

chapter 13

Overview: Nonequilibrium Community Theories: Chance, Variability, History, and Coexistence

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INTRODUCTION

To what extent are the attributes of natural communities predictable? The development of much ecological theory has proceeded under the assumption that natural communities can be described by models with stable equilibria. The stability of the equilibrium means that historical effects, chance factors, and occasional environmental perturbations play a small role. Because the system heads toward equilibrium, the effect of history disappears, environmental perturbations have no lasting effect, and chance is limited to a role in migration as it affects the arrival of species at a particular locality. Such models have been used to suggest that natural communities do indeed have a highly predictable structure. However, theories based on stable equilibria have been questioned on the grounds that (1) in natural systems the environment is continually changing, often with pronounced effects on populations, and (2) the species in many communities do not appear to have the attributes necessary for stable equilibria in models.

These findings demand that we enquire about

the roles of environmental variability and unstable population dynamics. Does environmental variability make the properties of communities unpredictable, or does it simply lead to different predictions? If a community has nothing like a stable equilibrium point, can it possibly have predictable properties, or will its structure be dominated by chance factors and historical effects? More generally, what sort of theory can community ecology hope to have? These are difficult questions, yet some interesting theoretical and empirical progress has been made, much of which is discussed in this book. It is the purpose of this chapter to review and synthesize this progress.

We begin with a discussion of the assumptions and conclusions of classical competition theory and its extensions. Key assumptions involve the notions of equilibrium and stability, which we define. We then discuss four different theoretical and empirical approaches to the questions above. Some of these approaches yield results that are similar to those of the classical theory and its extensions, yet emphasize rather different features of species such as life history traits and responses

to environmental change. Other approaches give quite different results and suggest that history, chance factors, migration rates, speciation rates, and climatic change all are important influences on community structure.

EQUILIBRIUM THEORIES OF COMMUNITY STRUCTURE

There are three major equilibrium theories of community structure: classical competition theory and two modifications of the classical theory.

Classical Competition Theory

Hutchinson (1959) argued that competition is the predominant process tending to limit species diversity and that competition leads to pattern in community structure. Although the mathematical modeling of competition had begun much earlier, Hutchinson's ideas led to a tremendous interest in the process of competition and to the development of a sophisticated theory of community structure that may be called classical competition theory. Armstrong and McGehee (1980) and Schoener (1982) review the key developments in the evolution of the theory, and Roughgarden (Chapter 30) presents a formulation of the theory.

The essential assumptions of classical competition theory are:

1. The life history characteristics of species can be adequately summarized by the population's per capita growth rate.
2. Deterministic equations can be used to model population growth; in particular, environmental fluctuations can be ignored.
3. The environment is spatially homogeneous, and migration is unimportant.
4. Competition is the only important biological interaction.
5. Coexistence requires a stable equilibrium point.

An early and key prediction of the theory is that at least n limiting resources are required for the coexistence of n species. The presence of n limiting resources is necessary, but not sufficient for the coexistence. Sufficient conditions involve the notion of *limiting similarity*: to coexist, the n

species must be sufficiently dissimilar in their use of the available n or more resources, that is, they must use the available resources in sufficiently dissimilar proportions. Dissimilarity in resource use of animals, when the resources are all types of food, is often expected to be reflected in body size differences, with larger animals concentrating on larger food.

This classical theory naturally became concerned with evolutionary notions and postulated that species in a community would evolve in response to interspecific competitive pressures. Such coevolution, coupled with repeated invasions of new species and extinctions of residents by competitive exclusion, was postulated to yield communities in which the theoretical limits to similarity are approximately achieved, endowing real-world communities with highly predictable properties. Schoener (1982) discusses these results in detail. Roughgarden (Chapter 30) argues that this approach is applicable to communities of Caribbean *Anolis* lizards.

Equilibrium Predation

If a predator is added to the equations of the classical theory, relaxing assumption 4, some of the predictions are changed. Broader limits to similarity of resource use may be possible (Roughgarden and Feldman 1975), and n species may be able to coexist on fewer than n resources. In this case predators may take the place of one or more resources and so may represent limiting factors (Levin 1970). The new theory then predicts that at least n limiting factors are required for the coexistence at equilibrium of n species. The precise predictions depend on the complexity of the predator's behavior (Chapter 29), including the possibility that a single predator may represent more than one limiting factor. Grubb, Buss, and Lubchenco apply this approach to communities of grassland plants and marine sessile invertebrates and plants (Chapters 12, 31, and 32).

Equilibrium Spatial Variation

If species compete for a single resource, but the environment favors different species in different patches, then it is possible for n species to coexist

in a system consisting of at least n patches (Chapter 30). Although a patchy environment, this is still an equilibrium situation: there are n different equilibria for each of the n patches, and these equilibria are stable. Variations on this theme are discussed by Levin (1974), Goh (1980), and Tilman (1982 and Chapter 22). An alternative to spatial variation in the environment is the existence of multiple stable points (Levin 1974), which provide spatially varying equilibria and permit coexistence under circumstances denied by the classical theory.

DEFINITIONS OF NONEQUILIBRIUM AND STABILITY

Equilibrium theories are currently under challenge, but as early as 1961 Hutchinson had proposed the beginnings of an alternative theory. His basic idea was that lack of equilibrium could be an explanation for species diversity. Recognizing that many more phytoplankton species coexist in lakes than can possibly be explained by the classical theory, he applied the logical contrapositive: If equilibrium implies that there can be no more species than limiting resources, the observation of more species than limiting resources implies that the hypothesis of equilibrium must be wrong. Hutchinson then went on to explain the diversity of phytoplankton communities in terms of intermediate-frequency temporal variation.

Hutchinson's idea was not given a great deal of attention, perhaps partly because other equilibrium explanations dominated the intellectual scene and perhaps partly because the mathematical theory of nonequilibrium situations was slow to develop. However, the observation that none of niche differentiation, predation, nor equilibrium spatial variation seems to be an adequate explanation of coexistence in some communities (Chapter 19; Sale 1977; Wiens 1977; Connell 1978; Hubbell 1979, 1980) and the finding of substantial temporal variation in densities, environmental variables, or population parameters (Chapters 9–12, 15–19, 30, 32, 33; Grubb 1977; Wiens 1977; Sale 1977, 1980; Hubbell 1980; Butler and Keough 1981; Keough 1983; Caffey 1985; Swarbrick 1984; Underwood and Denley

1984) argue for a close examination of Hutchinson's suggestion that the structure of some communities might best be explained by nonequilibrium ideas.

What Is a Nonequilibrium Explanation?

Although we have referred to "equilibrium" rather loosely until now, it is essential that we be more precise. In ecology there is no unanimity about the definition of equilibrium. There can be different kinds of equilibria depending on the way a system is modeled and the nature of the solution. A limit cycle can be regarded as an equilibrium and so can the strange attractors associated with chaotic population dynamics. For stochastic models solutions are often sought in terms of an equilibrium probability distribution. In multivariable systems we might expect some variables or composite variables to reach an equilibrium, while others drift about indeterminately. The equilibrium theory of island biogeography is a good example: species number is expected to reach an equilibrium point (or an equilibrium density function, depending on the formulation), while the set of species present is continually changing.

Nevertheless, the classical theory and its extensions involving predation and spatial variation are based almost exclusively on point equilibria at which species abundances remain constant over time. The second extension involves the idea that different spatial locations may have different point equilibria. Thus, at equilibrium there is variation in space in the densities of the species in the community, but the population density at each spatial location remains constant over time. We shall call *nonequilibrium* any situation where species densities do not remain constant over time at each spatial location. Clearly, questions of scale can arise with this definition because, as emphasized by Connell and Sousa (1983) and Murdoch et al. (1985), in the real world fluctuations on very small spatial scales necessarily occur, and such fluctuations on a small spatial scale may average out to yield relatively constant population densities on a larger spatial scale. However, from the point of view of developing theory, one asks whether the fluctuations are an

explanation of a community phenomenon of interest or are incidental to the explanation. If fluctuations or changes in population densities on some spatial scale are an essential part of a theory of some community phenomenon, then we shall refer to the theory as a nonequilibrium theory. From this perspective, "equilibrium island biogeography" is a nonequilibrium theory.

Some of the nonequilibrium theories discussed below depend on a patchy environment in which fluctuations occur on a local spatial scale, but populations may show constancy on a larger spatial scale. Other theories depend on fluctuations or changes in population densities on the largest spatial scales included in the model.

What Is Stability?

All of the equilibrium theories discussed above involve stability of the equilibrium, and in many cases the equilibrium is globally stable. Global stability of the equilibrium means that the system will return to equilibrium following any displacement. Such stability has four important consequences for community theory.

1. *Community conservation.* The community will show little tendency to lose species with time. Indeed, global stability implies that in the absence of external perturbations no loss of species will ever occur.
2. *Community recovery.* The community can recover from events that drive any of the species to low density.
3. *Community assembly.* The community can be built up by immigration of species from outside the system, for combinations of species that are capable of coexisting will increase to their equilibrium values.
4. *Irrelevance of history.* Because the community approaches equilibrium, the effects of past abundances of the species disappear. Note, however, that aspects of history such as the order of arrival of species will generally affect community structure unless species arrive over a time span that is so short that no extinctions have had time to occur. For example, a globally stable predator-prey system will nevertheless fail to form if the predator arrives first.

These aspects of stability may also be shared by the models of nonequilibrium theories. For example, systems that are nonequilibrium locally in space may still have an equilibrium for the total community as a sum of all the local communities, and this equilibrium may be globally stable, carrying with it the four properties listed above. More generally, for many nonequilibrium models the definition of coexistence is *invasibility* (see Chapter 14), which means that each species can increase from low density when all species are present in the community. The idea of invasibility applies to both deterministic and stochastic models of fluctuating populations. It is essentially the property of community recovery, and it implies community conservation and community assembly also. Invasibility often leads to the fourth property, irrelevance of history, because it often implies that the system will approach an equilibrium probability distribution for the abundances of the species in the system. Thus the system "forgets" previous abundances.

Properties 1 to 4 define what we shall call a *stable community*. As we have seen, the concept of a stable community is independent of the concept of equilibrium as defined here in terms of point equilibria. Many of the nonequilibrium theories below are indeed stable community theories. We now consider the different directions that have been taken in the approaches to nonequilibrium theory that are discussed in this book.

NEW THEORETICAL DIRECTIONS

Direction 1: Fluctuations and Continuous Competition

The simplest deviation from the assumptions of the classical theory is relaxation of the requirement of a point equilibrium, while retaining the idea that competition is important and occurs continuously. However, this simple deviation invalidates one of the key predictions of the classical theory. For instance, Armstrong and McGhee (1980) showed that if population dynamics lead intrinsically to limit cycles, then it is possible for many species to coexist on a single limiting resource.

In Armstrong's and McGhee's model the

environment does not vary in time. Instead, fluctuations in population densities and resource levels derive from instability of the model's point equilibrium. A fluctuating environment is more in line with Hutchinson's (1961) ideas about the effects of deviations from equilibrium. Indeed, a fluctuating environment can lead to predictions that differ from the classical theory, in particular, to the prediction that many species can coexist on a single limiting resource (Chapter 14). It is not necessary for fluctuations in resources or environmental variables to reduce the intensity of competition for these deviations from the classical theory to occur. What is important is that fluctuations occur in the competitive rankings of the species. Generally, these fluctuations are assumed to result from stochastic variation in the environment from year to year, but can also result from regular (for example, seasonal) environmental variation.

Temporal variation is the driving force in direction 1 theories. However, it has long been recognized that local populations and local environments may experience fluctuations that are out of phase from place to place. Elaborate community theories have been built on this premise, again with predictions differing substantially from those of the classical theories (Chapter 29; Atkinson and Shorrocks 1981; Chesson 1984, 1985; Comins and Noble 1985). These theories are compatible with continuous and intense interspecific competition, but competitive rankings of the species vary through time and space. The fluctuations in competitive rankings occur in two distinct ways. Fluctuations in migration rates into particular patches may occur, causing fluctuations in the numerical advantage that a species has in a particular patch. Alternatively, the competitive ability of individuals present in a patch may be environmentally dependent and therefore may fluctuate with the changes in the local environment.

Although these theories differ from the equilibrium theories by the absence of point equilibria and although many involve stochastic processes, they are all stable community theories as defined here. Thus, they have the properties of conservation, recovery, assembly, and irrelevance of history that the equilibrium theories possess.

In addition to stability properties, the theories

of direction 1 have a number of other features in common with the equilibrium theories. For instance, none of these theories predicts coexistence of identical species. Although the species may not differ in resource use, they will usually differ in some other sense. They may have different functional responses (different changes in resource capture rates with changes in resource density), as in Armstrong and McGhee (1980) and Hsu et al. (1978), or they may respond differently to temporal variation in the environment. In this sense these new theories may be considered as an enlargement of the classical theory rather than a strict alternative.

Despite similarities to the classical theory, these new theories suggest profound differences in the way communities should be studied. Clearly, the new theories emphasize that dynamic rather than purely static features are extremely important, and they also emphasize such species characteristics as functional responses and life history traits, including dispersal abilities. Indeed, life history characteristics can have profound effects in the presence of environmental fluctuations. For instance, Chesson (Chapter 14) shows that life history characteristics that tend to buffer a species against unfavorable environmental events (for example, long life and iteroparity) will also promote coexistence of competing species in a fluctuating environment. Other life history traits may promote competitive exclusion or have no effect on coexistence. Thus, it is not just the fluctuating environment that is important for coexistence, but the combination of a fluctuating environment and the possession of certain kinds of life history traits.

In the theoretical models of this direction, all members of a guild are assumed to have the same overall kind of life history (for example, are all long-lived and iteroparous). However, in the real world fundamental differences in life histories may well lead to important differences in responses to the environment. For example, they may lead to different time lags for responses to an event that two species find equally favorable or unfavorable. Thus, differences in life history traits, in addition to possession of particular kinds of life history traits, may be important factors in the coexistence of competitors in a variable environment.

These ideas suggest an explanation of coexistence of strongly competing species from very different taxonomic groups, for example, harvester ants, finches, and rodents (Chapter 3). Differences in life history, physiology, and behavior among these different organisms may lead to very different responses to the environment, so that a fluctuating environment promotes coexistence. On the other hand, congeners may have fewer opportunities for differential responses to the environment and therefore may more frequently show differences that lessen competition, for example, the differences in morphology and habitat distributions discussed in Chapters 5, 6, 10, 23, and 30 for closely related species of birds, lizards, or arid-zone plants.

Direction 2: Fluctuations and Discontinuous Density-Dependence or Competition

A second direction of deviation from classical theory emphasizes fluctuations in density or environmental variables as dominant processes. These fluctuations take place on an ecological time scale, and population dynamics may be density-independent much of the time. Strong, Kareiva, Grant, Grubb, and Wiens (Chapters 9–12 and 15) discuss the field evidence that many species fluctuate greatly in abundance, and that these fluctuations are often strongly related to environmental factors and only weakly related to population density or interactions with other species. Strong suggests that density-dependence may become more important at high and possibly very low densities, but that much of the time the dynamics of many species, especially insect species, are little influenced by density and are thus “density-vague.” In this view density-dependence sets the range over which population fluctuations occur, but most of the changes in population density occur in a density-independent manner.

Studies of populations with density-vague dynamics are unlikely to reveal any clear density signals except at the extremes of densities observed in nature. However, if one wishes to explain a population’s mean density, when sampled over time, a study of density-dependence at the population extremes will be necessary. Indeed,

density-dependence and density-independent fluctuations will interact to produce this mean density, as commonly observed in stochastic population models (e.g., May 1973a).

The community consequences of intermittent density-dependence and interspecific competition have been explored in models by a number of authors (Koch 1974, Huston 1979, Chesson 1983). In all cases fluctuations in environmental factors reduce the densities of several potentially competing species to levels where competition is weak and population growth is for a time insensitive to density. Thus both intra- and interspecific competition fluctuate in intensity with time. In all cases coexistence is promoted by these fluctuations. While these models do not explicitly address evolution, Wiens’s verbal model (discussed in Chapters 9 and 10) considers the effects of environmental fluctuations on the intensity of selection and the likelihood of character displacement.

Other community models in which environmental fluctuations can lead to periodic reductions in densities, reducing competition and promoting coexistence, involve a patchy environment (Slatkin 1974, Caswell 1978, Hastings 1980, Hanski 1983). In these models (also reviewed in Chapter 14) local extinctions wrought by environmental factors or predators open up space and may permit species to colonize and grow for a time without the influence of interspecific competition. Potential real-world examples involving forests and sessile marine organisms are discussed by Connell (1978), Fox (1979), and Paine and Vadas (1969).

It was pointed out above that the mean density in a population with density-vague dynamics results from the interaction between density-dependence and density-independent fluctuations. Similarly, properties of communities subject to intermittent competition may result from an interaction between density-independent fluctuations and competitive effects. This is especially clear in the lottery model with vacant space (Chesson 1983), where occasional density-dependence and environmental variation both have profound effects on the relative abundances of the two species. If space limitation is completely eliminated from this model, even slight differences between the two species can lead to the domination of a single species. However, the joint action of occa-

sional space limitation and environmental fluctuations can prevent this result.

The predictions of the nonequilibrium models of this second direction share many similarities with theories based on the absence of point equilibria, (direction 1) and, indeed, much of Chesson's discussion (Chapter 14) deals simultaneously with these two directions. Both directions can be looked upon as enlarging the standard theory. For instance, the patchy environment examples involve organisms doing different things from one another: Some are good dispersers, while others are good competitors. Moreover, in most cases coexistence occurs in the sense of invasibility, as discussed above, and so these theories are mostly stable community theories. Huston's theory is an exception, for coexistence in his theory does not depend on differences between species and it is not a stable community theory. It is discussed in detail under direction 4 below.

Direction 3: Changing Environmental Mean

Directions 1 and 2 consider fluctuations in the environment about some mean value, and generally the mean and the variance of these environmental fluctuations are assumed to be constant over time. However, Davis (Chapter 16) emphasizes that the mean of climatic environmental fluctuations cannot be considered to remain constant over any time scale that may reasonably be considered ecological time. Moreover, both Davis (Chapter 16) and Van Devender (Chapter 17) document community changes in response to changes in mean values of the year-to-year climatic fluctuations. Neither classical competition theory, nor its extensions based on point equilibria and a constant environment, nor the new stable community theories of directions 1 and 2 address this possibility. Does this mean that these theories must fail?

The answer to this question depends on the rate of change of the frequency distribution of the year-to-year environmental fluctuations (the mean and variance of these fluctuations) relative to the speed of community dynamics. Slow changes in this distribution imply that the community can track the predictions of the stable

community theories (assuming that the models on which they are based apply in the short term). For instance, if a stable community theory predicts the mean abundances of a number of species in a community as a function of the mean of the environmental fluctuations, then the actual community means can be expected to follow closely these predicted mean abundances as they change with the mean environment. In particular, present-day populations and communities can be explained on the basis of the environmental fluctuations that are observed at present without recourse to changes in the mean (and variance) of these fluctuations that have occurred historically. A number of different authors have studied such tracking behavior explicitly in simple models (Hubbell 1973; Roughgarden 1975b, 1979; Nisbet and Gurney 1982).

Davis suggests that short-lived organisms may well fit this picture since their population dynamics are fast relative to the rate of change of the mean environment. However, both Davis and Van Devender note that long-lived organisms, such as forest trees, respond to changes in the mean environment with considerable time lag; indeed, Davis notes that some present-day forests appear to be genetically maladapted to current conditions. For such communities, appeal to tracking cannot salvage the stable community theories.

In principle, it is simple to modify the models of the stable community theories—just make the mean of the environmental fluctuations change with time. The analysis of such models is not quite so simple, but more important, the amount of information necessary for a prediction increases enormously because stability property 4 (irrelevance of history) will no longer be true. Since the community is constantly adjusting to new conditions, but never completes the adjustment before conditions change again, past abundances of the species in the community remain relevant to the present abundances and community structure. In particular, the present community cannot be explained simply by studying it today.

Although clearly complex and likely to proceed largely as an empirical endeavor for some time, the study of communities from this direction appears rich and rewarding. For instance the

studies of Davis, Graham, and Van Devender (Chapters 16–18) show that the relationships among different species can change dramatically with climatic change. Life history characteristics and dispersal abilities have a profound influence on the tendency of species to track environmental change. During the Pleistocene forest trees were much poorer trackers of environmental change than herbs or mammals. Individual trees could withstand very long periods of unfavorable weather, sometimes only as below-ground biomass with the ability to recover with the return of more favorable climate. Such species therefore may persist at a locality longer than others, but also may reappear more quickly. Because of such differences in the tracking tendencies of different species, with each successive advance and retreat of the glaciers communities did not simply shift geographically back and forth. Rather, the entire community composition changed. These results suggest that the evolutionary histories of many species are likely to be quite varied.

Direction 4: Slow Competitive Displacement

Hubbell and Foster (Chapter 19) argue that many tropical forest tree species are essentially ecologically identical, having identical resource requirements and responding to the environment in identical ways. If this is true, then only reproductive incompatibility provides an ecological distinction between individuals of different species, and it follows that at any given time the difference in the densities of the two species is just as likely to increase as to decrease, quite independently of the environmental conditions or the population densities of the species. Fluctuations in numbers result simply from the uncertainty in the lives of individuals (within-individual variability; Chesson 1978), and these fluctuations lead to a random walk in population densities with no stabilizing tendencies at all. (Theoretical mean population growth rates are always zero.) Stable community theories clearly do not apply to this scenario. However, Hubbell and Foster show that in any reasonably large forest the time for competitive elimination of a species is long, and this is their explanation of coexistence. For the maintenance of diversity on long time scales, appeal

to speciation and migration is necessary, as discussed below.

Slow competitive elimination has been suggested as an explanation of coexistence in several other settings. Shmida and Ellner (1984) put forward the slow dynamics hypothesis in a deterministic model of species with similar competitive abilities. The similarity in competitive ability and the near equality of intra- and interspecific competition mean that competitive elimination will be slow. In the Hubbell-Foster model there is complete competitive equality in the community, and elimination occurs only as a result of random drift in numbers. It is implicit in both models that competition occurs continuously. On the other hand, Huston's (1979) theory relies on intermittent competition: Periodic reductions in population density reduce the frequency of intense competition and hence the speed at which species are competitively eliminated from the system. Overall similarity in growth rates enhances the opportunities for coexistence.

These theories of long times for extinction and slow competitive elimination satisfy only stability property 1 (community conservation). Thus, they are theories of conservation of the existing species pool and do not address the question of how that pool comes about in the first place. In this sense they are less complete than the stable community theories, which usually explain how a community can be assembled by the invasion of new species and coevolutionary adjustments among residents (Roughgarden 1979 and Chapter 30). In models with zero or near-zero mean growth rates there is no predictable community assembly. Only by chance population fluctuations will a potential invader increase in numbers and become part of the community. Indeed, it is most likely that a rare species will be eliminated quickly, and no species can be regarded as having any degree of permanence.

Communities obeying such slow elimination models may work rather like the neutral gene model in population genetics (see Roughgarden 1979). Given an ecological interpretation, this model says that newly arriving species increase and become part of a community purely by chance. The net number of species in the community is determined by the arrival rate relative to the population size. Species enter the community

as a result of speciation. Alternatively, or in addition, species arrive by migration from surrounding areas, but the ultimate answer is still, of course, speciation. Consistent with these ideas is the finding of Hubbell and Foster that the time for competitive elimination is comparable to the time for speciation.

For the sorts of communities discussed under direction 4, chance and history may be major factors shaping community structure. The time scale of slow elimination and slow input of species via speciation and migration will be on the order of the geological time scale. Past environments or conditions can play an important role in setting up communities in which slow but inevitable elimination occurs. For instance, it may be that the present tropical forests are derived by amalgamation of communities that were isolated during glacial periods (Haffer 1969, Vuilleumier 1971, Livingstone 1975). This isolation presumably led to genetic divergence and allopatric speciation, and so the present diversity of tropical forests may in some measure be a reflection of elevated speciation rates that occurred historically. Indeed, in such systems the actual number of species present will be critically dependent on speciation rates and historical changes in these rates, including climatic and geological events that divide or amalgamate communities. The structure of such systems therefore may well have a strong historical imprint.

CONCLUSIONS

Table 13.1 summarizes the general assumptions and predictions of equilibrium and nonequilibrium theories. It is necessarily an oversimplification and presents only the major emphases of these theories. The table makes no attempt to cover extensions of the theories to incorporate evolution and invasion.

The nonequilibrium theories of directions 1 and 2 differ in the way density-dependence and competition are perceived, but they produce similar results. The two theories can be considered enlargements or generalizations of classical competition theory and its equilibrium extensions, both in the nature of coexistence and in the predictions of the theories. These nonequilibrium theories are stable community theories, as we

have defined them, for coexistence involves the ability to recover from events that take a species to low density. This in turn implies a number of other properties generally associated with stability in equilibrium theories.

Like the equilibrium theories, directions 1 and 2 require that species must differ from one another if they are to coexist. However, the focus of these differences is not on how the species use resources, but on other factors such as fluctuating density-independent mortality. The species may be identical in their use of limiting resources, yet may still coexist because they have different responses to a fluctuating environment. Moreover, these two new directions emphasize that the life history characteristics of species are critically important. Coexistence thus results from the combined effects of fluctuations and the possession of certain kinds of life history traits.

Directions 3 and 4 are different from directions 1 and 2. Direction 3 puts great emphasis on historical factors and casts doubt on other directions, especially directions 1 and 2. Unless communities can be regarded as closely tracking gradual climatic change, we have at present no theory that can adequately handle the concerns of direction 3. Indeed, these concerns suggest that vastly different approaches to community ecology may be necessary. However, the empirical paleoecological approaches of this direction are revealing, and it is clear that they have much to offer to the understanding of communities that exist today. For instance, the suite of species present at a locality today may have a historical imprint that can be uncovered by looking back in time.

Although the major concern of direction 4 is still with coexistence, it is not a stable community theory, and it emphasizes overall similarity of species for their long-term coexistence, not the presence of differences. Species composition of a community is conserved because competitive exclusion is slow, but species composition will show no tendency to recover following a perturbation. Diversity of a community depends critically on rates at which similar species may competitively eliminate one another, relative to migration rates and speciation rates. Indeed, since this direction deals with events taking place on a long time scale, the history of climatic and

Table 13.1 EMPHASES OF DIFFERENT COMMUNITY THEORIES

	Equilibrium theories				New directions			
	Classical competition theory	Predation extension	Spatial variation	Spatial extension	(1) Fluctuations and continuous competition	(2) Fluctuations and discontinuous competition	(3) Changing environmental mean	(4) Slow competitive displacement
Assumptions								
No environmental fluctuations	Yes	Yes	Yes	Yes	No	No	—	Yes/no
Constant mean environment	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes
Spatial homogeneity	Yes	Yes	No	No	Yes/no	Yes/no	—	Yes
Life history traits adequately summarized by growth rates	Yes	Yes	Yes	Yes	No	No	No	Yes
Continuous competition	Yes	Yes	Yes	Yes	Yes	No	—	Yes/no
Predictions: Factors Involved in Coexistence of n species								
At least n resources, limiting factors, or patches	Yes	Yes	Yes	Yes	No	No	—	No
Limits to similarity of resource use	Yes	Yes/no	No	No	No	No	—	No
Differential responses to fluctuating environmental variables or resources	No	No	No	No	Yes	Yes	—	No
Particular kinds of life history traits	No	No	No	No	Yes	Yes	Yes	—
Shapes of functional responses	Yes	Yes	Yes	Yes	Yes	—	No	No
Overall similarity of species	No	No	No	No	No	No	—	Yes
History	No	No	No	No	No	No	Yes	Yes

A dash indicates that no particular emphasis has yet emerged.

Yes/no means that the theory suggests different answers in different circumstances.

geological change may well be very important to its predictions.

In dealing with chance, variability, and history, none of these approaches denies that predictions can be made about the properties of communities. The approaches all suggest a much more complicated world than classical competition theory, but even the largely historical approach of direction 3 allows us to relate community change in a changing environment to the life histories of the constituent species. As emphasized by Hubbell and Foster (Chapter 19), these new approaches to ecological theory may lead to predictions of a different nature, but they do not leave us without predictions.

These theories have already revealed a variety of new patterns that may be expected in guilds of competing species. While competition may be common in nature, as shown by field experiments (Connell 1983, Schoener 1983b), the new theories imply that classical patterns of resource partitioning, habitat segregation, or limitation by predators should not necessarily be expected. There has been much debate over whether patterns in nature do support classical competition theory (Schoener 1984, Simberloff 1984a). However, competition can still be important to community structure, as suggested by the new theories, without producing any of the patterns predicted by the classical theory.

Although our discussion of new theoretical directions has dealt mainly with a single trophic level, the results clearly have important ramifications for entire food webs and cast doubt on the deterministic modeling effort in that area. Indeed, some well-studied food webs have revealed a preponderance of nonequilibrium phenomena (e.g., Dayton 1975a).

Finally, we close with a plea for a pluralistic approach to the problem of diversity and species coexistence. It is quite reasonable to suppose that two species coexist in part because they have some differences in resource use, in part because they have different responses to the environment, and in part because the average net advantage that one species has over another is small, leading to a long competitive elimination time. Techniques that permit a quantitative partitioning of the components of an explanation are important for the study of systems that involve several determining factors, which undoubtedly constitute most of the ecological world.

ACKNOWLEDGMENTS

We are grateful for helpful comments on the manuscript by Joseph Connell, Theresa Dahlem, and Jared Diamond.