

Community Diversity: Relative Roles of Local and Regional Processes

ROBERT E. RICKLEFS

The species richness (diversity) of local plant and animal assemblages—biological communities—balances regional processes of species formation and geographic dispersal, which add species to communities, against local processes of predation, competitive exclusion, adaptation, and stochastic variation, which may promote local extinction. During the past three decades, ecologists have sought to explain differences in local diversity by the influence of the physical environment on local interactions among species, interactions that are generally believed to limit the number of coexisting species. But diversity of the biological community often fails to converge under similar physical conditions, and local diversity bears a demonstrable dependence upon regional diversity. These observations suggest that regional and historical processes, as well as unique events and circumstances, profoundly influence local community structure. Ecologists must broaden their concepts of community processes and incorporate data from systematics, biogeography, and paleontology into analyses of ecological patterns and tests of community theory.

INTEREST IN NATURAL DIVERSITY HAS RISEN IN THE PUBLIC conscience recently with concern over the imminent extinction of thousands of species as a result of pollution and habitat destruction (1). Ecologists are unable to calculate the consequences of this havoc for natural resources of use to mankind and for the intrinsic stability of natural systems. But many consider these consequences to be potentially disastrous (2). If we are to predict change in system function after depauperization, we need to understand processes responsible for generating and maintaining diversity in biological communities. Indeed, the diversity issue may have two faces: Can one comprehend the ruin of natural systems without understanding how they are built?

Present-day ecological investigations are largely founded on the premise that local diversity—the number of species living in a small, ecologically homogeneous area—is the deterministic outcome of local processes within the biological community. As a general rule, community diversity parallels variation in local physical conditions. For example, on all continents, diversity tends to decrease with increasing distance north or south from the equator (3). But whether such patterns are mediated by competition between species, predation and disease, or patchworks of natural disturbances is intensely debated without any sign of resolution soon (4, 5).

Competition has been advocated strongly (6–8) because coexistence requires that each species has some corner on a limited resource market. If coexistence were precluded when ecological

similarity exceeded some limit, or if a species could not persist when its ecological niche were reduced below some minimum viable size, the number of species in a community would be determined in a manner analogous to the packing of balls in a box. Accordingly, one would expect to find regular spacing between the positions of species within ecological space. Equivocal evidence for such spacing (9) has prevented the “competition hypothesis” from completely sweeping the discipline.

Predation is ubiquitous. The fact that predators can manipulate the dynamic relations between competing prey species has attracted many to the position that predation may influence diversity (10). Disturbances to the uniform fabric of the community caused by storms, erosion, predation, and natural deaths of individuals increase the heterogeneity of the environment and increase the amount of ecological space available (11). Disturbance itself, by interrupting the return of systems to equilibrium, may retard competitive exclusion and thereby promote diversity (12).

Almost certainly, these local factors influence local diversity. But a larger issue for ecologists is the degree to which they can explain local diversity solely by local processes, without considering the matrix of processes on larger spatial and temporal scales within which the community is imbedded. Ecologists are beginning to realize that local diversity bears the imprint of such global processes as dispersal and species production and of unique historical circumstance. These processes pose a challenge to community ecologists to expand the geographical and historical scope of their concepts and investigations.

Testing Predictions of Local-Process Theories

Regardless of the underlying mechanism, hypotheses that relate local diversity deterministically to local conditions make common predictions of (i) community convergence, (ii) resistance of the community to invasion, and (iii) independence of local and regional diversity. In two areas having different histories of biological development but similar physical conditions, adaptations of individuals and attributes of community structure and function should conform to limits imposed by local conditions. Although plant and animal form and function commonly converge in similar environments (13), accumulating counterexamples dispel belief that species diversity similarly converges (14, 15). Two examples will illustrate this important point. First, throughout the tropics, the boundary separating marine and terrestrial environments supports a mangrove-type vegetation consisting of species of trees uniquely (and convergently) adapted to the immersion of their roots in salt water. In the New World tropics and western Africa, mangrove communi-

The author is a professor in the Department of Biology, University of Pennsylvania, Philadelphia, PA 19104.

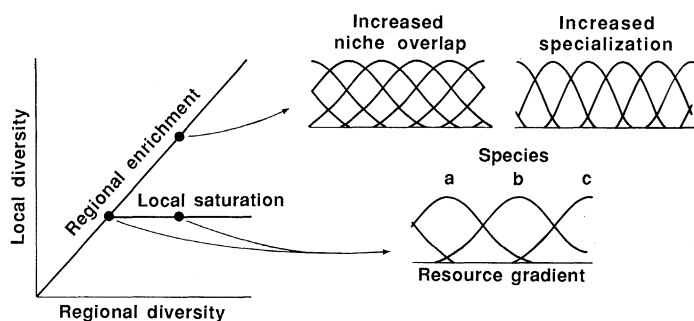


Fig. 1. Two models of the relation between local species richness and regional diversity. According to the saturation model, the coexistence of species is determined by their interactions, which impose a fixed limit whose value depends on the physical conditions of the environment. Variation in regional diversity due to rates of speciation and dispersal is accommodated by habitat specialization and increased geographical turnover of species. According to the regional enrichment model, variation in regional diversity influences local communities, where differences in diversity are accommodated by varying the degree of niche overlap or the degree of resource specialization.

ties consist of no more than the same three or four species throughout the region, each forming a distinctive zone with respect to tide level (16). In marked contrast, mangrove forests in similar physical environments on the coasts of Malaysia are formed by 17 "principal" and 23 "subsidiary" species loosely organized in five zones (17). Second, comparisons of the vegetation of chaparral (matorral) and coastal sage (phrygana) vegetation (Mediterranean climate) have revealed four times as many plant species in Israel as in southern California; local samples (0.1 ha) in Israel reveal almost twice the number of species as in southern California (18). Even where ecologists have claimed community convergence on the basis of similar local diversity in biotically distinct areas (19), they have failed to demonstrate statistically the uniformity of local diversity relative to the heterogeneity of regional diversity (20).

If species saturated biological communities within limits set by local conditions (that is, if the box were filled with balls of more or less fixed size), new species could not join the community without the compensating disappearance of others. If we assume saturation, communities should resist invasion because local species are better adapted than foreign ones to local conditions. Introductions provide only equivocal evidence. Many species have successfully invaded terrestrial and aquatic communities (21), but primarily in disturbed habitats and on depauperate islands (22). Successful introductions may lead to extinction of native forms, but usually by means of predation and disease rather than competition (23).

Finally, if local conditions determined local diversity, variation in regional diversity should have little influence on local diversity (Fig. 1). Replacement of species along ecological and geographical gradients would explain discrepancies between local and regional diversity (8). Ecologists have only recently tested the relation between local and regional diversity (24). Cornell (25, 26) has shown that the local diversity of cynipine gall-forming wasps on each species of oak (*Quercus*) in California depends on the overall number of wasp species recorded throughout the range of the oak (Fig. 2). Among small areas of matched, uniform habitat within the Caribbean region, including both mainland and island localities, songbirds (Passeriformes) also exhibit a direct relation between local diversity and regional diversity (27, 28) (Fig. 3). In these cases, local communities are not saturated, diversity is not prescribed by local condition, and the number of species found within small areas is sensitive to such regional processes as geographical dispersal and the historical accumulation of herbivore species on host plants.

Faced with mounting evidence against the predominance of local

determinism, ecologists are beginning to accept that processes beyond their normal scale of consideration may influence structure and function of ecological systems (26). Although ecologists recognize lack of convergence, most still regard history, geographic position, accident, and uniqueness as footnotes to a local ecological perspective. For example, while recognizing that "the marked differences in [regional] diversity between continents must have explanations with a strong component of history and chance," Cody (8, p. 238) maintained that patterns in local diversity "can be adequately explained by competition theory and by the constraint of a limiting similarity" and they "conform well with simple theoretical predictions that ignore history" (8, p. 238). In reviewing a recent symposium volume on community ecology, May (29, p. 1451) noted that "there has been an increasing awareness among community ecologists that the dynamical behavior of assemblies of plants and animals is likely to be highly dependent on the environmental and biological setting, and even on historical accidents." In a recent assessment of community convergence, Orians and Paine (14, p. 456) stated that "plant species richness, in contrast to plant growth forms, is not convergent. There is as yet no comprehensive theory or data base that allows us to assess the relative roles of direct competition, habitat heterogeneity, competition for pollinators and propagule dispersers, and selective grazing by herbivores in determining plant species richness. There is also strong evidence that plant species richness may continue to increase over long periods of evolutionary time." Why have ecologists been slow to adopt a regional perspective? The answer may be found in the development of the community concept.

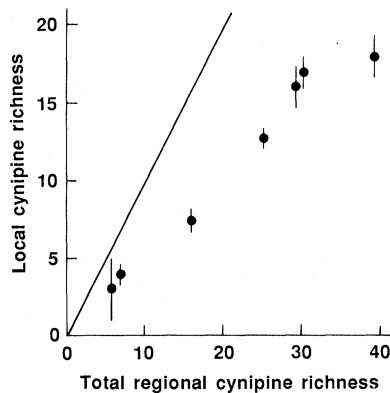
The Eclipse of History

At the turn of the century, most biologists accepted historical interpretations of species diversity patterns. This perspective led biogeographers and others concerned with regional and global patterns to speculate on diversity (30), but ecologists sidestepped the issue and focused on the structure and function of local systems (31). Starting in the 1920's, with the development of theory concerning the interactions of populations, attitudes began to shift; by the late 1950's, a concept had developed to relate community diversity to local interactions among species, the dynamics of which were determined by local physical conditions.

The transition began with Lotka's and Volterra's mathematical formulations of species interactions (32). Gause's experiments with laboratory populations demonstrated that species could not coexist on a single limited resource, thus verifying a theoretical prediction that came to be known as the "competitive exclusion principle" (33). In the 1940's, Lack applied Gause's principle to problems of ecological isolation and species diversification in nature (34). In the 1950's, Hutchinson extrapolated the concept of ecological isolation to the packing of species in multidimensional niche space and, by remarking on the apparent uniformity of observed size ratios between pairs of ecological counterparts, initiated the notion of limiting similarity (35). Building upon this concept in the 1960's, MacArthur and Levins (36) and May (37) used mathematical constructs to demonstrate deterministic, equilibrium properties of systems characterized by matrices of interactions among their component species. Thus, what Kingsland (38) referred to as the "eclipse of history" brought diversity into the realm of ecological study and caused a fundamental transformation of the discipline.

The key to divorcing local diversity from regional process and historical cause is the concept of limiting similarity: compression of the ecological niche below a certain threshold size, as by interspecific competition for resources, results in exclusion. Thus, diversity is

Fig. 2. Local richness of cynipine wasps on oaks is directly related to the total number of species of cynipines recorded from throughout the range of each oak species. Several local areas were sampled from within the range of each oak species. From low to high richness, the species of oaks (*Quercus*) are *dunnii*, *tomentella*, *agrifolia*, *durata*, *lobata*, *douglasii*, and *chrysolepis*. The solid line indicates local diversity equal to regional diversity (26).



more or less fixed at a level—the saturation point—above which the addition of new species is balanced by the extinction of old ones. Differences in regional diversity are accommodated by adjustment of the degree of habitat specialization (8). The concept of limiting similarity, by analogy, prevents compression of the size of balls as a way to pack more balls into the box.

The idea of limiting similarity began as an assertion. Ecologists rationalized it by the notion that population size decreases with ecological compression, thereby increasing the probability of extinction, especially in unpredictably variable environments (36). Neither theory nor observation suggests that there are minimum viable ecological breadths for species in particular environments or that saturation occurs at habitat-specific levels of diversity. Indeed, few ecologists would deny that saturation expresses a flexible equilibrium: local interactions causing extinction balance regional processes that augment local diversity. When habitat and niche size are specified, one can demonstrate theoretically a limit to the number of coexisting species (36, 39). But niche size responds to the number of species present (27, 40), and speciation and dispersal contribute new species to build up the diversity of local communities. In 1965, MacArthur (41, p. 510) offered a clear statement of the local-regional dichotomy: "... if the areas being compared are not saturated with species, an historical answer involving rates of speciation and length of time available will be appropriate; if the areas are saturated with species, then the answer must be expressed in terms of the size of the niche space ... and the limiting similarity of coexisting species."

Clearly, regional-historical issues stood in the way of bringing diversity into the realm of ecological investigation. Limiting similarity and saturation provided a convenient resolution of this dilemma, and ecologists rushed to embrace them (5, 6). Ecology chose to ignore history at this point for its own convenience and closed the door on its related disciplines of systematics, biogeography, and paleontology. As MacArthur (42, p. 239) phrased the distinction, "The ecologist and the physical scientist tend to be machinery oriented, whereas the paleontologist and most biogeographers tend to be history oriented. They tend to notice different things about nature." Even his acknowledgment that history may leave "an indelible mark even upon the equilibria so dear to the ecologist" (42, p. 239) emphasizes the developing gulf between the disciplines. Ironically, while historical uniqueness was being exorcised from local determinism, MacArthur and Wilson (43) developed their equilibrium theory of biogeography. This theory explicitly incorporated a regional process (immigration of species from mainland sources of colonists), whose expression depended on geographical circumstance, to balance local ecological processes governing coexistence and extinction. Although MacArthur (44) recognized that regional processes influence regional diversity, he largely retained the local-regional distinction: "The first explanation [of the great species diversity in the tropics], which is essentially historical,

allowing a future increase in the numbers of species, seems inconsistent with the others which predict a saturation with species, but even these can be mixed. Not only could some taxa have historical explanations while others have ecological, but also, the total fauna of a country could continue to grow ... while the local biota of any subdivision might have reached saturation" (44, p. 20).

While ecologists were abandoning history, the fields of paleontology, systematics, and biogeography experienced a resurgence of ideas and excitement (45, 46). Little of this revitalization has filtered back to community ecology. No discipline can resolve its major issues with narrow perspectives and incomplete concepts. Not surprisingly, then, ecologists have been divided on local diversity, and the premise of local determinism has finally unraveled.

The Balance Between Local and Regional Processes

The presence or absence of a species depends on the outcome of processes tending to increase or decrease its numbers. The latter are generally local in nature, including predation, disease, reduction of resource levels by competitors, small-scale disturbances, and periods of unfavorable climate. Most interactions between species are antagonistic, and selection favors increased competitive ability and predator efficiency. Thus, evolution, while fostering greater mutual accommodation among coexisting species, ultimately tends to reduce species richness. Balancing these negative factors is the intrinsic productivity of the population in a particular habitat and the immigration of individuals from other areas. The variety of immigrants to a particular place depends on such regional processes as the generation and dispersal of new species (speciation) and also on historical accidents and circumstances related to past climate history and geographical position of dispersal barriers and corridors. The stronger speciation and dispersal are, relative to local factors influencing adjustment of population size and adaptation of individuals, the deeper the imprint of history and geography on the local community.

In simple laboratory systems, competitive exclusion requires on the order of 10 to 100 generations (47). Stochastic (chance) extinction depends on the size of the population, but if n is 1,000 individuals (very small), an average extinction time of 10,000 generations is plausible (48). These periods seem brief compared to

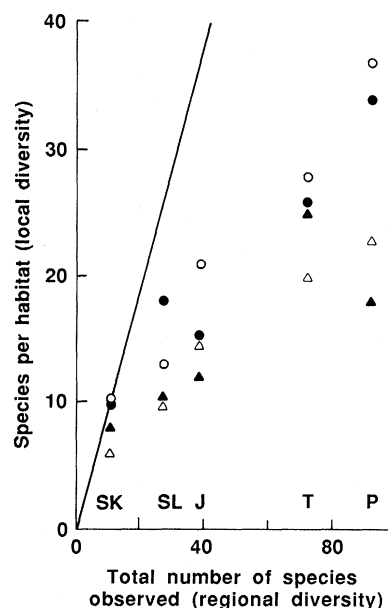


Fig. 3. Local species richness of birds in the Caribbean region is sensitive to regional diversity, which is determined primarily by biogeographic considerations. Areas sampled were St. Kitts (SK), St. Lucia (SL), Jamaica (J), Trinidad (T), and central Panama (P). Within each area, standardized counts were made of songbird species within small, homogeneous areas of habitat: secondary scrub (●), young secondary forest (○), mature lowland forest (▲), and cloud forest (△) (27, 28).

production of species, changes in climate and positions of landforms, and appearances of new genotypes that enable populations to expand ecologically into new communities. However, migration of individuals between local systems with different equilibria may slow the rate at which interactions between species move a system to a local equilibrium, perhaps to a level approaching the scale of evolutionary and biogeographic processes.

Consistent (convergent) patterns of diversity, such as the relation between species richness and geographical latitude, indicate deterministic equilibria with respect to physical conditions. But even here, regional processes, rather than or in addition to local interaction, may cause differences in diversity between areas. These processes include dispersal, evolutionary adaptation to new habitats, habitat specialization, and speciation. Ecologists must accept the possibility of communities in transition between equilibria; the equilibria may have been shifted by changes in climate and biogeographical setting or by the occurrence of local "hot spots" of species production. Conceivably, the equilibrium number of species may shift much more rapidly than the community can approach it. The processes responsible for the addition and removal of species from local communities may be mostly indifferent to the number of species present, but such ideas have been discussed only in terms of regional diversity (8, 46, 49).

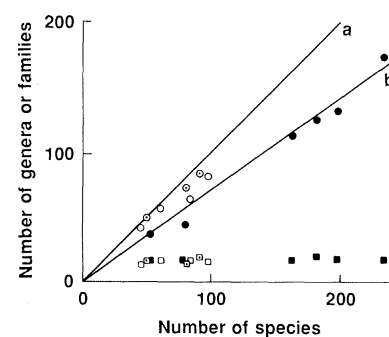
Evolutionary biology provides a useful analogy for ecologists. Evolution proceeds largely by a deterministic process of selection, but the particular manifestations of evolutionary history are unique and unpredictable. Form and function of organisms must obey certain physical laws, just as ecosystem function must obey the laws of thermodynamics. But a particular product of evolution—the elephant, for example—reflects a long sequence of historical events and circumstances; nature is indifferent to the specific quality of the elephant. Ecologists accept the unique taxonomic composition (history) of each community because community processes are similarly indifferent to biological species names. To the extent that this indifference extends to species number, we should expect each community's history of ecological, biogeographical, and evolutionary change to be revealed in local diversity as well.

An Expanded Program of Ecological Investigation

Ecologists ignored history because it was impractical to do otherwise. How can we regain a historical perspective and use it to resolve the major issues of community ecology? First, we must pay attention to developments in biogeography, paleontology, systematics, and evolutionary biology. New insights will arise at the intersection of the local-contemporary viewpoint of ecology and the global-historical viewpoint of its sister disciplines. Second, to deepen our insight, we must study the historical development of thought about community ecology and also reevaluate the conclusions of influential investigators. Third, we must rigorously examine the hypothesis of local equilibrium by putting community convergence and the independence of local and regional diversity to the test. Fourth, we must assimilate data on geographical distribution, habitat selection, and taxonomic status into the phenomenology of the community concept. Ecological data must match the spatial and temporal scales of processes that influence the properties of ecological systems.

Where dispersal occurs between habitats and geographical areas, equilibria are regional phenomena. In addition to contemplating coexistence in local areas of habitat, ecologists must examine patterns of coexistence within regions. The partitioning of habitats and of geographical area within regions has as much relevance for community structure as the partitioning of resources within habi-

Fig. 4. Relation between familial and generic diversity and species diversity in six local samples of passerine birds in lowland tropical forests. Solid symbols are observed numbers of families (squares) or genera (circles). Open symbols were obtained by systematically (symbols with enclosed points) or randomly (no enclosed points) deleting species from the more diverse South American censuses



(>150 species). The difference between the rarified samples (open symbols) and the Indonesian–New Guinean censuses (<100 species) indicates that the two were not drawn from the same distribution of species per genus. Lines a and b indicate 1.0 and 1.4 species per genus, respectively. Sample localities are, in order of increasing diversity: East Sepik, Papua New Guinea; Kilimantan Timur, Indonesia; Beni, Bolivia; Napo, Ecuador; Loreto, Peru; and Madre de Dios, Peru. Data are from Pearson (52).

tats; indeed, the two may manifest a single pattern of specialization (50). Local ecological distribution and population density bear a strong relation to geographical distribution and degree of taxonomic differentiation of the species (28, 51).

Taxonomic information provides clues to historical influence. Families have more ancient origins than genera and species, and patterns of familial diversity undoubtedly record the evolutionary, historical, and biogeographical settings of local communities more faithfully than do patterns of generic and, especially, specific diversity. For example, among assemblages of songbirds inhabiting small areas of lowland tropical forest between Indonesia, New Guinea, and the Amazon Basin of South America, differences in diversity arise at the generic rather than specific or familial levels (52) (Fig. 4). This feature suggests differences in the way that historic assembly of local communities determines contemporary diversity.

To the degree that rate of speciation depends on geographic or ecological isolation, this rate may vary systematically with conditions that promote reproductive isolation between populations and that enhance the rate of evolution. Thus, rate of speciation is a topic of concern for both ecologists and evolutionists, and its consequences may have a profound impact on the structure of local communities as well as on regional patterns of diversity.

The ecological community encompasses a hierarchy of structure discernable over a range of scales from those within the locality to those of the region and even the globe. In turn, a hierarchy of processes determines this structure, processes that act over correspondingly varied dimensions of time and space. Structures will generally match the scales of processes responsible for them (53). The scales of population processes leading to local exclusion of species, and those of the evolutionary and biogeographical processes that promote species richness, remain to be determined. To the degree that the scales of these processes match, local communities will reflect regional processes and historical events.

Conclusion

The regional-historical viewpoint provides a fundamental challenge to ecologists. Broadened concepts of the regulation of local community structure, incorporation of historical, systematic, and biogeographic information into the phenomenology of community ecology, and expanded investigations that address global variation in local species richness will help unite local and regional perspectives. Historical and regional causes are less accessible to experimentation than local processes in ecological time. But ecologists should

consider comparative studies, statistical analyses of pattern, and "natural experiments" (54) at a time when the discipline has begun to emphasize experimental approaches. Certain types of nonexperimental tests of hypotheses are possible, as illustrated here by examples, and new multivariate statistical applications (55) combined with novel logical structures may bring to ecology some of the resurgence enjoyed recently in the fields of systematics and biogeography.

The regional-historical viewpoint emphasizes the value of systematic and biogeographic data and argues for increased funding to support their collection and interpretation (56). It also argues that the integration of the traditional museum disciplines of systematics, paleontology, and biogeography into biology curricula may help to form a new synthesis of natural history and, perhaps, a resolution of some of the most fundamental and persistent issues in biology. Finally, the regional-historical viewpoint has implications for conservation and, particularly, for views on the relation between stability and diversity. The responsiveness of the equilibrium diversity of a locality to regional processes and historical circumstances argues that coevolved interrelations among component species do not buffer community structure against externally imposed change. Accordingly, the function of a system, including its stability, does not depend strongly on its diversity. The threat of habitat destruction and pollution derives primarily from direct impacts rather than from loss of system stability after depauperization. However, to the extent that local communities depend on regional processes, reduction and fragmentation of habitat area will initiate a decline in both regional and local diversity to a lower equilibrium, from which there can be no recovery.

REFERENCES AND NOTES

1. M. E. Soulé and B. A. Wilcox, Eds., *Conservation Biology: An Evolutionary Approach* (Sinauer, Sunderland, MA, 1980); P. R. Ehrlich and A. H. Ehrlich, *Extinction: The Causes and Consequences of the Disappearance of Species* (Random House, New York, 1981); R. Lewin, *Science* **221**, 1168 (1983); E. O. Wilson, *Issues Sci. Technol.* **2**, 20 (1985).
2. International Union for Conservation of Nature and Natural Resources (IUCN), *World Conservation Strategy* (IUCN, Gland, Switzerland, 1980); R. E. Ricklefs, Z. Navch, R. E. Turner, *Environmentalist* **4** (suppl. 8), 1 (1984).
3. A. G. Fischer, *Evolution* **14**, 64 (1960); E. R. Pianka, *Am. Nat.* **100**, 33 (1966).
4. D. R. Strong, Jr., D. Simberloff, L. G. Abele, A. B. Thistle, Eds., *Ecological Communities: Conceptual Issues and the Evidence* (Princeton Univ. Press, Princeton, NJ, 1984).
5. J. Diamond and T. J. Case, Eds., *Community Ecology* (Harper and Row, New York, 1986).
6. M. L. Cody and J. M. Diamond, Eds., *Ecology and Evolution of Communities* (Harvard Univ. Press, Cambridge, 1975).
7. P. R. Grant, *Am. Nat.* **100**, 451 (1966); M. L. Cody, *Competition and the Structure of Bird Communities* (Princeton Univ. Press, Princeton, NJ, 1974); J. M. Diamond, in (6), p. 342; E. R. Pianka, in *Theoretical Ecology*, R. M. May, Ed. (Princeton Univ. Press, Princeton, NJ, ed. 2, 1981); J. H. Brown, *Am. Zool.* **21**, 877 (1981).
8. M. L. Cody, in (6), p. 214.
9. E. F. Connor and D. Simberloff, *Ecology* **60**, 1132 (1979); D. R. Strong, L. A. Szyska, D. Simberloff, *Evolution* **33**, 897 (1979); R. E. Ricklefs and J. Travis, *Auk* **97**, 321 (1980); J. Travis and R. E. Ricklefs, *Oikos* **41**, 434 (1983).
10. R. T. Paine, in *Changing Scenes in the Natural Sciences, 1776-1976*, C. E. Goulden, Ed. (Academy of Natural Sciences, Philadelphia, 1977), p. 245; R. T. Paine, *J. Anim. Ecol.* **49**, 667 (1980); P. K. Dayton, in (4), p. 181.
11. J. H. Connell, *Science* **199**, 1302 (1978); R. G. Thiery, *Biol. Rev. Cambridge Philos. Soc.* **57**, 691 (1982); J. S. Denslow, in *The Ecology of Natural Disturbance and Patch Dynamics*, S. T. A. Pickett and P. S. White, Eds. (Academic Press, New York, 1985), p. 307.
12. S. P. Hubbell, *Science* **203**, 1299 (1979); M. Huston, *Am. Nat.* **113**, 81 (1979); P. L. Chesson, in (5), p. 240; S. P. Hubbell and R. B. Foster, *ibid.*, p. 314.
13. H. A. Mooney, Ed., *Convergent Evolution in Chile and California* (Dowden, Hutchinson & Ross, Stroudsburg, PA, 1977); G. H. Orians and O. T. Solbrig, Eds., *Convergent Evolution in Warm Deserts* (Dowden, Hutchinson & Ross, Stroudsburg, PA, 1977).
14. G. H. Orians and R. T. Paine, in *Coevolution*, D. J. Futuyma and M. Slatkin, Eds. (Sinauer, Sunderland, MA, 1983), p. 431.
15. J. H. Lawton, in (4), p. 67.
16. J. H. Davis, *Publ. Carnegie Inst.* **517**, 303 (1940).
17. J. G. Watson, *Malay. For. Rec.* **6** (1928).
18. H. Shmida, *Isr. J. Bot.* **30**, 105 (1981).
19. H. Recher, *Am. Nat.* **103**, 75 (1969); J. R. Karr and F. C. James, in (6), p. 258; M. L. Cody and H. A. Mooney, *Annu. Rev. Ecol. Syst.* **9**, 265 (1978).
20. D. Schluter, *Ecology* **67**, 1073 (1986).
21. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958); D. B. Quayle, *J. Fish. Res. Board Can.* **21**, 1155 (1964); J. L. Long, *Introduced Birds of the World* (Universe Books, New York, 1981).
22. M. P. Moulton and S. L. Pimm, in (5), p. 80.
23. J. Diamond and T. J. Case, *ibid.*, p. 65.
24. J. W. Terborgh and J. Faaborg, *Am. Nat.* **116**, 178 (1980).
25. H. V. Cornell, *Ecology* **66**, 1247 (1985).
26. ———, *Am. Nat.* **126**, 565 (1985).
27. G. W. Cox and R. E. Ricklefs, *Oikos* **29**, 60 (1977).
28. R. E. Ricklefs and G. W. Cox, *Am. Nat.* **112**, 875 (1978).
29. R. M. May, *Science* **231**, 1451 (1986).
30. J. C. Willis, *Age and Area* (Cambridge Univ. Press, Cambridge, 1922).
31. R. P. McIntosh, *The Background of Ecology: Concept and Theory* (Cambridge Univ. Press, Cambridge, 1985).
32. A. J. Lotka, *Elements of Physical Biology* (Williams and Wilkins, Baltimore, 1925); V. Volterra, in *Animal Ecology*, R. N. Chapman, Ed. (McGraw-Hill, New York, 1926).
33. G. F. Gause, *The Struggle for Existence* (Williams and Wilkins, Baltimore, 1934).
34. D. Lack, *Ibis* **86**, 260 (1944); *Darwin's Finches* (Cambridge Univ. Press, Cambridge, 1947); *Ecological Isolation in Birds* (Harvard Univ. Press, Cambridge, 1971).
35. G. E. Hutchinson, *Cold Spring Harbor Symp. Quant. Biol.* **22**, 415 (1957); *Am. Nat.* **93**, 145 (1959).
36. R. H. MacArthur and R. Levins, *Am. Nat.* **101**, 377 (1967).
37. J. H. Vandermeer, *Annu. Rev. Ecol. Syst.* **3**, 107 (1972); R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, 1973).
38. S. E. Kingsland, *Modeling Nature: Episodes in the History of Population Ecology* (Univ. of Chicago Press, Chicago, 1985).
39. R. M. May and R. H. MacArthur, *Proc. Natl. Acad. Sci. U.S.A.* **69**, 1109 (1972); J. Roughgarden, *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (Macmillan, New York, 1979).
40. K. L. Crowell, *Ecology* **43**, 75 (1962); R. H. MacArthur, J. M. Diamond, J. R. Karr, *ibid.* **53**, 330 (1972); T. J. Case, *ibid.* **56**, 3 (1975).
41. R. H. MacArthur, *Biol. Rev. Cambridge Philos. Soc.* **40**, 510 (1965).
42. ———, *Geographical Ecology: Patterns in the Distribution of Species* (Harper and Row, New York, 1972).
43. ——— and E. O. Wilson, *Evolution* **17**, 373 (1963); *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ, 1967).
44. R. H. MacArthur, *Biol. J. Linn. Soc.* **1**, 19 (1969).
45. T. J. M. Schopf, Ed., *Models in Paleobiology* (Freeman, Cooper, San Francisco, 1972); N. Eldredge and J. Cracraft, *Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology* (Columbia Univ. Press, New York, 1980); G. Nelson and N. Platnik, *Systematics and Biogeography: Cladistics and Vicariance* (Columbia Univ. Press, New York, 1981); G. Nelson and D. E. Rosen, Eds., *Vicariance Biogeography: A Critique* (Columbia Univ. Press, New York, 1981).
46. J. H. Brown and A. C. Gibson, *Biogeography* (Mosby, St. Louis, 1983).
47. R. S. Miller, *Adv. Ecol. Res.* **4**, 1 (1967).
48. E. C. Pielou, *An Introduction to Mathematical Ecology* (Wiley, New York, 1969).
49. M. L. Rosenzweig, in (6), p. 121; S. M. Stanley, *Macroevolution: Pattern and Process* (Freeman, San Francisco, 1979).
50. S. J. McNaughton and L. L. Wolf, *Science* **167**, 131 (1970); I. Hanski, *Oikos* **38**, 210 (1982).
51. E. O. Wilson, *Am. Nat.* **95**, 169 (1961); R. E. Ricklefs and G. W. Cox, *ibid.* **106**, 195 (1972); C. E. Bock and R. E. Ricklefs, *ibid.* **122**, 295 (1983).
52. D. L. Pearson, *Bol. Inf. Cient. Nac.* **13**, 3 (1972); *Publ. Mus. Hist. Nat. Javier Prado Ser. A Zool.* (no. 25), 1 (1974); *Pumapunku* **8**, 50 (1975); *Emu* **75**, 175 (1975); *Treubia* **28**, 157 (1975); in "Preliminary floral and faunal survey, Tambopata reserved zone, Madre de Dios, Peru" (unpublished, 1979).
53. T. F. H. Allen and T. B. Starr, *Hierarchy: Perspectives for Ecological Complexity* (Univ. of Chicago Press, Chicago, 1982).
54. J. Diamond, in (5), p. 3.
55. H. G. Gaugh, Jr., *Multivariate Analysis in Community Ecology* (Cambridge Univ. Press, Cambridge, 1982).
56. E. O. Wilson, *Science* **230**, 1227 (1985); R. E. Ricklefs, *ibid.* **231**, 1057 (1986).
57. I thank R. Burton, H. V. Cornell, J. Diamond, R. Karban, R. T. Paine, S. L. Pimm, J. Roughgarden, and N. Stoyan for comments.