Phylogenetic Perspectives on Community Ecology

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PHYLOGENETIC PERSPECTIVES ON COMMUNITY ECOLOGY[1]

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Abstract. Ecologists have long been interested in the differences that exist among communities. If species adapted rapidly and without constraint, and if any lineage could occur in any community, then we would expect differences in community structure to be indicative of environmental differences. Because lineages differ in their evolutionary potential and are geographically restricted, however, comparisons of community structure must take account of communities' histories. Phylogenetic information about the constituent lineages in a community can allow lineage effects to be factored out, thus allowing an assessment of environmental determinants of community structure. In addition, phylogenetic information permits understanding of how communities have evolved through time and suggests hypotheses that may be tested using extant communities. Methodological difficulties with the application of these methods to community ecological issues are also discussed.

Key words: Anolis; *community ecology; community evolution; community structure; comparative method; history and community structure; phylogeny; species diversity.*

INTRODUCTION

Community ecologists have traditionally been interested in both the proximate and ultimate causes of community structure. Proximate approaches to community ecology investigate the processes operating within communities and the effect these processes have on community structure. These approaches have been in the ascendancy over the past 20 yr because they are amenable to direct measurement and experimentation. By contrast, ultimate approaches to community ecology involve study of why communities have a particular organization and why differences exist between communities. Because historical effects on communities are long lived, ultimate questions cannot be answered solely from knowledge of present-day conditions (Mayden 1992, Ricklefs and Schluter 1993, and references therein). Rather, to understand the structure of contemporary communities, and why particular communities are convergent or distinctive, a firm understanding of the history of these communities is necessary. Although such questions historically held great interest to community ecologists (e.g., MacArthur 1972), the lack of a suitable methodology for their study caused the investigation of ultimate causes of community structure to fall from favor in the late 1970s. Recent years, however, have seen conceptual and methodological advances in our ability to study historical events. Use of these new phylogenetic methods allows community ecologists to once more investigate the ultimate causes of community structure and organization.

Although now common in comparative studies of species' ecology (e.g., Brooks and McLennan 1991, Harvey and Pagel 1991), phylogenetic approaches have been little used in elucidating the factors determining community structure. The goal of this paper is twofold: first, to illustrate how phylogenetic studies can aid in understanding community organization and composition, and, second, to illuminate some of the conceptual difficulties inherent in inferring historical processes from phylogenetic patterns.

PHYLOGENETIC APPROACHES AND COMMUNITY ECOLOGY

In this section, I first illustrate how historical contingency can confound community comparisons, then discuss how a wide variety of questions in community ecology can be conducted within a phylogenetic context and conclude by examining the situation in which a community is composed of a number of unrelated lineages.

In a world in which evolution was unconstrained and rapid and in which any lineage could occur in any region, communities in similar environments would be expected to be similar in structure (Orians and Paine 1983, Blondel et al. 1984, Schluter 1986*a*, 1990, Wiens 1989, Ricklefs and Schluter 1993). The observation of dissimilar community structures would suggest that communities were in dissimilar environments. However, in the real world, evolution is constrained and lineages are restricted in geographic distribution. Con-

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[1] For reprints of this Special Feature, see footnote 1, page 1319.

sequently, differences in the structure of communities may result as much from the differences in the lineages that occur in different communities as from differences in environmental conditions.

For example, members of the order Carnivora are more ecologically differentiated in Wyoming than in the Serengeti or Malaysia (Van Valkenburgh 1985, 1988). The proximate cause of these differences is the presence of a distinctive lineage of carnivores (the bears) in Yellowstone and their absence in the other two communities. Although environmental differences between regions could account for these observed differences in community composition, an alternative possibility is that the lineages that predominate in the different areas differ in their evolutionary potentialities (Cadle and Greene 1993, Morton 1993).

Consequently, correlations between community structure and the presence of particular lineages suggest that investigation may be directed more profitably toward explaining differences in lineages than differences in environmental conditions. Why have bears not colonized the Serengeti or the Malaysian lowland evergreen rain forest? Why are the other lineages present in the Serengeti and Malaysian rain forest (e.g., canids, felids) seemingly unable to evolve a bear-like morphology? Of course, environmental differences could account for the differences in community structure: maybe, for example, vegetation structure in the Serengeti both precludes ursine colonization and selects against other lineages evolving a more ursine aspect. Though possible, the explanation seems unlikely considering that bears have never crossed the Sahara and that no other extant carnivore lineage has produced a bear-like morphology. Framing the questions in the context of differences between lineages emphasizes that environmental differences are only one of a number of possible explanations; evolutionary and biogeographical considerations must be examined as well (see also Cogger 1984, Strauss 1987, Nee et al. 1991, Cadle and Greene 1993 [but see Winemiller 1991, Cotgreave and Harvey 1994]).

Phylogenetic approaches may be important not only for understanding why communities differ, but also for understanding why they are similar. For example, in the Lesser Antilles, which contain either one or two species of *Anolis* lizards, a remarkable regularity exists: on two-species islands, the species differ considerably in size, whereas one-species islands contain species that are intermediate in size (Schoener 1970). The pervasiveness of these patterns in the Lesser Antilles might suggest that the same ecological process has been operating throughout the region.

However, phylogenetic information again provides a different perspective by indicating that the cause of evolutionary changes in size has not been the same throughout the islands. The Lesser Antilles are occupied by two distinct lineages of *Anolis* lizards. Dominica and islands north contain species related to those on Puerto Rico, whereas islands to the south harbor species with South American affinities (Fig. 1). A phylogenetic analysis of size evolution in the two clades indicates that the patterns of size similarity may not have been generated in the same manner (Losos 1990*a*). In the northern Lesser Antilles, large and small size appear to have evolved simultaneously when two lineages came into sympatry (but see below, *Conceptual and methodological concerns in applying phylogenetic methods to community evolution: Methodological uncertainties*)—exactly the prediction of a hypothesis of character displacement (i.e., that species diverge morphologically in sympatry to minimize resource competition). By contrast, in the southern Lesser Antilles, evolutionary change in body size appears to have been unrelated to whether a species occurred in sympatry with congeners. Consequently, the existence of size patterns must have resulted from a process of ecological sorting in which only dissimilar-sized species can successfully colonize and coexist on the same island (Case 1983). Thus, the relative importance of coevolutionary processes in determining community

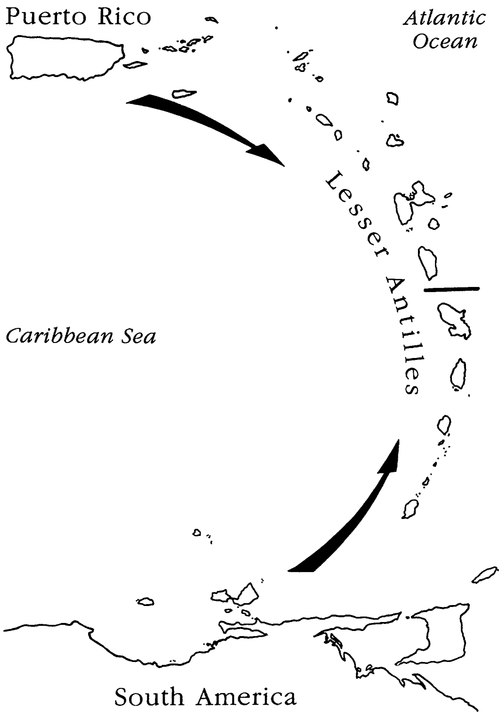

FIG. 1. The Lesser Antilles. The bar lies between Dominica and Martinique. Species of *Anolis* on islands north of the bar are related to anoles on Puerto Rico, whereas species on islands south of the bar are related to South American taxa.

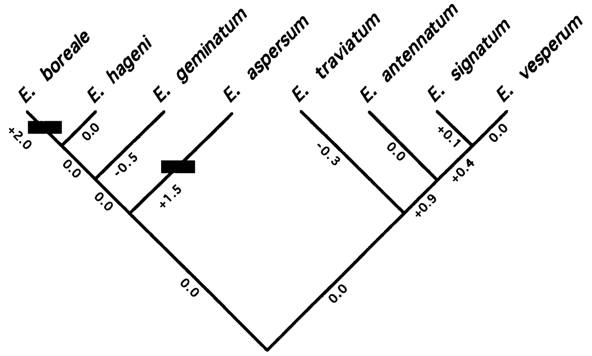

FIG. 2. The evolution of limb length in odonate larvae. Ancestrally, species occur in lakes occupied by fish. Bars represent transitions to occupying fishless lakes. Numbers represent the amount of evolutionary change in limb length between ancestor and descendant, as deduced using parsimony methods for reconstruction of ancestral character states (Maddison and Maddison 1992). Illustrated here is only one of the many equally parsimonious reconstructions of character evolution. All, however, indicate greater change on the two branches in which the transition to fishless lakes occurred than on other branches (based on McPeek 1995).

structure differs between the northern and southern Lesser Antilles, a result that is only apparent when these lizards are studied in a historical context.

The use of phylogenetic information to factor out historical effects

The previous section indicates how historical effects can potentially confound comparisons among communities that differ in lineage composition. By explicitly incorporating phylogenetic information into studies of community structure, however, such historical effects often can be factored out, thus allowing an assessment of the extent to which differences in structure among communities result from evolutionary responses to current environmental conditions. Further, historical approaches can direct inquiry away from proximate ecological circumstances and toward more appropriate evolutionary and/or biogeographical explanations for community patterns.

Communities can be compared both in terms of the attributes of their constituent species and in terms of the properties of the communities themselves. An example of a species-level community comparison is McPeek's (1995) study of North American odonate assemblages. The different characteristics of damselfly larvae in lakes with or without fish predators result because lineages moving into fishless lakes have evolved a distinctive set of morphological and behavioral characteristics, probably as a means of avoiding predation by dragonflies (Fig. 2; other examples are presented by Losos 1990*b*, Altaba 1991, Peterson 1993, and Miles 1994).

Hypotheses concerning environmentally caused evolutionary trends within lineages also invite phylogenetic analysis. For example, taxon cycle models suggest that a successional process of diversification occurs as a lineage first colonizes a new area and then specializes to use different microhabitats. Originally proposed to explain the evolution of ant community structure on islands throughout Polynesia (Wilson 1961), the taxon cycle model subsequently was applied to other taxa (e.g., Greenslade 1968, Ricklefs and Cox 1972; see also Roughgarden and Pacala 1989). Liebherr and Hajek (1990) used phylogenetic information to reconstruct the evolution of eight lineages of New World carabid beetles and found that only one lineage had diversified in a manner consistent with a taxon cycle hypothesis (see also Grandcolas [1993] on the evolution of habitat use in a lineage of cockroaches).

The evolution of communities themselves can also be investigated using phylogenetic methods; reconstructions of community evolution may be useful for both testing and generating hypotheses. For example, in many communities, species partition resources along several axes. Ecological theories differ in predictions about which axis (e.g., diet, habitat) should be the first to be partitioned as a community increases in diversity (e.g., MacArthur and Pianka 1966, Schoener 1974). Again, these are hypotheses that can be explicitly tested with phylogenetic information. The two communities subjected to phylogenetic analysis to date provide different results. Old World warbler assemblages apparently diverged early in prey size and only subsequently in habitat use (Richman and Price 1992), whereas the assemblages of *Anolis* lizards on Jamaica evolved in the opposite order (Losos 1992). Phylogenetic analysis also indicates that similarity in structure among communities of fish (Winemiller 1991), anoles (Losos 1992), and vultures (Hertel 1994) is the result of convergent evolution in similar environments.

Differences in the number of species among communities have long intrigued community ecologists. Many studies have looked to contemporary conditions as an explanation for differences in diversity among communities, but other considerations also may be important (MacArthur 1972, Ricklefs 1987). Although historical and/or geographical phenomena often have been considered to be of major importance in determining diversity (reviewed in Ricklefs and Schluter 1993), lineage effects rarely have been explored.

One possibility is that some lineages are inherently more likely to speciate or less vulnerable to extinction than others. Causes for lineage-based differences in speciation and/or extinction might be more related to intrinsic features, such as population structure, rather than a result of external environmental factors. Thus, differences in diversity among regions might result simply because one region contains lineages that tend to diversify more than another. Intercontinental differences in desert lizard diversity might be an example of this phenomenon (Losos 1994).

In addition, phylogenetic studies can suggest new avenues of investigation into community patterns. For example, species of *Anolis* have independently adapted to using grassy habitats in Cuba, Puerto Rico, Hispaniola, and Central America, but no such species occurs on Jamaica. One might ask: why are there no grass anoles in Jamaica? However, phylogenetic analysis indicates that other questions may be more appropriate. Phylogenetic reconstructions indicate that a predictable sequence of evolution of habitat specialists occurred on Greater Antillean islands. The grass habitat ecomorph (sensu Williams 1972) is the fifth in the sequence to evolve, but Jamaica has progressed to only the four-ecomorph stage (Williams 1972, 1983, Losos 1992). Thus, instead of focusing narrowly on the absence of a grass specialist, investigation might more profitably be directed toward the broader question of why Jamaica has only progressed to the four-habitat stage.

Communities as open systems: colonization, vicariance, and in situ evolution

The preceding section dealt with the case in which all members of an assemblage are descended from a single ancestor; consequently, speciation and adaptive change occurred in situ. This situation is not representative of most communities, which are usually composed of multiple trophic levels comprising many distantly related lineages (e.g., plants, microbes, vertebrates). Put another way, the nearest relatives of many taxa will occur outside of the community. Consequently, the composition and structure of such communities will result from a combination of colonization, geological events, and in situ ecological and evolutionary events. Accordingly, untangling the relative contribution of these different factors will require methods that can reveal historical changes in both ecology and geographical distribution (Mayden 1987, Brooks and McLennan 1991, 1993, Gorman 1993).

Combining phylogenetic and geographical information can thus provide an important perspective on community patterns. Consider, for example, anole assemblages on small islands in the western Caribbean. On Little Cayman Island, *A. sagrei* and *A. maynardi* (a member of the *carolinensis* species group) are sympatric and differ in habitat use. One hypothesis to explain this distribution is that the two species evolved differences in habitat use on Little Cayman to minimize competition. However, members of the *sagrei* and *carolinensis* lineages are sympatric in many locations throughout the Caribbean (including Cuba, where they both evolved), and in all cases, the two species show the same pattern of habitat partitioning. Although habitat partitioning may have evolved independently on each of these islands, this hypothesis is not parsimonious. An alternative explanation is that the evolution of habitat partitioning may not be a recent phenomenon, but, rather, evolved in the ancestors of the two lineages when they first came into sympatry in Cuba.

The historical analysis thus indicates that a study of the *cause* of habitat differences focusing on the anole community of Little Cayman would be inappropriate because habitat partitioning between these lineages originally evolved long ago on a different island. Nonetheless, competition may still be important in regulating community structure by, for example, preventing populations of *sagrei* from evolving to be more like *carolinensis* in habitat use or by preventing two members of the *carolinensis* lineage from coexisting. The historical perspective suggests an alternative possibility, however; ecological interactions between members of the two lineages may no longer occur, but the community structure that evolved in the past may persist nonetheless. These two hypotheses about the present-day importance of interspecific competition are testable because they make different predictions about whether interspecific interactions should occur in extant communities and what habitat use should be like on islands on which only one of the lineages is present (similar examples are discussed by Brooks and McLennan [1991, 1993]).

Historical explanations will only be appropriate when phylogenetic information suggests that a particular community structure arose prior to the origin of extant communities. If communities either do not contain the same lineages or if a lineage differs ecologically between the communities, then phenomena unique to one of the communities (e.g., colonization, extinction, in situ ecological change) will be implicated as an important determinant of community structure. On Jamaica, for example, *A. sagrei* occurs with members of the Jamaican anole radiation (Williams 1969). These lineages co-occur naturally nowhere else. Consequently, to understand the interactions that occur between *A. sagrei* and other Jamaican anoles, one need not look further than Jamaica—there is no historical component to the interactions between these taxa, which may be studied, at least initially, in an ahistorical context. Even in this case, however, it is possible that *A. sagrei* interacts with Jamaican anoles in the same manner in which it interacts with *A. carolinensis* elsewhere; hence, an historical perspective may still prove informative.

These approaches need not be confined to closely related taxa in a community. Historical information may prove informative whenever elements of community structure have a history of interaction. Indeed, there is a large body of literature concerned with investigating the extent to which evolutionary diversification in interacting components of a community, such as parasites or phytophagous insects and their hosts, has been linked (Farrell and Mitter 1993, and references therein). Historical influences on community structure can be examined among any elements of the community, such as predator–prey and multiple trophic-level interactions. All that one needs is historical information on all of the component lineages within each community considered in a study.

Brooks and McLennan (1991, 1993) devised a method to synthesize biogeographic, phylogenetic, and ecological information. Essentially, the method combines parsimony methods to reconstruct evolutionary change in ecology with vicariance biogeography methods to distinguish in situ speciation from colonization. Brooks and McLennan thus recognize four components contributing to community structure: (1) species that interact in the same way that their ancestors did in other communities (Fig. 3a) (such communities often are created by vicariant events [e.g., mountains rising and dividing a previously continuous community in two] rather than by colonization); (2) species that colonized a community but do not lead to ecological shifts (Fig. 3b) (thus, new associations of lineages are established, but ancestral ecologies are conserved); (3) species derived in situ that evolved different ecological requirements (Fig. 3c); and (4) species that colonize a community and interact with species already present, leading to ecological shifts in the colonizer, the resident, or both (Fig. 3d).

In all of these situations, the causal basis for the origination of a particular community structure must be sought at the appropriate historical level because the ecological forces responsible for the origination of a community's structure may not be the same as the processes maintaining that structure in extant communities. This is not a new idea (e.g., Connell 1980), but phylogenetic approaches now provide the appropriate methodology to test such hypotheses.

Studies of South American stingray parasites (Brooks and McLennan 1991, 1993) and North American freshwater fish (Gorman 1993) have used this approach. Both suggest that similarity between communities often results because vicariant events create communities composed of the same set of lineages, with each lineage remaining ecologically similar across communities.

Conceptual and Methodological Concerns in Applying Phylogenetic Methods to Community Evolution

Methodological uncertainties

The major drawback in applying phylogenetic methods to community ecology is the need for a robust phylogenetic hypothesis for lineages within communities. For many lineages, no phylogeny is available. Those that are available are often not strongly supported—the publication of new phylogenetic studies will often cause a reassessment of conclusions based on outdated phylogenies. For example, studies of the evolution of body size in *Anolis* of the northern Lesser Antilles based on a recent phylogenetic analysis indicate that character displacement is consistent with only one of several equally plausible scenarios (C. Schneider, J. B. Losos, and K. de Queiroz, *unpublished manuscript*). Further, although a number of methods are available to interpret evolutionary patterns based on a phylogeny (reviewed in Maddison and Maddison 1992, Swofford and Maddison 1992, Maddison 1994, Losos and Miles 1994), all methods require that assumptions be made about how evolutionary change occurs (e.g., gradual, punctuational, etc.); only rarely are data available to evaluate such assumptions.

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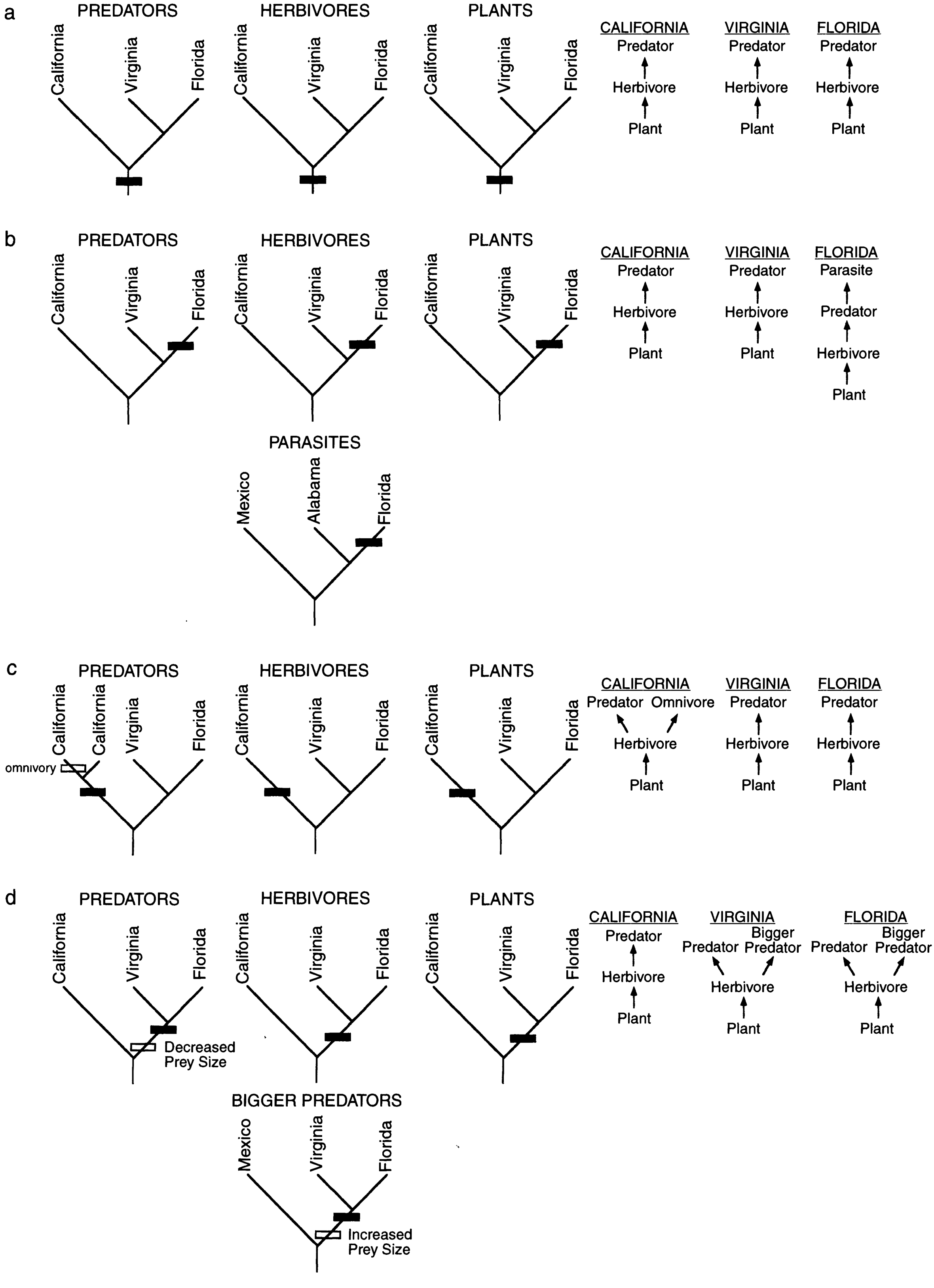
FIG. 3. Phylogenetic perspective on community structure. Cladograms illustrate the evolutionary relationships of the component species in food webs of several communities. Black bars indicate the point at which an association of species (i.e., a community) originated. Open bars indicate changes in ecology. (a) Communities composed of the same three lineages occur in three areas. Association of the three lineages predates any of the extant communities. Ecological interactions among the lineages are the same in all three communities. The three lineages may have once occurred in a community spanning North America; subsequent vicariant events led to speciation in each of the lineages and the formation of three ecologically identical communities. Studies focusing on why the California predator, for example, eats the particular California prey species (as opposed to another prey species not shown) should not focus on unique conditions in California. (b) Establishment of a new food web structure (=a new association of species, hence the black bar) in Florida. The parasite lineage does not occur with the other three lineages in California or Virginia, but has colonized the community in Florida, creating a new association of species. No interspecific shifts in ecology result from this colonization. (c) In situ speciation and ecological shift. The predator lineage in California speciated, adding another member to the community and creating a new association of species. In addition, the new species exhibits an ecological shift to omnivory, as indicated by the open bar. (d) Establishment of a new association causing alterations in patterns of ecological interactions. Another lineage of predators colonized the ancestral Virginia + Florida communities. Interactions between the predators may have caused a shift in diet in both the resident and colonizing bigger predator lineages. Investigation of this hypothesis should focus on the ancestral Virginia + Florida community.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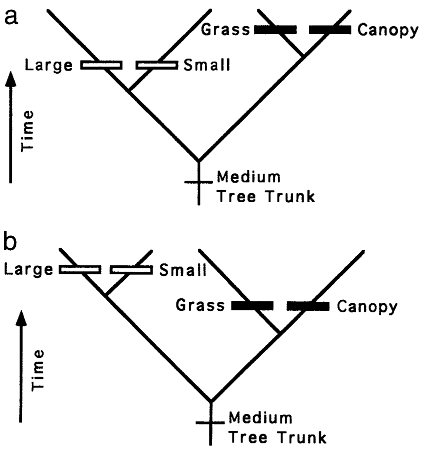

FIG. 4. Temporal component of phylogenetic reconstructions for in situ community evolution. Most phylogenies do not contain information on the temporal ordering of events. Consequently, different processes may produce identical phylogenetic patterns. The ancestor of a monophyletic lineage is medium sized and lives on tree trunks. (a) Diversification occurs first by divergence in body size; only subsequently do taxa specialize for different microhabitats. (b) The reverse ordering occurs. Diversification proceeds first by habitat specialization and subsequently by shifts in body size. Without information on the timing of speciation events, (a) and (b) cannot be distinguished.

As a result of the inherent uncertainties in phylogenetic relationships and inferences about evolutionary change based on these relationships, results of such studies must be treated cautiously. Consequently, the most prudent course will be to not focus solely on the "best" tree and a single model of evolution. Rather, many or all plausible trees should be examined, each with a variety of different models of evolutionary change (Harvey and Pagel 1991, Martins 1993, 1996, Losos 1994). Consistent results in all analyses will provide confidence in the results, whereas inconsistent results will emphasize the importance of recovering the correct phylogeny and mode of evolutionary change.

The problems just outlined pertain to attempts to reconstruct historical patterns of any sort using phylogenetic information. In addition, applications of such methods to studies of community evolution have unique difficulties. Most studies of community evolution will be interested in the temporal sequence of events. Unfortunately, most phylogenies do not provide information on divergence dates. Consequently, because most communities are composed of members of many different lineages, determining the ordering of events across lineages may prove difficult. For example, consider the four-species community illustrated in Fig. 4. Depending on the ordering of the speciation events among the lineages, one might suggest very different scenarios for community development.

This problem is compounded when some members of lineages occur in other areas. In such cases, one must infer not only the absolute timing of events, but also whether and when dispersal events occurred, because events occurring in other areas may not be relevant to the structure of the communities under study (Fig. 5). Methods developed in vicariant biogeography may prove useful (e.g., Brooks and McLennan, 1991, 1993), but these methods have the same problems as other phylogenetic methods: they rely on specific evolutionary models and only provide information on the relative ordering of events associated with divergence, rather than informing about the timing of evolutionary events. In some cases, however, molecular phylogenetic data may prove useful in providing the necessary temporal context (reviewed in Cunningham and Collins 1994).

Can comparative studies of community structure be conducted without phylogenetic information?

I have argued that ignoring the historical information provided by a phylogenetic perspective can lead to mistaken conclusions regarding both the evolutionary genesis and current maintenance of community structure.

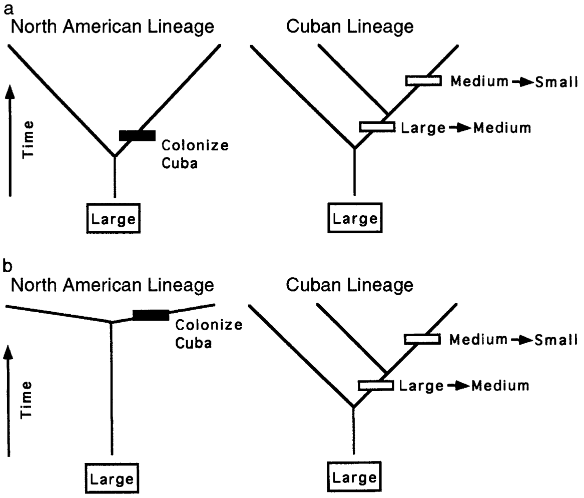

FIG. 5. Temporal component for phylogenetic reconstructions when a community is colonized by a new lineage. An extant community in Cuba contains three members of one lineage and one member of a second lineage that colonized from North America. (a) If the colonization event occurred prior to diversification in the Cuban lineage, then the presence of the larger species may have been responsible for the evolution of smaller size in the Cuban lineage. (b) Alternatively, if the colonization event was relatively recent, then the presence of a large species was not responsible for the evolution of small size. Again, these scenarios would not be distinguishable if one had only phylogenetic information without data on the temporal ordering of events.

Nonetheless, there are situations in which one can get by with minimal phylogenetic information.

Schluter (1986*a,* Schluter and Ricklefs 1993) has proposed a method to study whether communities in similar habitats are convergent in structure. In essence, the method works as follows: one collects data on the structure of communities (e.g., species number, mean nearest neighbor distance, etc.) in two or more continents or other large geographic areas. Within each continent, communities in several different habitat types (e.g., grassland, forest) are included. One then asks to what extent variation in community structure is explained by habitat type relative to the variation explained by continent and by the interaction of continent × habitat. To the extent that habitat type explains a significant portion of the variance, then the hypothesis that communities converge in structure in similar habitats is supported. Using this method, Schluter and Ricklefs (1993) found that convergence in diversity is common in bird, plant, and lizard communities (see also Pearson and Juliano 1993).

This method is implicitly phylogenetic in that it assumes that particular species are more closely related to species in other habitats on the same continent than they are to species in the same habitat on other continents. If this assumption is correct, then a similarity between species in the same habitat on different continents would be indicative of convergent evolution. Thus, minimally, one must know that occupants of one continent are monophyletic relative to taxa on other continents. This requirement is exactly the opposite of that in the method of Brooks and McLennan (1991, 1993), in which lineages must be shared among communities.

Monophyly vs. guild membership as the criterion for inclusion in studies of community structure

Recent years have seen widespread acceptance of the premise that comparative evolutionary studies must be conducted on monophyletic taxa—studies using paraphyletic (or polyphyletic) groups are likely to come to mistaken conclusions due to the omission of taxa (e.g., Cracraft 1981, Brooks and McLennan 1991, Wiley et al. 1991). Nonetheless, monophyly is not always the appropriate criterion for comparative studies of community structure. Rather, the most important criterion in ecological studies is that the taxa included be those likely to interact; such taxa need not be closely related. For example, members of a guild (sensu Terborgh and Robinson 1986) often come from very distinct lineages (e.g., Davidson et al. 1985, Schluter 1986*b*), whereas members of the same lineage may be so ecologically different that one would rarely consider including them together in studies of community structure (e.g., studies of mammal community ecology often exclude bats).

However, potentially the worst solution in deciding which taxa to include in community studies is to use Linnean taxonomy. Members of the same Linnean category often neither compose a monophyletic group nor are members of the same guild; thus, such groupings have neither ecological nor evolutionary relevance. For example, studies of lizard community ecology commonly include lizard taxa that have experienced limb loss or reduction. However, such studies rarely include snakes. Yet, snakes evolved from lizards (Estes et al. 1988); they are simply the most extreme of the 12 or more lineages of lizards that have experienced evolutionary limb loss (Edwards 1985). Further, some legless lizards are ecologically more similar to snakes than they are to other lizards (e.g., Patchell and Shine 1986). Thus, there is no justification for including most lineages of legless lizards in studies of lizard community ecology, but excluding one because it has been given its own Linnean category.

INTEGRATING EXPERIMENTAL AND HISTORICAL APPROACHES TO COMMUNITY ECOLOGY

Comparative studies have been revolutionized in the decade since Felsenstein's (1985) seminal paper. Phylogenetic approaches are now commonly used in comparative studies to test hypotheses (Miles and Dunham 1993). Now, the time has arrived for comparative biology to come full circle. Not only are phylogenetic approaches useful for testing hypotheses, but they may also serve as the source of hypotheses, which then can be tested using extant taxa and communities (e.g., Lauder 1989, Futuyma and McCafferty 1990, McLennan 1991).

For example, historical studies may suggest that certain processes (e.g., predation, competition) may have played an important role in community evolution. Studies on extant taxa could then test predictions stemming from such an hypothesis. Tests might include experimental investigation of whether the process is important in extant communities. If these manipulations could be maintained over sufficient periods of time, they might also test the prediction that the ecological consequences of the process would lead to microevolutionary change in the predicted direction.

For example, Gorman (1993) predicted that taxa that had a longer history of co-occurrence, as evidenced by phylogenetic analysis, would be less likely to experience competitive effects on habitat use than species that had more recently come into sympatry. Laboratory and field analyses confirmed this prediction. In a similar manner, Farrell and Mitter (1993) found that Peruvian plant species in lineages characterized by traits that promote species diversification have higher population densities than species in nondiverse lineages. Several studies currently are investigating whether interspecific interactions lead to microevolutionary change, as predicted by historical studies. None has run long enough to demonstrate evolutionary change, although Schluter (1994) has demonstrated that interspecific competition leads to selection favoring morphological divergence of competitors.

Phylogenetic approaches thus should be seen as an integral component of studies of the causal basis of community structure. In some cases, of course, phylogeny will not be relevant. If, for example, one were only interested in whether some process were currently operative, then the phylogenetic relationships among community members might not be important. But if one is interested in comparing the structure of communities or investigating how a community came to its present state, then phylogenetic information is indispensable for both generating and testing hypotheses.

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