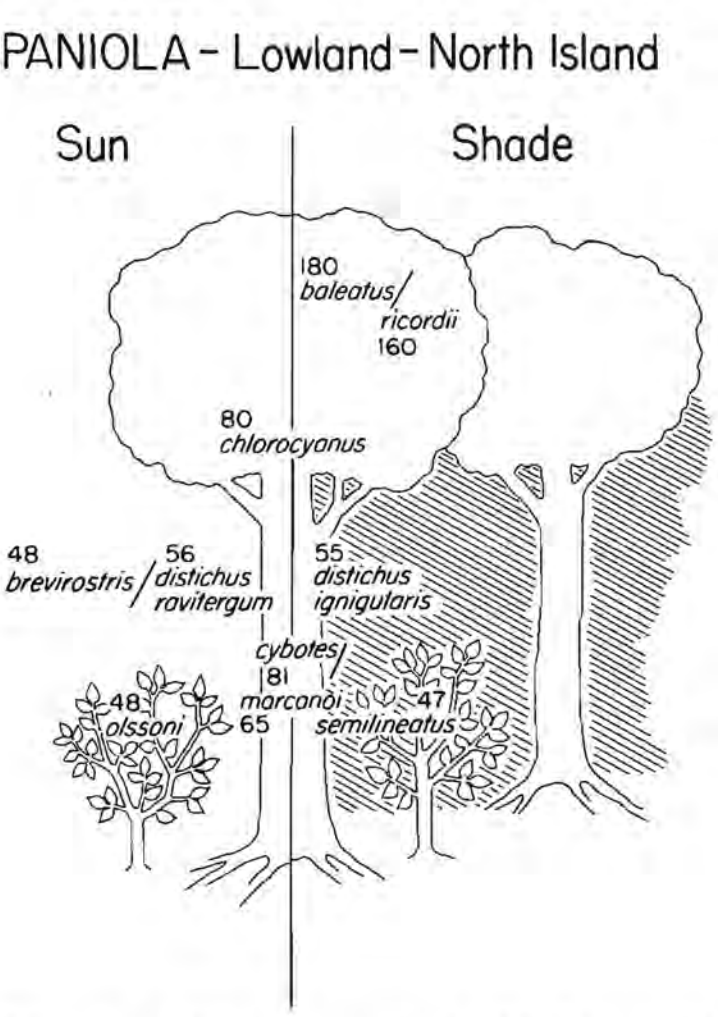

Figure 15.9 Perch and shade preferences of anoles of the lowlands of the north island of Hispaniola. All are standard sequence ecomorphs. Numbers are maximum adult male snout-vent sizes in mm. Species separated by a solidus (/) are allospecies.

another, that is, those that might be found in one tree or a few and their immediately adjacent bushes. These animals may usefully be regarded as syntopic. Three is a very usual count; the extreme count possible might be 6.

Where there are climatic vicariants interdigitation of habitats will sometimes permit species usually well separated to be seen within yards of one another. Table 15.7 lists some localities at which this situation

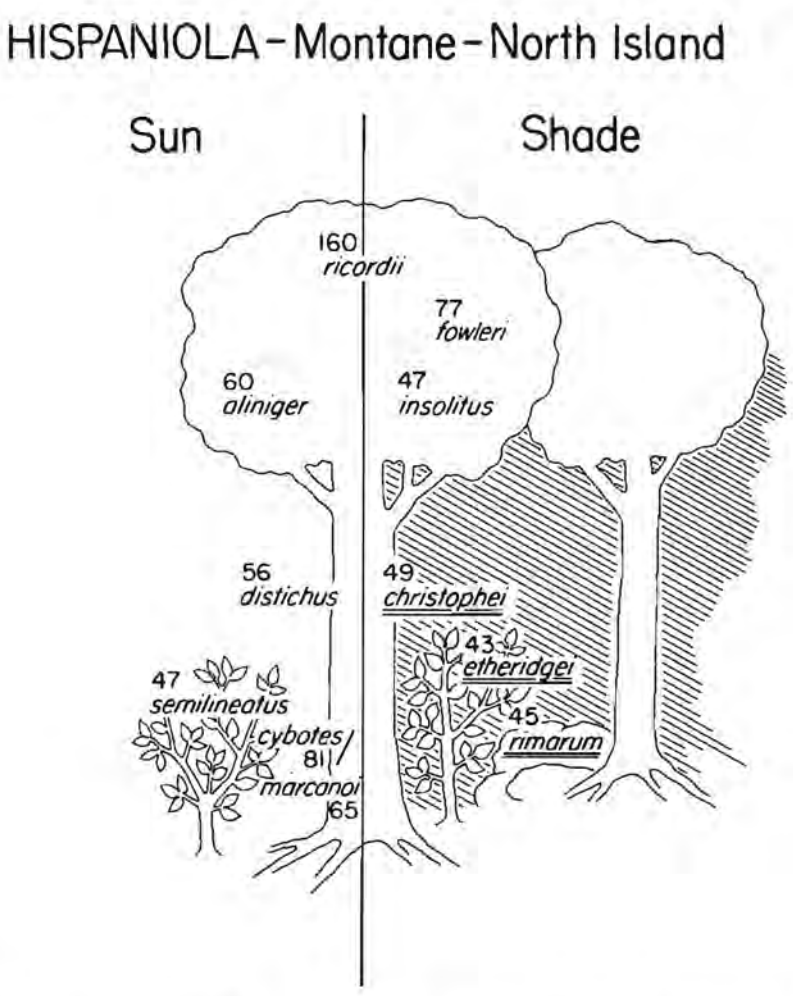

Figure 15.10 Perch and shade preferences of montane north island anoles in Hispaniola below the pine zone. Numbers are maximum adult male snout-vent sizes in mm. Species doubly underlined belong to the strictly montane *monticola* group. *Anolis shrevei* occur in the pine zone above these species.

would be seen. The extreme count of such species in Hispaniola or Cuba might be 10.

The tables cite maxima for specific localities. It should be remembered, however, that there are also minima, and that even on the largest islands in the densest faunas there are local situations and times in which faunas seem depauperate, despite apparent adequacy of habitat, and in which close observations find some to many fewer species than

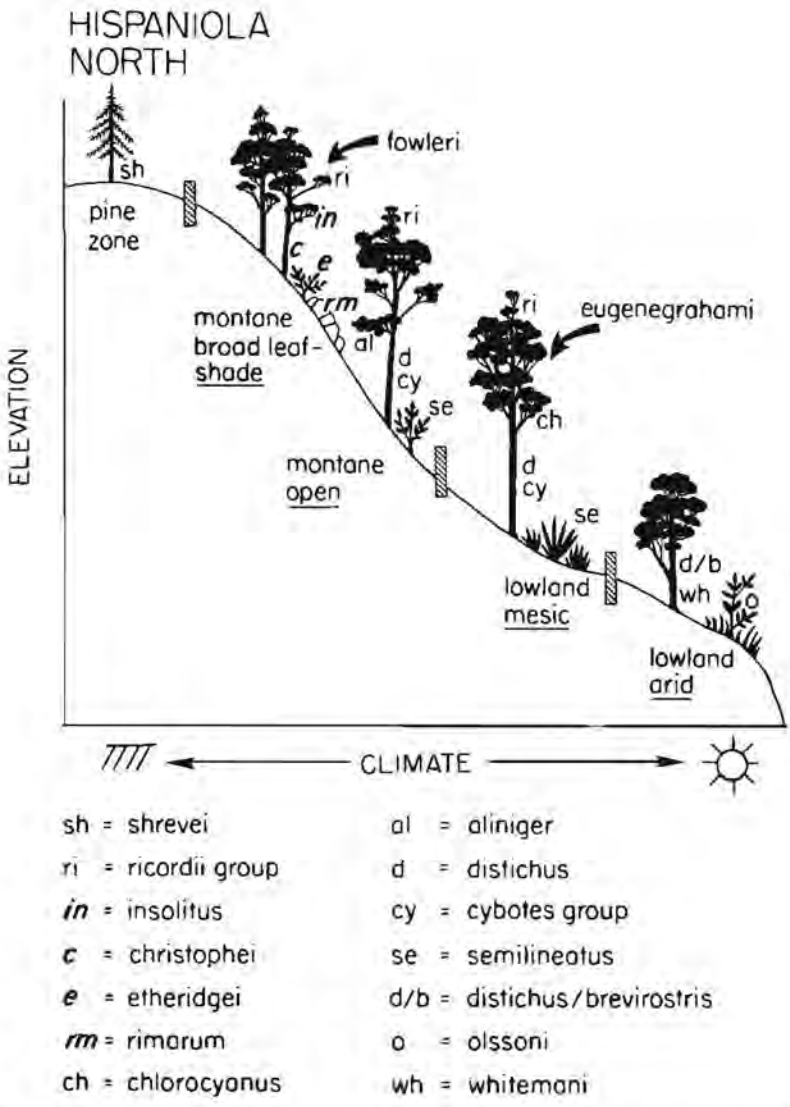

Figure 15.11 Profile showing variation in anole community structure on the north island of Hispaniola. Montane broadleaf and montane open communities are for the most part not closely related. Except in the case of *A. brevirostris* and *A. distichus*, which are complexly interdigitated, allospecies are not shown. Arrows indicate the occurrence of 2 recently discovered species that are poorly known.

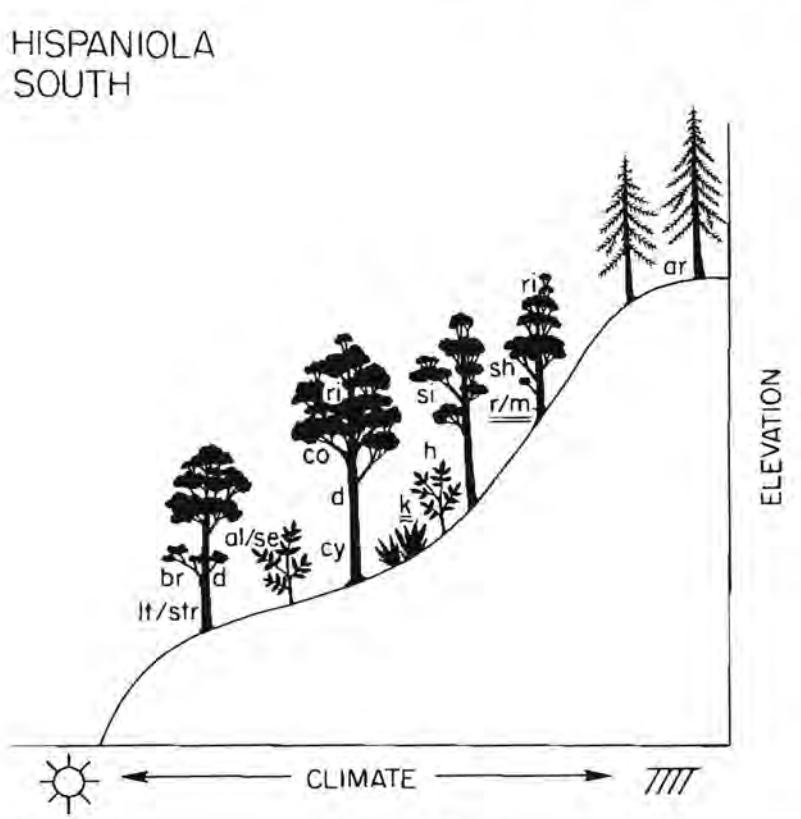

Figure 15.12 Diagrammatic profile of the anole communities of the south island of Hispaniola. Doubly underlined species belong to the *monticola* series.

might be expected. This may be a temporary phenomenon or an artifact of observation (or the individual observer), but such situations are sufficiently often confronted that they must be considered part of expected faunal variance, whether or not any ad hoc explanation can be devised. The maximal numbers of coexistent anoles given above for the larger

West Indian islands are not rare or even unusual, but they are not nearly modal.

Another local condition is not cited in any of the lists of Tables 15.6 and 15.7. This is the occasional doubling of species at the contact zones of allospecies, sibling species, or semispecies. There is sometimes a gap rather than overlap and then there is no doubling; one condition may be as frequent as the other. Thus on Hispaniola, *A. marcanoi* sometimes overlaps *A. cybotes, A. brevirostris* may be separated by an apparent gap from *A. distichus* or may contact that species (and may then hybridize or not, depending on locality), and Schwartz and Thomas (1975) report the overlap of *A. cybotes* with *A. armouri* and of *A. hendersoni* with *A. bahoruco ensis.*

The lists in Tables 15.6 and 15.7 represent essentially coadapted communities; they correspond to the results of the 3 axes of adaptation of *Anolis* in Figure 15.2 (size, perch, and climate). The contacts of allo-, sibling, and semispecies are not adaptive; they are the byproducts of an incomplete speciation process.

Thus 2 components to the size and complexity of anole faunas exist: (1) the high divisibility of the anole niche (speciation completed) and (2) the phenomenon of *species nascendi.*

Modes of Speciation, Modes of Colonization, Faunal Buildup

Most discussions of faunal buildup (Lack 1947, 1976; MacArthur and Wilson, 1967; Diamond, 1975) have used birds as their empirical examples. Classically faunal buildup in these models has been by multiple invasions—colonizations separated by time intervals and occurring across some discrete barrier, such as an oceanic strait. Invaders are considered to have already reached the level of species. The process so envisaged is one of accretion or accumulation.

This does seem to be the process by which island avifaunas originate. But Diamond (1977), who distinguishes 3 modes of allopatric speciation for Pacific land birds (continental, intra-archipelagal, and inter-archipelagal), goes on to make an observation very pertinent for anoline lizards: "For taxa whose dispersal ability and population density differ from those of birds, the relative contributions of the three modes may be very different. What is an island to one group of taxa may be a continent to another."

This is very much to the point. Clearly, to *Anolis* the Greater Antilles have been (relatively speaking) continents. In this regard the contrast between birds and lizards is very great.

Lack (1976:193) comments: "In the land birds, there has been virtually no adaptive radiation within the West Indies, though on Hispaniola the two species of todies and the two of endemic warblers represent a first step. Instead, as is usual in oceanic archipelagos elsewhere, each

Table 15.6 Syntopic or nearly syntopic anoles at selected localities on the three large islands.

Jamaica	Puerto Rico	Hispaniola
Mona forest, eastern Jamaica	El Yunque forest, eastern Puerto Rico	Vicinity of Santo Domingo, Dominican Republic
A. garmani	*A. cuvieri*	*A. baleatus scelestus*
A. valencienni	*A. occultus*	*A. chlorocyanus*
A. grahami grahami	*A. evermanni*	*A. cybotes*
A. opalinus	*A. gundlachi*	*A. distichus ignigularis*
A. lineatopus lineatopus	*A. krugi*	*A. semilineatus*
Whitehouse, western Jamaica	San Juan	La Palma, Dominican Republic (broadleaf forest)
A. garmani	*A. stratulus*	*A. baleatus sublimis*
A. valencienni	*A. cristatellus*	*A. insolitus*
A. grahami grahami	*A. pulchellus*	*A. christophei*
A. opalinus	Cabo Rojo, western Puerto Rico	*A. etheridgei*
A. sagrei	*A. cristatellus*	La Palma, Dominican Republic (open)
	A. cooki	*A. aliniger*
	A. poncensis	*A. cybotes*
	Culebra Island, Virgin Islands	*A. distichus ignigularis*
	A. stratulus	Barahona City, Dominican Republic
	A. cristatellus	*A. coelestinus*
	A. pulchellus	*A. cybotes*
		A. brevirostris wetmorei
		A. alumina
		Ducis, near Aux Cayes, Haiti
		A. coelestinus
		A. cybotes
		A. distichus vinosus

NOTE: Data from Rand and Williams (1969), Schoener and Schoener (1971a), Moermond (1979), and personal observation.

Table 15.7 Some localities on the three large islands at which sympatric (interdigitating) climatic vicariants occur.

Jamaica	Puerto Rico	Hispaniola
Mandeville (grounds of the Mandeville Hotel), central Jamaica *A. garmani* *A. valencienni* *A. grahami grahami* *A. opalinus* *A. lineatopus neckeri* *A. sagrei*	Maricao forest, western Puerto Rico *A. occultus* *A. evermanni* *A. stratulus* *A. gundlachi* *A. cristatellus* *A. krugi*	Oasis edge, Manneville, Haiti *A. chlorocyanus* *A. cybotes* *A. whitemani* *A. brevirostris brevirostris* *A. distichus dominicensis* *A. olssoni*
	El Verde Field Station, eastern Puerto Rico *A. cuvieri* *A. evermanni* *A. stratulus* *A. gundlachi* *A. cristatellus* *A. krugi* *A. pulchellus*	Ravine at ca. 1000 ft on road to Jarabacoa, Dominican Republic *A. chlorocyanus* *A. cybotes* *A. distichus ignigularis* *A. semilineatus* *A. christophei*
		Boutillier Road, south of Port-au-Prince, Haiti *A. coelestinus* *A. cybotes* *A. distichus dominicensis* *A. semilineatus* *A. olssoni* *A. hendersoni*

Les Platons, north of Aux Cayes, Haiti	
A. coelestinus	
A. cybotes	
A. distichus vinosus	
A. semilineatus	
A. dolichocephalus	
A. koopmani	
A. monticola	

NOTE: Data from Schoener and Schoener (1971b), Moermond (1979), and personal observation.

ecological niche is filled by a different colonist from the mainland. The Galapagos finches and the Hawaiian sicklebills are quite exceptional in this respect."

Lack notices the striking difference with *Anolis* and he suggests "that these lizards spread much more infrequently from one island to another than do land birds, so that it may have been possible for some of the colonists to become adapted to what, for *Anolis*, are unusual niches, without this being prevented by the arrival of a more efficient occupant of such a niche on the mainland."

The relative slowness of lizard colonization compared with that of birds is certainly part of the story. Beyond this, however, there are the correlates of this slowness, its difficulty and its selectivity: few lizard invaders ever came from the mainlands, and these were apparently moderate generalists. In lizards, the specialists are not, in general, good colonizers (Williams, 1969). Specialization—the differentiation of ecomorphs—occurred in situ on the islands.

Given slowness, difficulty, and selectivity of colonization, *Anolis* speciation on islands has, for the most part, been not by accumulation but by radiation. This requires a different use of space. Space between islands not on the same bank slows the process too much to play a major role in the formation of the larger *Anolis* faunas. Space within islands, at least within island banks, which are, sometimes, for *Anolis* demicontinents, serves instead.

However, some islands do not show internal speciation. All the Lesser Antilles seem to belong to this class. Although 2 quite different phyletic stocks inhabit the northern and southern islands and although there are a great many islands from the very small to many times larger, there are 1 to 2 anoles per island, never more, and, in all cases (see Lazell, 1972, for one version of the possible histories) the 2 species faunas appear to have been built up by cross-water invasion.

Yet 4 species of *Anolis* can clearly live in sympatry on islands far smaller than the major islands of the Lesser Antilles. Four species coexist, for example, on Bimini, in numbers that should resist extinction except by major geological, meteorological, or climatic catastrophes. The failure of the Lesser Antilles to have more than 2 anoles per island must depend therefore on 2 factors: (1) the difficulty, almost to the point of impossibility, of colonization in the face of filled faunas or broadly adapted species; (2) the similar apparent impossibility or near impossibility of speciation, that is, the full genetic partition of species, within islands below a certain size.

Note, however, there is not a failure to respond to environmental pressures. Geographic differentiation can be sharp and spectacular (for example, in *A. marmoratus* cited above) and is at least in part a response to climatic factors. But in the Lesser Antilles strong differentiation ex-

cept in size is always infraspecific and involves usually color, much more rarely scales.

Apart from size, indeed, differences within species, either solitary or a member of a species pair, may be stronger and more conspicuous than between species. Between species pairs there are, as was said above, ecological differences—thermal preference, perch—but these are not, as was also said, very strong, nor are the morphological correlates of thermal preference and perch very marked. Differences exist—the members are displaced ecologically and morphologically with respect to one another, the species have moved apart—but except in size not very much.

In contrast to the Lesser Antillean anoles, the faunas of the Greater Antilles all have utilized for the origin of at least a major part of their species number intraisland space, and the differences between their several island faunas is probably best understood in terms of the space available for speciation.

Although on the Greater Antilles intraisland speciation has clearly occurred, much of its mode and detail remains obscured by the "fog of time" (Williams, 1969). The speciation process has gone to completion for all members of the faunas on 2 of the islands, Jamaica and Puerto Rico, but for Hispaniola (and Cuba) this is untrue.

All species of Jamaica, except *A. reconditus*, are fully sympatric. But, except for *A. sagrei*, an obvious invader, which is not part of the problem, their mode of speciation is not understood. For geographic speciation, as commonly understood, there are obvious difficulties. Jamaica is very much a unit island, with only a few small and close-in satellite islands on its bank. Physiographic barriers within the island are not obvious, and vegetational fragmentation sharp enough to permit the evolution of full species status is not obvious either, certainly not at the present time. It is, indeed, easier to explain the absence of some members of the standard sequence—the absence of bush-grass or trunk ecomorphs—than to explain the existence of 5 full species plus 1 quite distinct montane isolate. Quite obviously the failure of Jamaica to develop climatic vicariants or allospecies is, given its topographic unity and simplicity, the least of problems.

The happiest solution may be to suppose that in Jamaica the operational areas for allopatric speciation were vegetational islands—the products of the very sharp climatic transitions that can occur on islands—possibly assisted by near-inshore islands separated by narrow water gaps (cf. Lazell, 1966). The mechanism—capture of a fragment of a species by the alternative environment—proposed by Vanzolini and Williams (1981) was suggested as an explanation of climatically vicariant species. In modified form it may assist in explaining the evolution of ecomorphs. Ruled out apparently is chromosomal speciation; the karyotypes of the Jamaican anoles are too similar. There is intraspecific

polymorphism, rampant in *A. grahami* (Judith Blake, in preparation), but there is a single karyotype present in common in all the native Jamaican species.

But the absence of climatic vicariants at the species level in Jamaica does not imply a failure to respond genetically to local environmental pressures. Again the genetic response is infraspecific; the named subspecies of *A. lineatopus*—all of them color races with or without minimal scale differences (compare Puerto Rican vicariant species below)—have a clear correlation with the major climatic regions within Jamaica: *A. lineatopus lineatopus* with the dry south central region, *A. l. neckeri* with the wetter central mountains and the west, *A. l. merope* with the dry north coast, *A. l. ahenobarbus* with the very wet eastern region. In fact, the climatic differentiation of *A. lineatopus* is subtler than the named taxa imply (personal observation) and local populations may differ from valley to valley. Of the two recognized subspecies of *A. grahami*, *A. g. aquarum* applies to the population of the wet eastern region that borders the John Crow Mountains. It is sharply distinct in color and in 1 scale character from *A. grahami grahami*, which occupies the remainder of the island. There are differences within the latter (see Jenssen, 1981) but these are not as clearly associated with ecological aspects of the habitat. The others of the Jamaican species (*A. garmani*, *A. opalinus*) show geographic variation but, like that within *A. grahami grahami*, it is neither sharp nor well bounded.

For all that, the native anoles of Jamaica are distinct full species, all but *A. reconditus* sympatric, all fully isolated reproductively. Despite their differentiation of true ecomorphs, they are, except for *A. valencienni*, morphologically more alike and behaviorally less constrained than are their parallels on the 3 other large islands. Within the spectrum of differentiation and specialization from the smallest to the largest islands, these animals clearly fit below the level of those of the other large islands, although well above those of the Lesser Antilles.

In terms of the usual models of allopatric speciation, Puerto Rico is, at least at a superficial level, an easier case than Jamaica. Its total bank is much larger than that of Jamaica and, more important, it divides into 2 distinct sections, the main island of Puerto Rico and the remainder of its bank, the almost linear series of small islands, the Virgins. Most of the main island is mesic (although the extreme southwest is very arid), while the Virgins are relatively xeric but not maximally so. As I wrote in 1972, there is clearly enough geographic complexity for the allopatric model of speciation, although its details are not easy to make out.

Judged on the results, the Puerto Rican bank has been optimally fragmented for the speciation process. Alone of the 3 large islands, all its species are both fully reproductively isolated and ecologically well constrained. Not only the ecomorphs but the climatic vicariants are all also

morphologically well separated. Puerto Rico presents a tidy picture, all clean lines and no shadows.

Climatically vicariant species first occur on this island and within 3 of the 5 ecomorphs. The color and scale differences between these climatic vicariants in each case show interesting parallels. The shade-wet-preferring *A. evermanni* of the trunk-crown ecomorph is green and large; the more open-dry-adapted *A. stratulus* is gray-brown and smaller. Both have uniform dorsal scales. In the trunk-ground and grass-bush climatic series there are in each case 3 species ranging the spectrum from wet to drier to arid habitats. In neither series is there any important size difference between the species, although in each case the arid-adapted species tends to be smallest. There is in each case a series in body color from wet to dry—dark brown to lighter brown to gray-brown—and in each an increase in scale size from wet to arid.

The curious fact here is that, although involving different parameters, the species difference between climatic vicariants is as sharp as that between ecomorphs, that is to say, the species level does appear to have the potential to heighten ecological adaptation.

Hispaniola is quite another case, being a huge island divided into 2 parts by a trough that is partly below sea level. It has a great deal of physiographic complexity, but in no way can it be said to be fragmented in the sense that the Puerto Rican bank is fragmented. As the description of its anole fauna above has plainly indicated, the north-south island division is of very limited aid in the explanation of its faunal complexity. In fact, the absence of more than one major physiographic barrier in so large an area may be, in major part, the explanation for the species level untidiness that is characteristic of the island. In a number of cases the speciation process in Hispaniola has not been able to advance as far toward completion as have all the species of Puerto Rico.

Hispaniola has, indeed, by the usual method of counting, more than 3 times (37) the number of species of anoles that the Puerto Rican bank has (11). But only some of these 37 species are genuine equivalents of Puerto Rico's clearly defined 11. Twenty-four of the named species of Hispaniola are allospecies or semispecies. Only 13 are so distinct or show their distinctness so clearly by extensive sympatry with their closest relatives that they can be called species in quite the same sense that the species of Puerto Rico are so called.

The phenomenon we confront here is, of course, much more common than just the anoles of Hispaniola. It was for this sort of situation that Mayr and Short (1970) invented the term "zoogeographical species," which they succinctly explain as follows: "The basic units of our analysis are the 'zoogeographical species.' These are superspecies (Mayr, 1963; Amadon, 1966) or individual species not belonging to a superspecies. When several species comprise a superspecies they are counted as *one*

zoogeographical species just as is each species not belonging to a superspecies."

A count of zoogeographical species shows Hispaniola with 20 anoles (13 species not in superspecies and 7 superspecies). Twenty is not a great increase beyond 11 and not impressive at all when the areas of Hispaniola and Puerto Rico (even including its bank) are compared. Clearly Hispaniola has been permissive of the initiation of the species process, but, by the same token, it has not forced completion of that process.

Forced may be a key word. Sympatry is clearly less easily achieved than reproductive isolation. Looking back now at Jamaica and Puerto Rico, we can see these islands as large enough to permit speciation but small enough to impose intense competition for successful completion of speciation.

Any speciation process will include aborted examples: incipient and nascent species that in the end are left by the waysides of faunal history. These are not visible in the transect of Recent time available to us and because of their low level of differentiation are unlikely to be discoverable in the fossil record.

I believe it safe to assume that every *Anolis* species sympatric with others now was once—sometimes, perhaps, a number of speciation events back—an allospecies. We may also assume that over the course of faunal history some allospecies (and some full species) have lost out. These are part of that "invisible history" that I have commented on elsewhere (Williams, 1969). We can track them, if at all, only by their effect upon the surviving faunas. This is not an issue that can be dwelt on here, but it should always be kept in mind.

There is another phenomenon in Hispaniola that requires comment, the montane faunas. I have remarked above that there are not one but several montane faunas in Hispaniola. The montane faunas of the Cordillera Central and of the Sierra de Baoruco and of the Massif de la Hotte have elements in common with each other and with the lowland faunas but the differences are more impressive. The montane faunas are islands within islands and their resemblances can be charged to past connections between them and present connections within the lowlands, their differences to periods of isolation like the present.

The sizes of the present montane islands must have varied greatly in the past and there is a further factor to be considered: the montane areas of Hispaniola have 2 types of forest, pine forest (on the highest and least favorable areas) and montane broadleaf forest. The pine forests are relatively unfavorable for *Anolis; A. shrevei* in the Cordillera Central and *A. armouri* in the Massif de La Selle are known inhabitants of pine forests. It is therefore faunas of the broadleaf forests that we particularly think of when the term montane faunas is used and the area of broadleaf forest must, under all climatic regimes, have been significantly smaller than the total montane area.

It is possible therefore that the montane broadleaf forests of Hispaniola, or some of them, correspond to the missing intermediate term in the island sizes between the largest of the Lesser Antilles and the smallest of the Greater Antilles. Is it not possible then that the seemingly anomalous montane anole fauna of Hispaniola—an alternative sequence, as I have called it above—at least that of the broadleaf forest, corresponds to some stage in the evolution of the main sequence ecomorphs so well represented in the lowlands of this and the other Greater Antilles? If we suppose that this has been true, an enlarged view of the evolution of faunas may be necessary. The intermediate evolutionary stages may have been more experimental than I supposed in 1972; the strict sequence that I propounded in 1972 from giant ecomorph to twig ecomorph to trunk-crown ecomorph to grass-bush ecomorph may quite underestimate the ecological variability of the transitional stages of faunal evolution. The main sequence may be just the survivors of more varied and variable faunas. On the smaller islands they would be the only survivors, while on the large islands the permissiveness of greater area may have allowed the survival of such specialists as *A. eugenegrahami* on Hispaniola (or its analogue *A. vermiculatus* on Cuba).

The untidiness of Hispaniola as compared with the tidiness of Puerto Rico does suggest that tidiness is a secondary phenomenon, the end result of a severe weeding out process. There is another suggestion: Puerto Rico (and perhaps Jamaica) may be at its faunal climax, with only further loss a probability. Hispaniola, on the other hand (and presumably Cuba), may still be in a formative phase with active coadjustment going on—some species still forming, others now dying.

Of course, whatever the evolutionary process in the West Indies may have been before human contact, the hand of man has been heavy on these islands. All of them correspond to gardens in which those patches of "natural" vegetation that survive are only those that have been unfavorable for gardening. We are looking at a scarred and ruined picture, the subject and lesson of which may have been difficult to interpret when pristine but are far more difficult to discover now. In attempting to assess the history of West Indian faunas, we contend not only with the fog of time but with human-imposed distortions.

Coda

This has obviously been a close rather than a distant view of faunal radiations in the sense I have earlier used (1969) (see also Lack, 1976). Similarly, my paper on the origin of faunas (1972) was a close rather than a distant view. In presenting these detailed synopses of lizard biogeography in the West Indies, I have not at all intended to denigrate efforts (MacArthur and Wilson, 1967, and others) to obtain generality by a distant view. However, for my part, I am very conscious of a need to assure myself of the homogeneity of the data that are being used for gen-

eralization. The distant view is, it appears to me, best reinforced or emended by a close view.

In this regard, the present case appears to provide a very significant warning against any too simple attempts at estimating the meaning of area for species number. (I point out that in 1972 I was guilty of just this simplification.) Counting of species assumes as a first premise the equivalence of the entities counted. In the series of faunas we have just examined, this equivalence is not present. The allospecies of Hispaniola and the local and specialist species of all the large islands are not biologically or evolutionarily equivalent to the fully sympatric species of Puerto Rico or Jamaica or the Lesser Antilles. We obscure a part of biological reality when we count all of these together.

This failure of species to be equivalent should be less apparent in island birds than in island lizards. The very factors that permit intra-island radiation in lizards (and presumably in other slow colonizers) have the consequence that some species are caught *in statu nascendi*.

Diamond's 1977 warning is very pertinent: differences in dispersal ability and population density may mean very different end results. In this study we have seen substantive differences between similar faunas that seem to have resulted from the different areas and topographies of different island banks. But even the largest islands are several grades in area and complexity below the continental mainlands. Even for lizards Hispaniola is not really quite a continent.

Island anoles, both those of the large and the small islands, are abundant, conspicuous, and dominant in island ecology. Precisely because they are so major a feature of the areas they inhabit, they can be treated as if evolving alone (Williams, 1969). They can be treated, in fact, as if the only factors important in their evolution were two: (1) interactions within the genus and (2) constraints that physical habitat, in particular areal size, place upon these interactions.

These phenomena, which tend to be characteristic of many island species, make the biota of islands easy systems to study and make a close view of whole sections of faunas far more feasible and attractive than parallel studies on mainland. But by the same token, there is imperfect correspondence between the histories and the effective factors in the evolution of biotas in the 2 classes of areas. Partial correspondence there is, but a simple transference of concepts from one frame to the other is not possible. As we have found in this study, when areas of differing magnitudes are compared, there is as much change as there is congruence.

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