

INTEGRATIVE APPROACHES TO EVOLUTIONARY ECOLOGY: *Anolis* Lizards as Model Systems

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Abstract

Two approaches characterize the study of evolutionary ecology. Prospective studies investigate how present-day ecological processes may lead to evolutionary change; retrospective studies ask how present-day ecological conditions can be understood as the outcome of historical events. I argue that the most appropriate test of an evolutionary ecological hypothesis requires an integration of these approaches. I illustrate this approach by examining the hypothesis that interspecific competition has been the driving force behind the evolutionary radiation of *Anolis* lizards in the Caribbean. This hypothesis is supported by four lines of evidence: 1. Anole communities are structured by competition; 2. Populations alter resource use in the presence of congeners; 3. Microevolutionary adaptation occurs in response to resource shifts; and 4. Macroevolutionary patterns are consistent with interspecific competition as the driving force behind anole adaptive radiation.

INTRODUCTION

A schism exists in the field of evolutionary ecology. To some, evolutionary ecology is prospective, inquiring how present-day ecological processes may lead to evolutionary change, whereas for others, the emphasis is retrospective, asking how present-day ecological conditions can be understood as the out-

come of historical events. This dichotomy can be seen by comparing Pianka's (89) ecologically oriented *Evolutionary Ecology* with Cockburn's considerably more evolutionary *Introduction to Evolutionary Ecology* (11) or by perusing the pages of the journal *Evolutionary Ecology*.

Although some authors suggest that "evolutionary ecology" should include both perspectives (e.g. 3, 101), most practitioners in the field usually consider only one. For example, I examined all papers in the first four volumes of the journal *Evolutionary Ecology* in addition to a haphazard survey of papers, books, and symposia with "evolutionary ecology" in the title. Of the papers surveyed, only 5.3% considered both aspects of evolutionary ecology. By contrast, 85.3% focused on prospective approaches and 9.3% dealt with historical determinants of currently observed ecological patterns.

Although both retrospective and prospective studies are interesting in their own right, each of these approaches is limited in scope. By their nature, historical studies concern patterns and their interpretation; experimentation is not possible. Thus, for example, one may make deductions about historical sequences or how the evolutionarily-acquired features of taxa limit or channel their ecology, but these inferences can be tested only in a correlational manner with historical data. On the other hand, although one can directly measure and experimentally verify the existence and magnitude of currently operative ecological processes, one cannot demonstrate either that these processes have operated in the past, or that the processes, extrapolated over time, are sufficient to explain evolutionary patterns.

An integrative approach, by contrast, can provide broad insight into the factors regulating biological diversity. The prospective and retrospective approaches are complementary. Historical approaches can suggest hypotheses about which processes have been important in shaping biological diversity. Prospective studies can verify the importance of these processes, at least in contemporary communities, and can examine whether they lead to microevolutionary change in the direction predicted by historical studies. Consider, for example, a hypothesis, addressed below, that interspecific competition has been the driving force behind adaptive radiation in a given lineage. This hypothesis entails three predictions: 1. Historical patterns implicate competition as a cause of evolutionary diversification; 2. interspecific competition is demonstrably important in present-day communities; and 3. such competition leads to microevolutionary change which, if extrapolated sufficiently over time, would produce observed macroevolutionary patterns. Confirmation of all three premises would strongly support the hypothesis that competition has been the primary force determining community structure and diversification.

One of the first attempts to integrate phylogenetic and prospective approaches to evolutionary ecology was a pioneering analysis of the evolution of communities of *Anolis* lizards in the Caribbean (141). In that paper, Williams

argued that interspecific competition was the driving force behind the diversification of Caribbean anoles. The subsequent 22 years have seen both a tremendous amount of research on *Anolis* ecology and evolution and major conceptual advances in how these fields are studied.

The goals of this paper are two-fold. First, the body of the paper attempts to demonstrate the power of an integrative approach by focusing on the hypothesis that interspecific competition has been the major force guiding the community structure and evolution of Caribbean *Anolis* lizards. I address the three predictions detailed above by arguing that competition is a potent force structuring present-day anole communities, that anoles have evolved adaptations to allow resource partitioning, and that historical analyses implicate competition as a driving force in the anole adaptive radiation. Second, in the latter part of the paper, I return to a broader discussion of integrative approaches to evolutionary ecology and particularly address the question of how to interpret situations in which independent lines of investigation are inconsistent with respect to a given hypothesis.

BACKGROUND ON ANOLIS

Anolis is one of the largest vertebrate genera, with approximately 300 described species, half of which occur on Caribbean islands. Anoles are typically small, arboreal insectivores, but interspecific variation exists in size, habitat, and diet (see 130). Most of the small islands in the Caribbean contain 1–2 species of anoles, although islands that were part of considerably larger landmasses within the past 10,000 years, such as the Bahamas and satellite islands in the Greater Antilles, may have larger anole faunas (96, 123). Radiations on each of the Greater Antilles, however, have been more extensive, resulting in local communities with as many as ten sympatric species; total diversity exceeds 40 species on both Hispaniola and Cuba (142; Figure 1).

These radiations have produced essentially the same set of ecological types, termed “ecomorphs,” on each island. An ecomorph is a group of “species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phylogenetically” (141, p. 82). Quantitative morphological measurements indicate that members of each ecomorph type are truly convergent in morphology; species do indeed cluster in morphological space by ecomorph type rather than by phylogenetic affinity (69, 80). These differences in morphology correlate with differences in ecology and behavior (65, 67, 82, 83); functional studies indicate that differences in locomotor capabilities are responsible for these ecomorphological correlations (66, 75).

Ecomorphs are named for the microhabitat they normally utilize. Four ecomorph types (trunk-ground, trunk-crown, crown-giant, and twig) are common to all four Greater Antillean islands. The grass-bush ecomorph is present

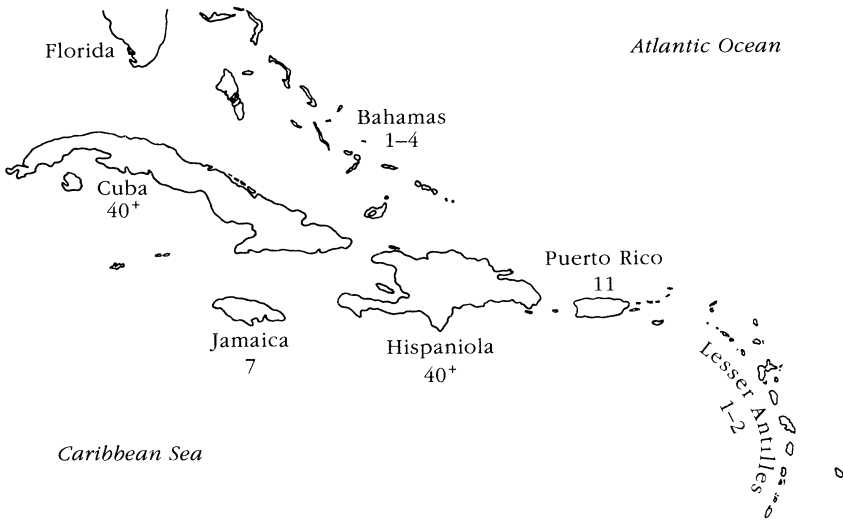


Figure 1 Caribbean islands and their anole species diversity.

on three of the islands but absent in Jamaica, whereas the trunk ecomorph is found only on Hispaniola and Cuba.

Higher-level phylogenetic relationships within anoline lizards are still controversial (5, 7, 33, 34, 37, 143), but reliable phylogenies exist for the radiations on Jamaica and Puerto Rico (see 69). Despite uncertainty about anoline relationships, the radiations on the islands clearly have been, for the most part, independent (142). Consequently, members of an ecomorph type are similar as a result of convergent evolution rather than recency of common ancestry.

INTERSPECIFIC INTERACTIONS AND THE EVOLUTION OF COMMUNITY STRUCTURE

Interspecific competition has often been invoked as the underlying driving force in adaptive radiation in general (22, 29, 114), and in the Caribbean anoline radiation in particular (69, 104, 141). Although particular hypotheses differ in details (69, 104, 141), all share a common scenario: Ecologically similar species compete strongly, creating strong selective pressure for species to diverge in resource use, thereby allowing coexistence. These competitive processes, extended over macroevolutionary time, are postulated to have produced the adaptive radiations observed today.

Four explicit predictions stem from the hypothesis that interspecific competition drives adaptive radiation:

1. Anole communities are structured by competition.
2. To minimize competitive pressures, populations alter their resource use as a function of which competitors are sympatric.
3. Microevolutionary (defined here as equivalent to within-species) changes in physiology, morphology, and behavior occur as populations adapt to alterations in resource use.
4. Macroevolutionary patterns are consistent with a scenario of adaptation to specialized niches in response to interspecific competition.

In the following, I illustrate that the evidence for these four propositions is strong.

Anole Communities Are Structured by Competition

SYMPATRIC ANOLES DIFFER IN RESOURCE USE Differences in resource use among sympatric species have often been taken as evidence of ongoing and/or past competition (13, 124). *Anolis* species partition resources along three axes (93, 94, 98, 142): prey size, which is strongly correlated with body size (102, 115, 116, 125; but see 21); structural habitat, usually defined by measurements of perch height and diameter; and microclimate (i.e. thermal habitat). In the Greater Antilles, sympatric species invariably differ on at least one of these axes, with partitioning by structural habitat being most common (98, 116, 121; 126, 127). By contrast, in the Lesser Antilles, sympatric species invariably differ along at least two axes (106).

Variation in which resource axes are partitioned The relative importance of these resource axes exhibits geographic and lineage-based differences. In the Lesser Antilles, species on two-species islands always differ greatly in body size, with one exception (118). However, the species differ in which the other resource axis is partitioned. In the northern Lesser Antilles, species (*bimaculatus* series) differ more in structural than in climatic microhabitat, whereas in the southern Lesser Antilles (*roquet* lineage), the reverse is true (106).

Similarly, in the Greater Antilles, where sympatric species partition resources on at least one axis, variation exists in which axis is partitioned by sympatric members of the same ecomorph [a null model confirms that sympatric members of the same ecomorph are more ecologically distinctive than expected by chance (118); exceptions occur at zones of contact between parapatric species (142)]. In contrast to the situation in the Lesser Antilles, however, the variation correlates with differences in structural habitat, rather

than geography or lineage (127). The more terrestrial trunk-ground and grass-bush ecomorphs partition climatic microhabitats when two members of either type occur sympatrically. This partitioning is so strong that sympatric members of either ecomorph type often are almost allotopic, only overlapping at ecotones (e.g. forest edge—93, 107). These distributions are probably driven by physiological adaptation to different microhabitats (see *Comparative Studies Among Closely Related Taxa*), which explains why different species will occupy the same spot at different times of the day (119). Closely related members of these ecomorph types that use different climatic microhabitats differ only slightly in body size.

In contrast to these more terrestrial ecomorphs, sympatric members of the more arboreal trunk-crown, crown-giant, and twig ecomorphs differ substantially in body size (123, 142). Although sympatric trunk-crown anoles also differ in microclimate, these differences are considerably less marked than those displayed by trunk-ground and grass-bush anoles and do not prevent the species from occurring syntopically (119, 126, 127). Schoener & Schoener (127) proposed an explanation for the relationship between degree of arboreality and axis of resource partitioning.

Body size varies depending upon which congeners are sympatric Resource partitioning is also evident when body size distributions are compared. In both the Lesser and Greater Antilles, when ecologically similar species are absent, anole species tend toward a similar body size, whereas communities composed of ecologically similar species often contain species diverging from this size. These observations suggest the possibility that an optimal body size may exist for anoles, but that competition in multi-species communities forces species to diverge from this optimum (117, 118).

Most (> 80%) of the anole populations occurring on one-species islands in both the Lesser and Greater Antilles (Greater Antillean one-species islands occur primarily in the Bahamas, Virgin Islands, and fringing islands in Cuba and Hispaniola) exhibit an adult body size that falls within a relatively narrow range (63, 117). Although it is possible that lizards of this size are more likely to be successful colonizers (see 117, 141), some of these islands were connected to larger mainlands historically and presumably originally contained more species; consequently, differential colonizing ability as a function of body size cannot be the sole explanation for the size of species on one-species islands. Rather, these data suggest that an optimal size appears to exist for one-species islands (117). The body size predicted to be optimal from a model incorporating energetic and physiological information corresponds closely with the size of species on these islands (85).

An optimal size may also exist for ecomorphs in multi-species communities

in the Greater Antilles. On Cuba and Hispaniola, species that are similar in structural habitat and do not occur with other members of the same ecomorph type tend to be similar to each other in size (118).

However, the presence of sympatric congeners leads to deviations from the putatively optimal size both on two-species islands in the Lesser Antilles and in Greater Antillean communities containing two species of the same ecomorph type. In the Lesser Antilles, two-species islands are, with one exception, occupied by species greatly different in size (118). Null models indicate that these differences are greater than would be expected if species on two-species islands were randomly sampled from a source pool (68, 123). Similarly, in the Greater Antilles, syntopic members of the same ecomorph tend to differ greatly in size (118). As discussed above, this disparity in size occurs primarily among the more arboreal ecomorphs, whereas sympatric members of the more terrestrial ecomorphs are frequently of similar size and allotopic.

These deviations from the optimal size could result from evolutionary adjustments in sympatry or from differential colonization or extinction as a function of size similarity (8, 9, 68, 104). Distinguishing between these alternatives generally is difficult without an historical perspective (8, 68; see below), but in some cases, evolutionary adjustment seems probable. For example, *A. porcatus* is considerably smaller in central Cuba, where it is sympatric with the larger *A. allisoni*, than on the eastern and western thirds of the island, where the larger *A. allisoni* does not occur (121).

RESOURCE PARTITIONING DIMINISHES THE EFFECTS OF INTERSPECIFIC COMPETITION The importance of resource partitioning in minimizing competition is demonstrated in two ways. First, experiments conducted in the Lesser Antilles demonstrated that two species with relatively minor differences in size and structural habitat competed strongly, whereas two species that partitioned resources along these axes had almost no effect on each other (86, 87, 105, 110). In the latter case, experimental habitat alterations that forced the species to overlap in structural habitat to a greater extent led to increased competitive effects on one of the species (110).

Second, the success of anole introductions (most accidental) is a function of how ecologically similar the introduced species is to the native species. Of 11 species introduced to islands on which no ecologically similar species occurred (ecological similarity defined in terms of overlap in the resource axes discussed above), 7 have achieved relatively large geographic ranges and none has become extinct. By contrast, of 12 species introduced to islands that already had an ecologically similar species, none has become widespread and 2 have become extinct (73).

Populations Alter Resource Use in the Presence of Congeners

HABITAT SHIFTS For interspecific competition to have evolutionary consequences, the presence of competitors must lead to alterations in resource use. A large body of evidence documents shifts in habitat use in anoles as a function of sympatry with other species. Although anoles partition resources along three axes, few studies have looked for competitive effects on diet or microclimatic habitat use. One exception is a set of experimental studies in the Lesser Antilles, in which ecologically similar species alter their diet and use of microclimatic habitats when sympatric, but ecologically dissimilar species do not (87, 110). Shifts in microclimatic habitat use were also detected in an experimental removal in Florida (111).

In contrast to the paucity of studies examining effects on the diet and microclimate resource axes, a number of studies document shifts in structural habitat use. These studies, which include behavioral observations of species interactions, experimental manipulations, and geographical and temporal comparisons, are summarized in Table 1. Two general results emerge from these studies. First, in the presence of congeners, anoles tend to alter their habitat use so as to minimize overlap (e.g. in the presence of a more terrestrial

Table 1 Studies demonstrating habitat shift in anoles in the presence of congeners.

Focal species	Locality	Context	Reference
<i>opalinus</i>	Jamaica	Observations made when <i>lineatopus</i> is present or absent	54
<i>porcatus, sagrei</i>	Cuba	Observations made when both or only one species present	12
<i>sagrei</i>	Florida	Experimental removal of <i>crisatellus</i>	111
<i>gingivinus</i>	St. Maarten	Experimental enclosures with and without <i>wattsii pogus</i>	87
<i>wattsii wattsii, bimaculatus</i>	St. Eustatius	Experimental enclosures with each species alone or both species together	87, 100
<i>pulchellus</i>	Puerto Rico	Experimental removal of <i>crisatellus</i>	38
<i>carolinensis, distinctus, grahami, sagrei</i>	Caribbean islands	Comparisons of sites with or without other species, corrected for habitat availability	120
<i>sagrei</i>	Caribbean islands	Comparisons of sites with or without other species	62
<i>cooki</i>	Puerto Rico	Comparison of sites with or without <i>crisatellus</i>	55
<i>conspersus</i>	Grand Cayman	Comparison of habitat use before and after introduction of <i>sagrei</i>	73

congener, species become more arboreal). Second, when two species are sympatric, habitat shift is sometimes more apparent in the smaller of the two species.

Particularly instructive are the experimental studies by Roughgarden and colleagues in the Lesser Antilles in which different combinations of species were introduced into enclosed areas or onto a small island (86, 87, 105, 110; see 35 for a critique of the design of these experiments). On St. Maarten, the relatively ecologically similar species *A. wattsi pogus* and *A. gingivinus* both alter their habitat use when sympatric. By contrast, *A. bimaculatus* and *A. w. wattsi* on St. Eustatius are considerably more ecologically distinct, and only one of the species (the smaller *A. w. wattsi*) shifts its habitat use in sympatry. Not only is *A. bimaculatus* unaffected by the presence of *A. w. wattsi* on St. Eustatius, but the fitness effects on *A. w. wattsi* are also much less than the effects experienced by *A. w. pogus* on St. Maarten (86, 87, 110).

ECOLOGICAL RELEASE If interspecific competition leads to partitioning of resources, then in the absence of competitors, a species may broaden its use of resources. This phenomenon, termed ecological release, has been widely sought among insular populations of various vertebrates, including anoles (reviewed in 122). Several studies looked for ecological release in climatic habitat use among Lesser Antillean anole species (44, 51, 97, 102, 108). Interpretation of such studies is problematic, however, because the ancestors of these populations may never have occurred in communities with other congeners; thus, no pre-ecological release comparison is possible (44, 62). Indeed, broad resource use may be a prerequisite for successful colonizers, rather than a result of post-colonization evolution (44).

By contrast, taxa clearly derived from ecologically specialized Greater Antillean species are potential candidates to exhibit ecological release and can be compared to close relatives in multi-species communities in the Greater Antilles. In several such species, ecological release in terms of climatic and structural habitat appears to occur (44, 58, 62; but see 26, 109).

Microevolutionary Adaptation Occurs in Response to Resource Shifts

EXPERIMENTAL AND ACCIDENTAL INTRODUCTIONS Interspecific competition may lead not only to behavioral shifts in resource use, as described above, but also to changes in the selective environment, favoring microevolutionary adaptation to the new regime of resource use (reviewed in 135). No study to date has documented interspecific competition driving natural selection to produce microevolutionary change in anoles. However, one study attempted to show that populations transplanted into habitats greatly different from their native

habitat experienced strong directional selection (76). Although the experimental design has been questioned (57, 60), this study does indicate that strong directional selection did occur in at least one population, and that population, coincidentally or not, was the one transplanted from the most different habitat (montane rainforest to xeric scrub).

Whether microevolutionary change occurs when populations use new habitats has also been investigated experimentally (JB Losos, KI Warheit, TW Schoener, unpublished). In this study it was also possible to make a priori predictions about the direction of adaptive morphological divergence. Populations of *A. sagrei* were introduced to extremely small islands in the Bahamas in 1977 (128). The vegetation available on these islands consisted of bushes and small trees, providing a habitat matrix of smaller-diameter supports than was available in the habitat of the source population. Based on the relationship between limb morphology and support diameter among species of Greater Antillean anoles (65, 82, 83, 91), one would predict that the populations should evolve relatively shorter limbs. Fifteen years after the introductions, the populations had diverged morphologically from the source population in the expected direction; further, the degree of divergence was correlated with how different was the island vegetationally on which a population occurred, relative to the source island. Studies are currently underway to assess the extent to which differences in relative limb length could be environmentally induced by differences in habitat.

Rapid microevolutionary change has also been documented in *A. leachi*, a large species that has increased to an even greater size since its introduction to Bermuda in the 1940s (92). In this case, the cause of the change is not clear, although one possibility is that the larger size of *A. leachi* evolved because the other species of *Anolis* on Bermuda (also introduced) are larger than the species with which *A. leachi* is sympatric on Barbuda and Antigua (70). However, the genetic basis for differences in body size in anoles still requires investigation (cf. 103).

COMPARATIVE STUDIES AMONG CLOSELY RELATED TAXA The studies just discussed document rapid morphological change in populations experiencing new environments, but they do not clearly implicate the presence of competing species as the impetus for this change (although it is suggested for *A. leachi*). Such evidence is provided by comparisons among populations occurring sympatrically and allopatrically with other species. Such comparisons indicate that microevolutionary adaptation occurs in response to shifts in resource use on all three axes. Divergence along the prey-size axis is illustrated by several widespread species in which body size decreases as a function of the number of sympatric competitors (117). Adaptation to shifts in structural habitat occurs in Bahamian populations of *A. carolinensis* and *A. sagrei*. Both species differ

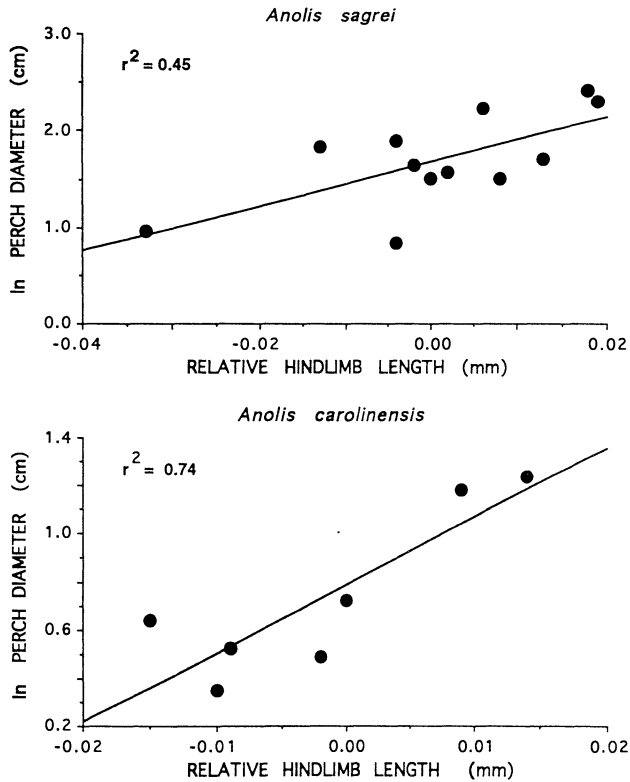


Figure 2 Relationship between hindlimb length and perch diameter among Bahamian populations of *A. carolinensis* (top) and *A. sagrei* (bottom; from 72).

in habitat use as a function of which competitors are present (120) and exhibit a relationship between relative limb length and structural habitat use (72; Figure 2). Finally, adaptive differences in thermal physiology are often exhibited by closely related taxa that partition resources along the microclimate axis (25; 42, 45, 48, 52, 107), although this result is not universal (40, 42, 43, 46; see also 78).

Macroevolutionary Patterns Are Consistent with Interspecific Competition as the Driving Force Behind Anole Adaptive Radiation

If interspecific competition has been the driving force behind the anole adaptive radiation in the Caribbean, then the preceding discussion suggests that two patterns should be evident in an historical analysis: First, adaptation for

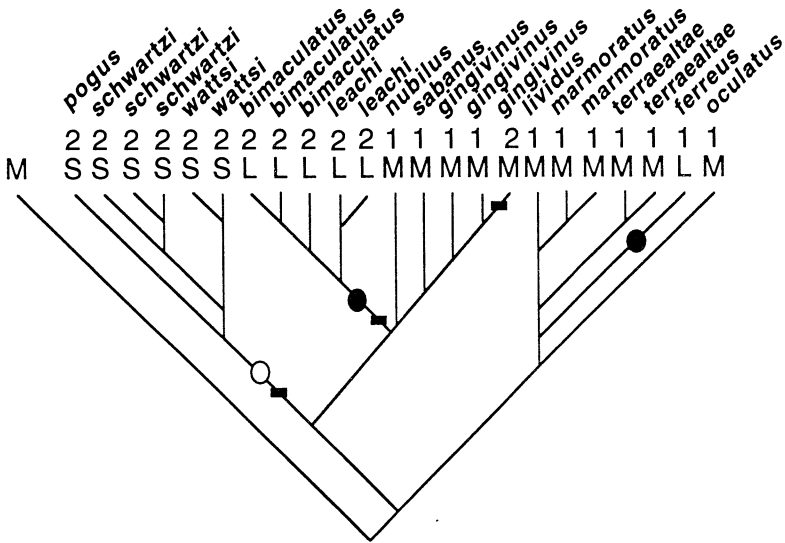


Figure 3 Evolution of body size in *Anolis* lizards of the northern Lesser Antilles (based on 68, 104). Numbers indicate the number of *Anolis* species on the island occupied by each taxon. Letters indicate body size (small, medium, or large). Circles represent major evolutionary changes in body size (solid = increase; open = decrease); bars represent the transition from an ancestor on a one-species island to a descendant on a two-species island. The statistical analysis in (68) used actual values rather than categorical variables. Perch height and body size are strongly correlated among these lizards (106); consequently, the evolution of perch height proceeded in an essentially identical manner. (Figure from 69 with permission)

resource specialization should evolve as additional species join a community. Second, based on the apparent prevalence of structural habitat partitioning in the Greater Antilles (see Sympatric Anoles Differ in Resource Use), evolutionary specialization should occur first along the structural habitat axis and only subsequently on the prey-size and microclimate axes. These hypotheses can be tested by using phylogenetic methods to reconstruct character evolution, assuming that a robust phylogenetic hypothesis exists for the group in question (4, 14, 36, 50, 59, 74).

The evidence is mixed concerning the prediction that the addition of species to a community leads to resource specialization in the Lesser Antilles. Supporting evidence comes from a phylogenetic analysis of the anole radiation in the northern Lesser Antilles, which indicates that divergence along two resource axes occurred when taxa came into sympatry (68; Figure 3). However, this result must be qualified owing to uncertainties about phylogenetic relationships and the existence of alternative evolutionary scenarios that require

equally or only slightly less parsimonious reconstructions of character evolution (D Miles, A Dunham, unpublished; C Schneider, K de Queiroz, J Losos, unpublished). By contrast, analysis of the diversification of anoles in the southern Lesser Antilles does not indicate that evolutionary change in resource use was associated with the attainment of sympatry with competitors. For these taxa, ecological differences appear to have evolved in allopatry and have subsequently allowed coexistence of taxa (68).

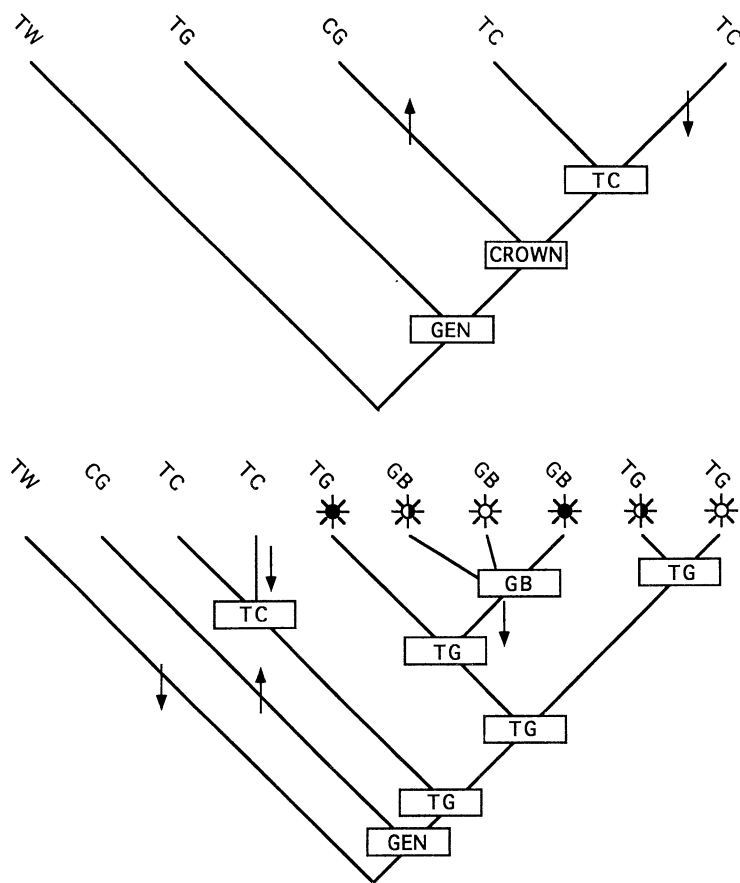


Figure 4 The evolution of *Anolis* community structure in Jamaica (left) and Puerto Rico (right; see 69 for methodological details). The names of the ecomorphs refer to the habitat they normally utilize (TW, twig; CG, crown-giant; TG, trunk-ground; TC, trunk-crown; GB, grass-bush). One ancestral taxon was reconstructed as inhabiting the crown, but not as belonging clearly to either of the crown ecomorphs (GEN, generalist). Arrows indicate the evolution of large or small size from the ancestral, intermediate body size. Circular symbols represent species that have specialized to distinctive climatic habitats (*open*—xeric, hot; *half-shaded*—lowland, moderate; *shaded*—montane, cool).

For Greater Antillean anoles, suitable phylogenies currently only exist for the Jamaican and Puerto Rican radiations (reviewed in 69). Comparison of macroevolutionary patterns in these two radiations indicates not only that resource specialization has occurred as species are added to the community, but also that the two islands have followed an almost identical sequence in the evolution of ecomorphs (69; Figure 4). This unexpected finding suggests that a deterministic trajectory exists by which anole communities increase in species number and complexity. Further, this analysis suggests a proximate explanation for the absence of grass-bush anoles in Jamaica. Rather than occurring as a result of the lack of appropriate available resources, the absence of a grass-bush ecomorph on Jamaica may result simply because Jamaica has only reached the four-ecomorph stage, and the grass-bush anole is the fifth ecomorph to evolve in the community-evolution sequence. This explanation shifts inquiry from why the grass-bush ecomorph has not evolved to why Jamaica has not reached the five-ecomorph stage in the community-evolution sequence (69, 142).

Phylogenetic analysis also indicates that structural habitat specialization often precedes climatic or diet specialization (Figure 4). For example, on both Jamaica and Puerto Rico, prey-size divergence occurs within a clade of trunk-crown anoles. Further, on Puerto Rico, climatic specialization occurs subsequent to structural habitat specialization in both the trunk-ground and grass-bush ecomorphs. By contrast, the phylogenetic analysis indicates no cases in which climatic or diet specialization precedes structural habitat specialization (although several cases of substantial change in body size occur simultaneously with specialization to a particular microhabitat, such as the concordant evolution of small size and twig specialization in Puerto Rico). In addition, both phylogenies document that specialization for a particular microclimate evolved multiple times but that each ecomorph type evolved only once. Thus, it appears that a structural habitat niche, once filled, can be subdivided easily along microclimate lines but generally is resistant to evolutionary invasion by another lineage differentiating on the same island. [However, the successful invasion of Jamaica in recent years by the Cuban trunk-ground anole *A. sagrei* (140) indicates that other lineages may ecologically invade if they have already evolved the necessary specialization.]

Without a phylogeny for the anole radiations of Hispaniola and Cuba, the hypothesis that differentiation in structural habitat occurs prior to differentiation on other axes is difficult to test. Nonetheless, evolutionary inference is possible in cases in which closely related species (e.g. members of the same species complex) are all members of a single ecomorph type, yet have diverged in microclimate or prey size specialization. Specialization to different microclimates has occurred among closely related members of the same ecomorph type in the trunk-ground (Hispaniola: 46, 129, 138; Cuba: 107) and, perhaps, grass-bush (Hispaniola: 41) ecomorphs, whereas prey-size specialization, as

represented by body size, has occurred in the trunk-crown (Cuba: 121; Hispaniola: 139) and twig (Hispaniola: 142) ecomorphs. These examples indicate that microclimate and prey-size partitioning often occur subsequent to structural habitat specialization (assuming that the ancestor of these closely related groups of species was the same ecomorph as all of its descendants). However, in contrast to the Jamaican and Puerto Rican radiations, several of the ecomorphs may have evolved multiple times on Hispaniola and Cuba (5, 142), although without a robust phylogenetic hypothesis, this statement must be tentative. Further, most multiple origins of an ecomorph type appear to have occurred in the unusual montane faunas of these islands (142).

Competition, Predation, or Parasitism?

The data reviewed here make a compelling case that interspecific interactions not only are important in structuring extant anole communities in the Caribbean, but also have played an important role in shaping community evolution and adaptive radiation. Interspecific competition has generally been considered the process responsible for these patterns, but they could also be produced by other ecological processes. Recently, it has been suggested that predation or parasitism may be the driving force structuring anole communities. Although the importance, and even the incidence, of these processes has been neglected in studies of anole ecology, it is unlikely that either is a dominant structuring force in anole communities.

PREDATION In recent years, theorists have suggested that patterns attributed to interspecific competition could also result from predation (31, 49, 53). Predation could exert its influence in two ways: either via the erstwhile competitors eating each other or via a predator that eats both species. In the anole communities of the Caribbean, both processes are unlikely to be important in shaping community structure.

Many species of *Anolis* have been reported to eat vertebrates occasionally, including other anoles (e.g. 19, 71, 95, 134). Most incidents of one *Anolis* eating another ("intra-guild predation"—90) involve an adult eating a juvenile or an adult of one species eating an individual of a considerably smaller species (19, 95). In some cases, such predation may affect habitat use of the prey species such as juvenile *A. aeneus* (134) and the small Hispaniolan *A. bahorucoensis* (19).

However, intraguild predation does not provide a general explanation for anole habitat partitioning for the simple reason that the species and size classes that interact most strongly are those least likely to prey on each other. Anoles are probably only capable of eating organisms considerably smaller than they are. Naganuma & Roughgarden (85) estimate the maximum prey size as one third of an anole's snout-vent length (based on 132; see also 134). Consequently, the effects of predation should be most strongly manifested in com-

parisons among different-sized taxa; adults of all but the smallest species should be immune to predation from other anoles, except perhaps from large crown-giants (71).

The data, however, indicate that the strongest interspecific effects on fitness parameters occur between similar-sized species, as noted above. Further, Schoener (120) documented that the strongest interspecific effects on habitat use were between relatively similar size-classes [e.g. females of a larger species and males of a smaller species or subadult males and adult females of similar-sized species; females are generally smaller than males in Caribbean species (117)], rather than between the size-classes most dissimilar in size and thus most likely to exhibit the effects of predation. Thus, intraguild predation cannot explain the large interspecific effects between similar-sized lizards, although it may explain habitat and behavioral shifts documented in females and juveniles of some species.

A second possibility is that sympatric anoles alter habitat use, not to minimize resource competition, but to avoid predators. It is possible that predators specialize, either evolutionarily or cognitively, to capture prey in particular habitats. Thus, by diverging in habitat use, anole species could, in theory, minimize predation pressure.

This is a difficult hypothesis to reject out-of-hand because so little is known about predation on anoles. Probably the most common anole predators in the Caribbean are certain birds (1, 81, 136, 137, 144, 146) and snakes (39) and perhaps sometimes mammals and invertebrates (136). On some islands, predation may be relatively intense (81, 136). Could the foraging behavior of these predators be responsible for patterns of anole resource partitioning and evolutionary diversification?

I suggest that this hypothesis is unlikely for several reasons:

1. Resources appear to be limiting for Caribbean anole populations. Supplementation experiments on anoles generally indicate that they are food-limited (reviewed in 32, 145).
2. Interspecific aggression sometimes occurs between ecologically similar species. In a number of instances, ecologically similar species exhibit interspecific territoriality and higher levels of interspecific agonistic behavior where they co-occur (references in 47).
3. Anoles respond in behavioral time to the presence of competitors. Several studies indicate that anoles alter their habitat use when individuals of other species are present (12, 54), which implicates interactions between the lizards themselves, rather than a mutual predator, as the most likely cause.
4. Experimental Studies of interspecific interactions Studies on St. Maarten indicated that, when one species was experimentally removed, the other species exhibited higher measures of body condition, prey intake, and egg

production. By contrast, on St. Eustatius, where two ecologically dissimilar species occur, removals had considerably less effect (87, 110).

A hypothesis that interspecific competition structures anole populations would predict each of these observations. Individual anoles are limited by food, defend resources against other species, and behaviorally alter their resource use when potential competitors are present. Further, the presence of competing species adversely affects anoles.

Of course, it is possible to formulate scenarios in which predation could produce the same results, but most such scenarios are fairly convoluted. For example, the presence of other anole species might attract more predators; thus, behavioral shifts could be a response to this increased risk of predation. Similarly, in the Lesser Antillean experiments, the removal of one species might reduce predation pressure, allowing the remaining species to alter resource use and exploit previously unavailable resources. Still, to explain these results, one must assume that *A. w. pogus* and *A. gingivinus* on St. Maarten share predators, but *A. w. wattsi* and *A. bimaculatus* on St. Eustatius do not. Many such scenarios seem implausible, but only experimental manipulations can demonstrate conclusively the role predators play in structuring anole communities.

PARASITISM Differential susceptibility to parasites also has been invoked recently as an important determinant of community structure (e.g. 31, 131). On St. Maarten, *A. gingivinus* is more susceptible to malaria than *A. wattsi pogus*. The parasite is patchily distributed and, with one exception, *A. w. pogus* only occurs in areas in which malaria is found, whereas *A. gingivinus* occurs throughout the island. Thus, malarial infection may alter competitive relationships and allow coexistence of the two species (112). This finding is particularly significant because St. Maarten is the only island in the Lesser Antilles in which two relatively similar-sized species co-occur.

A similar hypothesis has been proposed for the anole fauna of Puerto Rico, in which malaria is prevalent in only one (*A. gundlachi*) of five species examined (113). Schall & Vogt (113) hypothesized that malaria mediates coexistence between *A. evermanni* and *A. gundlachi*. However, the situation in Puerto Rico does not parallel that in St. Maarten. In contrast to the species on St. Maarten, *A. evermanni* and *A. gundlachi* exhibit substantial differences in structural habitat use (64, 65, 93, 99, 127), foraging behavior (67), and time of activity (43). These differences are comparable to those displayed by other sympatric Greater Antillean anoles. Consequently, the coexistence of *A. evermanni* and *A. gundlachi* needs no special explanation. Indeed, in more open lowland habitats in Puerto Rico, *A. evermanni* is able to coexist with *A. cristatellus* (93, 127), a species quite similar to *A. gundlachi* in structural

habitat and morphology, even though neither species is prone to malaria (113). Thus, at this point, the evidence does not indicate that susceptibility to malaria is an important determinant of community composition in the Greater Antilles.

DISCUSSION

Several lines of evidence implicate interspecific competition as an important force structuring communities of *Anolis* lizards in ecological and evolutionary time: sympatric species usually differ in resource use along one or more of three resource axes; when ecologically similar species cooccur, competitive effects on fitness occur; species alter their resource use in the presence of ecologically similar species; species adapt evolutionarily to shifts in resource use; and phylogenetic reconstructions are consistent with competition as a driving force behind the anole radiations. The congruence among these approaches provides strong support for the competition hypothesis.

Below, I first discuss integrative approaches to evolutionary ecology, and how one may interpret situations in which different lines of investigation provide inconsistent results, and then I discuss future directions in the study of anole communities.

Integrative Approaches to Evolutionary Ecology

Historical effects on the biological diversity of communities and regions are widely recognized (e.g. 6, 27, 100, 104). The cause of such effects, and how they may be studied, can be quite varied. In some cases, rare phenomena such as asteroid impacts, cycles of forest contraction and expansion, or the appearance of new taxa such as eutherian mammals, may produce large and long-standing effects on diversity. Because these are unique or infrequent events of large magnitude, they generally can only be studied using historical methods.

An alternative class of historical effects on diversity results from the evolutionary outcome of ongoing ecological processes. Such effects occur because ecological processes often have effects on fitness. If genetic variation exists for relevant traits among affected individuals, then fitness differentials may lead to microevolutionary change. Over time, these changes can be extrapolated to produce observed macroevolutionary patterns (e.g. 29).

To study this latter class of historical effects, both historical and ecological data are needed. In particular, an evolutionary ecological hypothesis may be corroborated if three premises are confirmed:

1. A given ecological process is an important determinant of community structure;
2. Selection studies indicate that the process leads to microevolutionary change.

3. Historical analyses yield macroevolutionary patterns similar to those that would have been predicted if observed microevolutionary processes were extrapolated over long periods of time.

These criteria obviously lead to a prescription for integrative studies of organismal diversity, incorporating phylogenetic and ecological studies. Confirmation of these three hypotheses would provide strong support to the premise that the process is and has been an important determinant of biological diversity. But what if one (or more) of these postulates is not confirmed? A number of possible explanations exist:

1. *Ecological processes may not have evolutionary effects.* Ecological processes could have important effects but not have any net evolutionary impact. This could result if no genetic variation existed for relevant traits, if all genetic variants were equally affected by the ecological process (i.e. no differential selective effect), or if the magnitude and direction of the selective effect varied through time such that the net effect over time was zero (e.g. 24).
2. *Microevolutionary change might not accumulate over time to produce macroevolutionary patterns.* The extent to which the processes governing macroevolutionary change are distinct from those operating within species is controversial (10, 28, 61). To the extent that speciation leads to large-scale changes of a fundamentally different nature than those that occur during anagenesis, then one may not be able to extrapolate from microevolutionary process to macroevolutionary pattern.
3. *The processes important in structuring extant communities may not be the same processes that have molded biological diversity historically.* The processes that regulate community structure probably depend on which taxa are present (88), but the composition of a community is constantly in flux as a result of immigration, extinction, speciation, and successional changes. In addition, environmental change may also lead to shifts in the relative importance of different ecological processes (56).
4. *Ecological or historical studies may be misleading.* Rare events of large impact may play a more important role in directing large-scale patterns than day-to-day processes (30, 133), but such events may rarely be observed in most short-term ecological studies. In a similar vein, historical analyses reconstruct past events relying on assumptions (e.g. parsimony) that may not always be correct. Thus, incongruence between ecological and historical analyses may result because one approach is simply mistaken about the importance of a particular process.

These possibilities underscore the advantages of taking an integrative approach to evolutionary ecology. By combining studies at several hierarchical

scales, one can not only look for overall congruence between pattern and process, but one can also generate predictions at one level that can then be tested at another. Further, when analyses at different levels produce differing conclusions, additional testable hypotheses about the forces regulating biological diversity may be formulated. Because biological diversity ultimately reflects the interplay of ecological and evolutionary processes, only by considering both can we come to fully appreciate its genesis and maintenance.

Future Directions in Anole Evolutionary Ecology

For many years, community ecologists were preoccupied with documenting and comparing the structure of communities. However, observed ecological patterns often may result from a number of different processes (9, 15). In an effort to distinguish among competing hypotheses, ecologists in recent years have turned to either experimental or mechanistic approaches to understand community organization. Although both approaches have been used to some extent to understand anole communities, I suggest below several additional areas in which these approaches could prove fruitful.

INTERSPECIFIC INTERACTIONS Given the tractability of anoles, it is surprising that they have not been used more in experimental studies. Examination of the relative importance of competition, predation, and parasites in mediating coexistence may prove particularly enlightening. Because these processes can produce very similar patterns, however, detailed mechanistic studies of interspecific interactions may be necessary to disentangle the relative importance of these processes. In addition, experimental studies could determine the extent to which resource partitioning is an evolutionarily fixed result of historical interactions as opposed to a behavioral response to ongoing interactions. Although a variety of data suggest that interactions occur between some ecomorphs (e.g. trunk-ground and trunk-crown ecomorphs), it would not be surprising to find that other ecomorphs (e.g. twig and crown-giant) do not currently compete.

On the other hand, the possible importance of other factors such as predation and parasitism is still uncertain. More detailed studies of community dynamics may yet yield surprises such as the possible importance of parasites in regulating anole interactions on St. Maarten (112). Examination of these questions may require a combined mechanistic/experimental approach to understand how the addition or removal of species affects other sympatric species.

RESOURCE PARTITIONING Resource partitioning needs to be examined mechanistically at several levels. First, although anoles partition climatic and spatial resources, it is not clear how populations are limited by these resources. One possibility is that partitioning along these axes leads to differences in prey

utilization. Surprisingly little information is available on whether sympatric anoles partition prey by taxon. A more detailed understanding of anole natural history and community dynamics, combined with experimental alterations of resource availability (including habitat), would be useful. In the one such study conducted to date, Rummel & Roughgarden (110) altered available perch heights and concluded that perch height and prey size are not independent resource axes in the Lesser Antilles.

Second, how do the specific adaptations of taxa allow them to use particular habitats more successfully? A correlation exists between morphology, habitat use, and behavior among anoles (65, 77, 82–84, 91). Further, differences in morphology lead to ecologically relevant differences in functional capacities such as running and jumping ability (65, 66, 75). These differences in performance also correlate with differences in behavior and habitat (65). What is needed now is an understanding of why different capabilities are required in different habitats. Why, for example, is greater sprinting speed correlated with the use of broad surfaces? Are lizards in these habitats farther from prey or cover? Do they face faster predators or prey? Is fast sprint speed not advantageous in cluttered habitats? Again, more detailed understanding of anole natural history is required.

EVOLUTIONARY CHANGE Recent years have seen a proliferation of studies attempting to detect the operation of natural selection in nature (16). However, in the absence of information about how organisms interact with their environment, studies of selection can be difficult to interpret because a plausible explanation can be advanced for any result (16, 23). Selection studies are most informative when conducted on phenotypic traits for which the functional and behavioral significance is well understood. Well-studied taxa such as *Anolis* are thus obvious choices to understand the working of natural selection.

In addition, selection studies can be designed to test key components of hypotheses concerning anole adaptive radiation. A number of factors have been implicated as important in driving the anole radiation. Because humans have altered anole communities through both addition and subtraction, many species may currently experience directional selection. Selection studies can thus verify whether species using new habitats or species sympatric with new combinations of species actually do experience selective pressures to change in the hypothesized manner and whether, over several generations, microevolutionary change actually occurs. A robust understanding of the relationship between ecological process and microevolutionary response thus can test an important underlying hypothesis concerning anole adaptive radiation. Experimental introductions may also be used to test these hypotheses.

SPECIATION Theories concerning anole radiation have focused on the cause of morphological differentiation among species but have paid little attention

to how speciation actually occurs. Macro- and microvicariant models have been postulated as a prerequisite for the determination of allopatric speciation in the Greater Antilles (e.g. 142), but these models are usually speculative.

Most studies of evolutionary diversification draw a distinction between the population-genetic phenomena occurring during speciation and the subsequent ecological processes that affect survival and proliferation of new species. However, in anoles it is possible that speciation and ecology are intimately linked. Species-recognition in anoles relies upon visual signals, including the shape, color, and pattern of the dewlap and the pattern of head-bobbing (references in 20, 47). These features are also important in intraspecific communication. Further, the optimal visual signal may differ as a function of habitat (17, 18, 20). For example, a brightly colored dewlap may be most visible in a sun-lit habitat, whereas in dark forest, lighter colors may be more effective. Indeed, a relationship exists between dewlap color and habitat use among Greater Antillean anoles (20).

This raises the possibility that shifts in habitat use by an anole population may lead to shifts in signals to maximize intraspecific communication. Because the same signals are used for both intraspecific communication and species recognition, these changes may lead to the establishment of a new species-recognition signal. Hence, adaptation for increased communicative success may have the incidental effect of reproductively isolating a population from other populations in a species, thus causing speciation (e.g. 17, 79). Hence, the forces that promote ecological differentiation may also be responsible for the high rates of speciation in *Anolis*. This hypothesis can best be tested by combining historical and ecological approaches.

CONCLUSIONS

Biological diversity is the result of processes occurring presently and in the past. Understanding why some communities or regions are more diverse than others thus requires both studies of present-day ecology and inferences about processes operating in the past. Historical and ecological approaches are complementary: Each makes predictions that can be tested by reference to the other. The synergism resulting from the integration of the two is the most effective means by which we may understand the origin and structure of natural communities.

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