REVIEW

The coexistence of species

La coexistencia de especies

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ABSTRACT

This paper is a critical literature review on the topic of the coexistence of similar species within ecological communities. A conceptual framework is provided for dividing coexistence studies and concepts into three distinct time scales. The first six sections deal primarily with ecological-scale, or mesoscale coexistence, defined as coexistence in the classic sense of the competitive exclusion principle and Lotka-Volterra models, wherein interacting populations have had enough time to reach equilibrium. The first four sections briefly review resource partitioning studies and competitive coexistence models, and discuss the relative contributions of, and interaction between empirical and theoretical approaches to the problem of ecological-scale coexistence. The next two sections discuss the importance of biological trade-offs and the role of competition in structuring ecological communities. Based on compelling empirical evidence on both sides of the competition debate, a view of competition's role in structuring communities is proposed wherein the effects of competition are important but incomplete. The next section briefly reviews coexistence as it has been incorporated into habitat selection models, which represents coexistence at a finer time scale generated by the behavioral decisions of individual organisms. Linkages between this type of coexistence and mesoscale coexistence are discussed. Finally, a larger scale of coexistence is explored in which the assumptions of fixed niches, habitats, and species pools in communities are relaxed. This section links global and evolutionary species diversity literature to mesoscale ecological coexistence, focusing on the effects of ecosystem productivity and province size. Factors that govern diversity at large scales may be used to calibrate expectations and make predictions about mesoscale coexistence within particular communities. The study of diversity dynamics at geologic time scales suggests some sort of competitive saturation process, yet community dynamics on the scale of glacial oscillations often appear unsaturated and non-equilibrial. This provides additional support for the idea that competition has an important, but only partial structuring effect on biological communities. Because coexistence is affected by competitive as well as non-competitive influences, both must be incorporated to develop accurate models, make useful predictions, and gain fuller understanding of the coexistence of species within ecological communities.

Key words: coexistence, competition, community structure, resource partitioning, niche.

RESUMEN

Este artículo es una síntesis critica de la literatura sobre la coexistencia de especies similares en comunidades ecológicas. Se propone una estructura conceptual para dividir los estudios y conceptos sobre la coexistencia a tres escalas distintas de tiempo. Las primeras seis secciones se refieren principalmente a la coexistencia a una meso-escala, o escala ecológica, definida como coexistencia en el sentido clásico del principio de exclusión competitiva, y el modelo Lotka-Volterra, en el cual las poblaciones han interactuado por un tiempo suficiente para llegar a un equilibrio. Las primeras cuatro secciones revisan brevemente los estudios de división de recursos y los modelos de coexistencia en la literatura teórica, y discuten las contribuciones relativas de, y la interacción entre los enfoques empíricos y teóricos al estudio de la coexistencia en una meso-escala. En las próximas dos secciones, se considera la importancia de compromisos biológicos y la competencia en la estructuración de comunidades ecológicas. Considerando la fuerte evidencia que presentan ambos bandos del debate sobre la competencia, se propone una organización conceptual de la estructura comunitaria en la cual los efectos de la competencia son importantes pero incompletos. La próxima sección examina la coexistencia a una escala temporal mas fina tal como se ha incorporado en los modelos de selección de hábitat. A esta escala, la dinámica de las interacciones refleja el comportamiento de organismos individuales. Se discute la relación entre la coexistencia a este nivel y la coexistencia a la meso-escala. Finalmente, se explora un nivel de escala más amplio de coexistencia, en el cual las suposiciones de nichos, hábitats, y especies fijos son relajadas. Esta parte enlaza la literatura sobre la diversidad global y evolutiva de especies con la coexistencia ecológica a la meso-escala dentro de comunidades específicas. El estudio de las dinámicas de la diversidad a la escala geológica parece revelar

algún proceso de saturación competitiva. Sin embargo, las dinámicas de comunidades en la escala de oscilaciones glaciales frecuentemente no parecen saturadas ni en equilibrio. Estas observaciones apoyan la idea que el efecto de la competencia sobre la estructura comunitaria es importante pero parcial. Ya que la coexistencia puede ser afectada por fuerzas competitivas a la par que es influenciada por factores no competitivos. Para desarrollar modelos precisos, hacer predicciones útiles, y obtener un entendimiento más completo de la coexistencia de especies dentro de comunidades ecológicas es necesario tomar en cuento ambos tipos de factores.

Palabras clave: coexistencia, competencia, estructura comunitaria, división de recursos, nicho.

INTRODUCTION

The coexistence of similar species in ecological communities is one of the oldest, most studied, and most perplexing problems in ecology. Dating back to theoretical and experimental studies in the early part of this century, the coexistence problem has provided a conceptual basis for a vast and diverse body of research. This research has produced a rich diversity of modeling tools and a wide base of empirical data that have illuminated many aspects of the structure and functioning of ecological communities. Ecological coexistence continues to be a popular research paradigm today, yet the very size and importance of the body of coexistence research have contributed to its current state of disorganization. Today, studies with the word "coexistence" in the title may have almost nothing in common except their conceptual origin. Several different areas of research centered on coexistence are not feeding back to one another. Terms are being used in unclear and heterogeneous ways. Scales of space and time are often not clearly defined.

The goals of this review are twofold. The first is to summarize what we have learned about ecological coexistence to date. This section is a critical review of resource partitioning studies and a more comprehensive review of coexistence theoretical studies, which represent the two major approaches to the ecological coexistence problem. The strengths and limitations of these two approaches are discussed, as well as the relative roles of empiricism and theory in the study of ecological coexistence.

The second goal of this review is to draw together ideas from several other areas of research that have made important contributions to our understanding of ecological coexistence. Studies of habitat selection help us to understand coexistence at a finer scale of space and time, giving us a more mechanistic basis for understanding coexistence at the ecological scale. Studies of global species diversity patterns have revealed how species coexist at larger scales of space and time, illuminating evolutionary constraints that govern coexistence at the ecological scale. Finally, the debate over the role of competition in structuring ecological communities is reviewed, focusing on the implications for the coexistence of species in ecological communities.

Defining ecological coexistence

The problem of ecological coexistence was crystallized by the results of Gause (1934). His laboratory experiments with paramecia showed that when two competitor species were introduced together in a lab culture, one or the other species would always go extinct. This led to "Gause's principle" or, "the competitive exclusion principle" (Hardin 1960) which states that two species with identical niches cannot coexist.

This principle has served as the conceptual basis for a legacy of investigations of ecological coexistence. I define ecological coexistence as coexistence in the sense of Gause. This is the classical coexistence problem as it is most commonly treated in ecological literature. At this scale, we are integrating over many smaller-scale interactions, behaviors, and decisions of individual paramecia, and over the entire test tube. We are studying the system at the point where some sort of ecological equilibrium can potentially have been reached. One or the other species may have been driven extinct through competition. The niches and habitats of species, as well as the species pools of communities or regions are fixed.

Resource partitioning studies

The empirical approach to the ecological coexistence problem is embodied by resource partitioning studies. In the words of Schoener (1974), "The major purpose of resource partitioning studies is to analyze the limits interspecific competition place on the number of species that can stably coexist." The essence of this highly popular research paradigm is to go into nature, find coexisting sets of ecologically-similar species and measure niche differences among them. But how

do you measure niches in nature? G. E. Hutchinson (1957) codified the concept of the niche by describing it as a hypervolume with "n" dimensions (or niche axes) corresponding to the number of biotic and abiotic factors to which species may exhibit differential responses. It is impossible to identify all of the relevant niche axes in a given community or assemblage. Even among those variables that can be identified as important niche axes in certain situations, there are many that are difficult or impossible to measure empirically.

Thus, the reality is that resource partitioning studies do not measure overall niche differences between species. Instead they measure the variation along one, or several environmental or biological axes that represent an unknown fraction of "n". This places an important limitation on the interpretation of resource partitioning studies in the context of ecological coexistence. Lack of observed variation cannot be taken as a rejection of Gause's principle because it does not necessarily mean that species' niches are identical. In fact, where niche differences cannot be found in resource partitioning studies, they are routinely assumed to be manifest on unmeasured niche axes, "...similarity of species along one dimension should imply dissimilarity along another..." (Schoener 1974).

Nonetheless, resource partitioning studies are critically valuable as empirical observations, and have revealed much about patterns of ecological coexistence in nature. Given that resource partitioning studies do not measure all niche axes but merely a subset, it is important to ascertain whether there are biases within this subset. The variables and study systems that ecologists have chosen for resource partitioning studies are not chosen at random. They are biased towards well-known organisms and easily-measured environmental and biological axes. At best, these biases are not correlated with features of community structure. If this is true, then the overall results from these studies are generally representative of a larger biological phenomenon. At worst, ecologists have selected cases that confirm preexisting opinions or that otherwise represent a skewed subset of overall community patterns. We have few tools for separating these two scenarios and obtaining unbiased conclusions.

One way to avoid subjective biases in resource partitioning studies is to seek patterns of a different nature than those sought by the authors of individual data sets. Irene Wishieu (1998) used this approach to study the importance of different mechanisms of community organization among resource partitioning studies published between 1983 and 1993 in the U.S. journal, *Ecology*. She found that two patterns were predominant, each representing about 41% of published cases in which appropriate data were collected. The first is distinct preference organization (MacArthur & Levins 1967) in which each species' realized niche corresponds with the most preferred part of its fundamental niche. The second is shared preference organization (Rosenzweig 1991) in which all species prefer the same region of a niche axis (an overall better, or more productive part). In the latter scenario, realized niches are spread out along the axis according to a hierarchy in which the competitively-superior species occupy the best part of the axis, and the competitively-inferior species are relegated to worse parts of the axis. The weakest competitors must also be the most tolerant of poor conditions in order to survive. The actual prevalence of shared-preference organization may be higher than Wishieu's 41% as this type of organization was twice as common as distinct preference organization among studies that used more discriminatory experimental manipulations. Wishieu was also able to make additional generalizations about when and where to expect shared- vs. distinct-preference community organization. Shared-preference scenarios were more likely to occur along gradual, or quantitative gradients (e.g., temperature) as opposed to disjunct, or qualitative gradients (e.g., specific host species). Shared-preferences were also more prevalent among autotrophs than among heterotrophs, and among vertebrates than among invertebrates.

Despite important limitations, resource partitioning studies have the advantage of biological reality. Ecologists have documented ecological segregation of coexisting species along many different environmental and biological gradients. By considering the results of many resource partitioning studies together, we have identified patterns in nature which point to some generalities about ecological coexistence mechanisms (Schoener 1974, Wishieu 1998).

Two widespread practices within studies of resource partitioning indicate that these empirical approaches may only have scratched the surface of the array of niche axes that are partitioned among species in nature. The first is the use of body size as a niche axis (Wilson 1975, Basset 1995). This variable is not really a niche axis because it does not describe a relationship between an organism and its environment. It is rather a black box with an array of different niche axes implicitly subsumed within it. Various authors have explained the ecological significance of body size as a function of birth and death rates (Ziv 1998), resource harvesting efficiencies

(Reichman & Roberts 1994), metabolic requirements (Wilson 1975), home range size (Basset 1995), or other factors that vary with body size. In essence, the variable of body size is used as a proxy for the myriad environmental and biological variables that scale exponentially with body size (Peters 1983, Calder 1984). Because of the scaling effect, the ecologically-relevant variables, themselves, correspond well with body size and may include any factor that scales in this way. Examples of apparent resource partitioning by body size are prevalent in the literature, including well-known patterns of constant size ratios among ecologically-similar coexisting species (Hutchinson 1959, Horn & May 1977). This suggests that many of the niche axes that provide a basis for niche separation in nature are not commonly measured in resource partitioning studies. Many of these would be impossible to measure directly.

The other black box in resource partitioning studies is the use of taxonomically-circumscribed sets of species (e.g., Johnson 1986, Fletcher & Underwood 1987, Dickman 1988). In essence, this widespread practice represents the use of shared ancestry as a proxy for ecological similarity (Azofsky 1996). Using taxonomically-circumscribed sets of species in resource partitioning studies makes the assumption that interspecific competition should be greater among closely-related species than among distantly related species, even in the absence of any a priori ecological explanation for this difference. This assumption has often been confirmed when tested (Thompson et al. 1991 but see Jaksic et al. 1993 for a counter example). The actual mechanism behind this pattern is the set of unknown physiological, behavioral, and ecological differences that provide niche segregation between taxonomically-distant species. These differences constitute niche axes that are difficult to identify and/or measure but that account for ecological coexistence nonetheless.

Coexistence theoretical studies

The multi-dimensional, unmeasurable nature of ecological niches is not the only problem confronting empirical studies of coexistence. It is also difficult to measure other important attributes such as the fitness functions of individuals along niche axes, or the fundamental vs. actual preferences of individuals. One way to get around these problems is to analyze coexistence using idealized mathematical models. This has permitted ecologists to ask sophisticated questions regarding ecological coexistence that have been out of

the reach of empiricists. These questions include: What are the limits to the ecological similarity of coexisting species? How is ecological coexistence affected by such factors as different carrying capacities, different resource utilization functions, different levels of variability or environmental patchiness? A variety of mathematical approaches have made substantial contributions to our understanding of ecological coexistence.

The Lotka-Volterra model and analogues

The largest category among mathematical approaches to ecological coexistence includes studies that model the dynamics of systems of ordinary differential equations. The vast majority of such studies have used the Lotka-Volterra model (eq. 1).

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \sum\limits_{j \neq i}^{n} \alpha_{ij} N_j}{K_i} \right) \quad (1)$$

This equation models the growth of competing species (change in population size, N for species i through j in time) as functions of the species' intrinsic rates of growth (r), carrying capacities (K) and competitive effects on one another (α). In such studies, the criterion for coexistence of species is that they increase when rare. Classical studies of coexistence theory are primarily concerned with describing the mathematical dynamics of this system with various values, behaviors, and alternative forms of the parameters, r, K, and α.

Competitive coexistence has been shown to result from interspecific differences in any of these parameters (May 1974, Abrams 1975, 1983, Roughgarden & Feldman 1975, Armstrong & McGehee 1980). In general, coexistence is facilitated in these models when parameter values exhibit density-dependent behavior (Abrams 1975, Roughgarden & Feldman 1975, Armstrong & McGehee 1980), or different patterns of variability (Abrams 1976, Chesson & Warner 1981, Turelli 1978, 1981, Levins 1979).

One limitation of Lotka-Volterra-based studies of ecological coexistence is that many have analyzed only the behavior of the system at equilibrium. Some theoreticians have shown increased possibilities for competitive coexistence in nonequilibrial conditions (Armstrong & McGehee 1980, Caswell 1982).

Another limitation is that most Lotka-Volterra modelers assume that all species have identically-shaped resource utilization curves. Several theoreticians have shown that competitive coexistence is facilitated when interacting species have differently-shaped curves (Roughgarden 1974). Another assumption in many Lotka-Volterra competitive coexistence studies is that niches differ only along a single niche axis. The incorporation of multi-dimensional variation in niches also results in increased opportunities for competitive coexistence (MacArthur & Levins 1967, May 1974, Pianka 1974).

Still other dynamical modeling studies of competitive coexistence have used analogues to the Lotka-Volterra model and have shown additional theoretical possibilities for competitive coexistence (Abrams 1975, Turelli 1978, Armstrong & McGehee 1980).

The Lotka-Volterra-based approach to ecological coexistence problems saw its greatest period of popularity during the 1970's, at which time it was one of the favorite subjects of MacArthur, May, Levins, and many other ecological theoreticians. This began with the influential, "limiting similarity" paper of MacArthur & Levins (1967), who studied the equilibrial behavior of a Lotka-Volterra system with species showing distinct preference organization along a single niche axis. They achieved a result consistent with Gause's principle, that ecologically-identical species could not coexist. They then went a step further to attempt to describe the limits to the ecological similarity of coexisting competitors mathematically. This paper was a stimulus for a multitude of subsequent papers dealing with the theory of limiting similarity, and with the conditions for competitive coexistence in general. Abrams reviewed the area of limiting similarity theory in 1983 and concluded that it had generally been unsuccessful. He noted that the limiting similarity relationship was highly sensitive to the structure of parameters, resource utilization curves, and relationships in the models (Abrams 1983). Rosenzweig has described limiting similarity theory as, "...quicksand that trapped the energies of community ecologists for more than ten years and nearly killed the sub-discipline" (Rosenzweig 1995). The virtual extinction of studies published in the tradition of limiting similarity theory after Abrams' review is a testament to the fact that this area was generally deemed to be unfruitful by ecologists.

The fall of limiting similarity theory contains an important lesson that applies to the role of mathematical approaches to the ecological co-existence problem, and within the field of ecology in general. The original conclusion of MacArthur & Levins (1967) was that the means of the species' resource utilization curves had to be separated by a minimum distance (d) of the standard deviation of the curves (w). This particular result was highly sensitive to model structure such that, "The limiting similarity relationship (could) be affected by most aspects of the population biology of a group of interacting species." (Abrams 1983). This rendered the d>w result biologically irrelevant, yet we have learned much about the factors that influence the qualitative behavior of competitive coexistence dynamics from MacArthur and Levins', and related models. The principal error of limiting similarity theory was merely that it attempted to push the interpretation of a mathematical model beyond a justifiable level of resolution. Limiting similarity theoreticians were not necessarily using flawed models but were essentially reading their results out to too many significant digits given the biological precision of the parameters and fitness functions in Lotka-Volterra models.

Lotka-Volterra model with metapopulation dynamics

While limiting similarity studies and studies of Lotka-Volterra-based models in general have declined in recent decades, one area that has lived on, and even flourished since Abrams' review, is the study of Lotka-Volterra competition models with patchiness. The idea that colonization and extinction dynamics of patches could promote the coexistence of competitors was first conceptualized in Hutchinson's notion of a fugitive species (Hutchinson 1951). A fugitive species always loses out in in-patch competition, but its proficiency at colonizing new patches prevents it from being competitively excluded from the entire matrix of patches, so long as the subpopulations (within single patches) of the competitive dominant species have a non-trivial probability of going extinct. The colonization of new patches allows the fugitive species to continually "flee" from competition as long as the landscape contains some unoccupied patches. This sort of coexistence depends on a trade-off between competitive ability and dispersal ability (Tilman 1994).

Mathematical representations of this idea began with an extension of Levins' original metapopulation model (Levins 1969) which included two species competition as in equations 2a and b from Hastings (1980).

$$\frac{dp_1}{dt} = c_1 p_1 (1 - p_1) - m_1 p_1 \qquad (2a)$$

$$\frac{dp_2}{dt} = c_2 p_2 (1 - p_1 - p_2) - m_2 p_2 - c_1 p_1 p_2 \qquad (2b)$$

In this model, p_i is the proportion of patches occupied by species, i, c is its rate of colonizing new patches, and m is the rate at which local populations (in a single patch) go extinct. This model incorporates a competitive hierarchy among species. For the competitively-dominant species, growth depends only on its own rates of c and p, whereas the growth of the competitively-inferior (fugitive) species depends on the c's and p's of both itself, and of the dominant species, since the dominant can always exclude the inferior species from a given patch.

Versions of this model were used to develop the idea of regional coexistence of species (Cohen 1970, Levins & Culver 1971, Horn & MacArthur 1972, Slatkin 1974, Hanski & Ranta 1983). Slatkin (1974) showed that with certain assumptions, the equations used by Levins and Culver and Horn and MacArthur were, "...formally the same as the Lotka-Volterra competition equations, and the criteria for coexistence and exclusion (could) be written down directly." Slatkin also relaxed the assumption of independent distributions of species and extended the results of this model to non-equilibrial solutions.

A number of studies have developed the idea of regional coexistence further. Several authors have focused on the evolution of different dispersal strategies adapted to particular spatio-temporal mosaics of patches (Levin et al. 1984, Cohen & Levin 1991). Hanski (1981) analyzed the effects of predation on the coexistence of competitors in a metapopulation. Hanski and Zhang (1993) included several costs of migration and showed that increased dispersal in such models was not always beneficial. Tilman (1994) showed that coexistence was possible for an unlimited number of species in a metapopulation model as long as the dispersal rate of each successive competitively-inferior species increased by an amount proportional to the abundance of the competitively superior species (a new limiting similarity relationship). He also showed that increased longevity of species had the same effect as increased colonization rates in allowing a species to coexist with a competitive dominant.

Recently, several studies have applied metapopulation Lotka-Volterra coexistence models to situations with disturbance, habitat destruction, and fragmentation. These studies have generally shown that increased disturbance and fragmentation in metapopulations favor the fugitive species relative to the competitive dominants (Nee & May 1992, Dytham 1994, Tilman et al. 1994, Moilanen & Hanski 1995, Tilman et al. 1997, but see McCarthy et al. 1997). In general, these influences favor fugitives by increasing the importance of colonization relative to in-patch competition. Disturbance and/or fragmentation can elevate local extinction probabilities, which produces more patch vacancies for fugitives. Fragmentation and habitat destruction raise inter-patch distances, putting an additional premium on dispersal. The result is, "...a community composed of more rapidly dispersing, weedy species." (Tilman et al. 1997). Moilanen and Hanski (1995) looked at particular spatial distributions of patches and showed that for a given level of habitat destruction, the competitive dominants do best if patches are aggregated rather than highly interspersed. This is because patch aggregation maintains short interpatch dispersal distances, which enable even the less-dispersive species to recolonize patches.

Consumer-resource theory

In the Lotka-Volterra model, interspecific competition is represented by the α parameter. But what does α represent? What mechanisms are really driving the competition? Some modelers were unsatisfied with this "black box" representation of competition. They described to the Lotka-Volterra model as "phenomenological" and sought a more "mechanistic" model to explicitly represent competition (Tilman 1980, 1987). Tilman (1980) invented such a class of models, known as consumer-resource theory, which has become the basis for a substantial body of recent work on competitive coexistence. Tilman noted that in classical Lotka-Volterra studies, coexistence was often explained based on implicit relationships between consumers and resources, i.e., that the resources are what the competitors exploit, partition, etc. Tilman's consumer-resource model explicitly includes the dynamics of both the consumers and the resources. Consumer species compete not through a mysterious parameter, but directly, through the consumption of common resources.

Graphical representations have provided a useful tool for interpreting the criteria for coexistence of competing consumers in consumer-resource models. Zero net growth isoclines (ZNGI's) can be plotted for each consumer species in a two-dimensional state space defined by

the density of two different resources (one on each axis). Points on the ZNGI represent resource levels when the consumer species is at equilibrium (zero net growth). The consumption vector for a consumer species represents the amount of each resource eaten by that consumer. Analyses have shown that in order for two consumers to coexist, two conditions must be met. First, their ZNGI's must cross. Second, the slope of each species' ZNGI must be shallower than that of the other with respect to the resource that forms the larger component of that species' consumption vector. In other words, each species must consume more of the resource that is more limiting to its own growth. Any intersection point between isoclines is an equilibrium point with both species coexisting, but the equilibrium is only stable if the second condition is met (Tilman 1980, Vincent et al. 1996).

The primary advantage of consumer-resource theory in modeling ecological coexistence is its explicit, mechanistic treatment of resource-based competition. This has made consumer-resource theory especially useful for exploring community dynamics with different types of resources. For example, some have modeled the coexistence of consumers on essential (nonsubstitutable) vs. substitutable resources (Tilman 1980, Abrams 88, Vincent et al. 1996). Consumer-resource theory has also been extended to coexistence problems with varying productivity and consumer functional responses (Abrams 88), spatially separate-vs. intermixed resources (Vincent et al. 1996), communities with guild structure (Morris & Knight 1996), and optimally-foraging consumers (Vincent et al. 1996).

Consumer-resource models have more parameters and variables per species than basic, Lotka-Volterra models of competition. In general, consumer-resource models added a level of complexity by including explicit resource dynamics. Certain advantages were thereby gained, but only at the cost of decreased analytical tractability, simplicity, and flexibility. As a result, consumer-resource models have not been applied to as wide a variety of problems as have Lotka-Volterra models. For example, no one has yet modeled the coexistence of more than two species in a consumer-resource model. Authors who have sought to extend consumer-resource theory to multi-species problems such as productivity-diversity relationships (Abrams 1988), and community composition (Morris & Knight 1996), have done so strictly by extrapolation from two-species coexistence scenarios. The added complexity of consumer-resource theory is also the likely explanation for why these models have not been success-

fully extended to spatial, or non-equilibrium problems, and for why Lotka-Volterra models continue to be the model of choice in metapopulation coexistence studies.

Keystone predators and food-web theory

In the midst of the limiting similarity theory era, Levin (1970) published a paper in which he noted that competitive exclusion could result not only from resource-based competition, but from competitive dynamics with respect to any limiting factor, including predation. He cited Paine's (1966) famous demonstration of predator-mediated competitive coexistence as an example. He included a diagram that showed how consumer dynamics were linked to the dynamics of both resources and predators in an ecosystem. This gave rise to food-web models, which have provided another important mathematical tool for studying competitive coexistence dynamics.

Food web models are essentially another outgrowth of Lotka-Volterra models that can get even more mechanistic than consumer-resource theory. These models include separate equations representing the dynamics of a top predator, one or two consumer (=prey) species, and a resource. Coexistence criteria parallel those of consumer resource models. ZNGI's are plotted for consumer species not in resource-resource phase space, but in resource-predator phase space. As in consumer-resource theory, coexistence requires that the ZNGI's cross. There is also a similar requirement regarding the relative impacts and slopes of the ZNGI's (see discussion of consumer-resource theory). In essence, the predators must rely more heavily on the species that is the better resource exploiter (lower ZNGI intercept on resource axis) (Holt et al. 1994, McPeek 1996). This amounts to another trade-off criterion for coexistence (see later section on trade-offs).

Food-web theory has provided new insights into ecological coexistence primarily by virtue of its explicit, mechanistic treatment of competition. This competition can be either resource-based, as in consumer-resource theory, or predator-based. Predator-mediated competition causes competing prey species to divide niche space not along resource utilization dimensions, but along predator avoidance dimensions. This is an important innovation of food-web models, and has provided the basis for a great deal of overlap between food-web models and predator-prey theory (see references in Vance 1978, Holt et al. 1994, Liebold 1996). In particular, most food-web models have focused on the keystone predator effect, i.e., they

assume that a single predator species can prey on all species of consumer (Vance 1978, Holt et al. 1994, Liebold 1996). These models have sometimes left out explicit resource dynamics altogether and replaced them with parameters that govern consumer growth as in the Lotka-Volterra model (Vance 1978, Holt et al. 1994).

As a consequence of the complexity of food-web models, the analytical and flexibility constraints on these models are even more severe than for consumer-resource models. The most simple food-web models typically have around 10 parameters (8 in Liebold 1996, 12 in Holt et al. 1994 and McPeek 1996). Coexistence studies have been limited to equilibrial, two species, consumer species, and fixed-parameter cases. McPeek (1996) incorporated spatial variability by studying the requisites for species to be able to coexist in multiple, spatially-separate habitat types (habitat generalists). This is a simplified and less-explicit treatment of spatial heterogeneity than in other coexistence modeling approaches. Liebold (1996) extended the results of a food web model to spatially-heterogeneous cases and the productivity-diversity relationship, but this was based on somewhat speculative extrapolation rather than a rigorous treatment of these scenarios in his model.

Spatially more sophisticated models

All of the classes of ecological coexistence models discussed up until this point are based on systems of ordinary differential equations (ODE). As such, they all share a number of constraints and limitations common to this type of modeling approach. Such models are only analytically tractable with a small number of variables and parameters. While simplicity in modeling has its advantages, there are some cases where additional complexity is desirable. ODE models are not spatially explicit. As a result, treatment of spatial effects and heterogeneity has been limited (Eckshmitt & Breckling 1994, but see metapopulation section). Many of our ideas on community structure and niche evolution involve spatial heterogeneity. A variety of alternative modeling approaches have provided some more spatially sophisticated insights into the issue of ecological coexistence.

Partial differential equations (PDE) allow modelers to incorporate spatial and temporal dynamics simultaneously. This has provided a way to treat spatial effects more extensively than in ODE models of ecological coexistence (Holmes et al. 1994). Most PDE coexistence models have

used a diffusion system to represent spatial movements in a Lotka-Volterra-based competitive model (e.g., Merino 1996). Several such models have shown that competitive coexistence is facilitated by variation in dispersal rates among species (Shigesada & Roughgarden 1982, Schat et al. 1996). In a model by Mimura et al. (1991), diffusion movements in a two-island system produced spatial segregation of competitors leading to coexistence in the absence of any interspecific differences.

Others have incorporated more realistic movement patterns, especially convection and intraspecific avoidance (Namba 1989) or attraction. Intraspecific attraction produces aggregation effects in PDE models, which can allow competitors to coexist even in homogeneous environments (Britton 1989, Holmes et al 1994). This parallels empirical studies that have suggested that intraspecific aggregation promotes coexistence in *Drosophila* communities (Shorrocks & Sevenster 1995), insect communities associated with dung pads and carcasses (Hanski & Cambefort 1991), and possibly other cases. The principal limitation of PDE models is that they are analytically difficult. As a result, models are less manipulable and the results are less generalizable than in ODE models.

Another way that ecologists have incorporated spatial processes in studies of competitive coexistence is with cellular automaton models. These models are comprised of grids of cells that define space explicitly. Each cell represents a population or patch that is described by a particular state at any given time unit. The cells in these models shift among different states discretely in time according to a set of uniform and constant rules (Halley et al. 1994). The models are run through simulations consisting of various numbers of time steps, and then the resulting distribution of states in the model is analyzed. Coexistence is assessed based on species' continued persistence at the end of simulations.

Competition has been incorporated into such models in several ways. Some have included discrete versions (difference equations) of the Lotka-Volterra system as an interaction rule in the model (Dytham & Shorrocks 1992, Comins & Hassell 1996). Others have simply specified that one species can always exclude another from a cell (Halley et al. 1994). Ziv (1998) included explicit competition for common resources (as in consumer-resource theory) into his model.

Many studies have explained competitive coexistence in these models as a result of self-organizing patterns of spatial aggregation that develop (Dytham & Shorrocks 1992, Halley et al. 1994,

Comins & Hassell 1996). Dytham & Shorrocks (1992) showed that such aggregation could result from an intraspecific attraction probability, but other models have produced such aggregations and competitive coexistence even in the absence of intraspecific attraction, and in homogeneous environments (Halley et al. 1994, Comins & Hassell 1996).

Dytham (1994) used a cellular automaton model to reproduce and extend the results of Nee & May's (1992) Lotka-Volterra metapopulation model, which looked at the effects of habitat destruction and fragmentation on competitive coexistence. Like Nee & May, he showed that habitat destruction and fragmentation favor dispersive species relative to sedentary species (fugitives and competitive dominants, respectively, see earlier section). Dytham's model further showed that the sedentary species were least depressed in parts of the "world" that contained aggregations of remaining intact habitat patches. This is consistent with the result of Moilanen & Hanski's (1995) metapopulation model. Dytham also showed that in certain parts of the world, patches of intact, suitable habitat could become isolated and remain uninhabited by any species.

Cellular automaton models do not have the analytical difficulties of many other types of models, and are particularly useful for studying spatial processes. However, this method has its own limitations and constraints. Some have noted that interaction rules are usually less realistic than in differential equation models (Halley et al. 1994, but see Ziv 1998). An important constraint is that rules are uniform over the grid and constant through time. This makes it difficult to incorporate density dependent effects, or varied and nonlinear functional responses. Another difficulty with cellular automaton models is the inherent complexity of being spatially explicit. Results are often sensitive to the size and shape of the grid of cells (Molofsky 1994). Complicated spatial patterns are often interpreted qualitatively for their resemblance to natural patterns (Halley et al. 1994) rather than being analytically compared with quantitative predictions.

Other modeling approaches

The most complex models of ecological coexistence are individual-based simulation models. Such models are similar to cellular automaton models in that they define states and interaction rules, and then run simulations consisting of a number of discrete time steps. One difference is that individual-based models may (e.g., van der

Laan et al. 1995), or may not (e.g., Hansson 1995) be spatially-explicit. The primary distinction of individual-based models is their high level of biological detail. They model states and interactions among individuals, whereas the smallest unit in a cellular automaton model is usually a subpopulation. The fine resolution of individual-based models permits the incorporation of detailed life-history information. Reichman & Roberts (1994), used such a model to study the coexistence of three rodent species on seed patches of different densities based on optimal foraging behaviors and allometrically-scaling metabolic requirements of differently-sized individuals.

One class of simulation models has paralleled consumer-resource theory by modeling the coexistence of multiple consumer species competing for common resources that obey their own, explicit dynamics. These have explored consumer coexistence with varying time scales of consumers and resources (Loreau 1992), varying underground nutrient mixing processes (Huston & DeAngelis 1994), and source-sink resource dynamics (Loreau & DeAngelis 1997). Van der Laan et al. (1995) included a dazzling amount of life-history information into a model of herbivore-mediated competition between two species of oak trees. Hansson (1995) used individual-based simulation models to study competitive niche shifts in communities of competing predator species and their prey. He used 288 different models to represent all possible permutations of several different numbers of predator and prey species, competition intensities, and rates and regulation of prey growth.

Individual-based models are the empiricist's dream and the modeler's nightmare. They are the former because they can incorporate lots of ecological detail, especially life-history information and spatial effects that have been difficult to handle in other types of models. They are the latter because the high complexity largely defeats the primary purpose of ecological modeling: to understand the processes and mechanisms that underlie ecological patterns. With so many different variables and relationships influencing the outcomes of individual-based simulations, it is hard to disentangle the effects of each one. Few tools exist for quantitatively analyzing the outputs of such models. Some individual-based models have included smaller amounts of detail and have been an effective tool for studying processes that are hard to include in other types of models (e.g., Reichman & Roberts 1994). More detailed models may be useful tools for specific management applications but their generality is limited.

Tanner et al. (1994) used a projection matrix model to study ecological coexistence. The parameters in the matrix were constructed empirically from an extensive data set of transition probabilities to and from each of ten species of coral in the Great Barrier Reef. They ran the model through discrete time steps that produced successional dynamics. They observed patterns analogous to fugitive species coexistence, with short-lived, good colonists peaking in abundance early after disturbance and longer-lived, poor colonists exhibiting a more gradual rise, peaking when the community appeared to reach an equilibrium. However, matrix models assume that all transitions between species are first-order Markovian processes. In other words, they assume that the probability of a given species appearing at a given point is strictly a function of the previous occupant. This makes such a model a powerful tool for studying successional dynamics (see references in Tanner et al. 1994), where transitions may obey this assumption, but makes it difficult to apply to ecological coexistence problems which may include zero-order replacement (random) or higher order interactions such as density dependence, or priority effects (Tanner et al. 1994).

Another modeling approach that has recently been applied to ecological coexistence is game theory. Such models start with a fitness-generating function (G-function) which defines the dynamics of population density as affected by various parameters. Examples could include any of the ODE competitive coexistence models discussed earlier. Rather than assume that parameter values are fixed, game theory treats these parameters as "strategies" that are permitted to evolve, and that approach values at which fitness is maximized (Vincent & Vincent 1996). I discuss game-theoretical models of coexistence here because they are theoretical models of coexistence, and because they incorporate an ecological-scale model such as a Lotka-Volterra or consumer-resource model within it. Game theoretical models are a bit out of place in this section, however, because they have extended mathematical models to the problem of coexistence at a larger time scale. They model shifting life-history traits, behaviors, or niches in evolutionary time.

Vincent & Vincent (1996) used a consumer-resource model as a G- function in such a model to study the coexistence of plants with different root-shoot allocation strategies. Their result was that when evolution proceeded to equilibrium, there was only a single species that possessed the optimum root-shoot allocation strategy. They showed that the G-function would have to have humps (multiple peaks) in order to achieve multispecies coexistence. They suggested that such non-linearities in G-functions would represent complex interactions between strategy parameters and other parameters. One example of such an interaction would be a trade-off between the strategy parameter and some other life history parameter (see later section on trade-offs).

In one sense, game theory has provided an important innovation to coexistence theory by extending mathematical models to larger time scales. On the other hand, looking at the problem at this scale has served as a humbling lesson regarding the inadequacy of our ecological-scale models for dealing with larger-scale coexistence problems. There is no current theoretical or empirical basis for constructing realistic G-functions that would incorporate multiple humps to allow for the coexistence of multiple species (strategies). Even if such a function could be constructed it would not be adequate for modeling niche evolution because such functions are not fixed in evolutionary time. The processes of coevolution and environmental change should cause changes not only in the parameter values, but in the very fitness optima that those parameter values are approaching as well.

Empiricism, mathematics and coexistence

One curious development within the field of ecological coexistence research is the virtual lack of interchange between empirical and theoretical studies (Abrams 1983, but see Schoener 1974). On the one hand, empiricists cannot seem to interest theoreticians in their results. Perhaps because logistical constraints prevent them from measuring variables such as total niche similarity, competition, and resource overlap (Abrams 1983). On the other hand, theoreticians cannot convince the empiricists that their results are biologically relevant because of the simplifying assumptions that are necessary for their models (Simberloff 1983). Indeed, both sides have powerful advantages as well as strong limitations, and both have taught us much about species coexistence. However, the chasm between these two conceptually linked areas is troubling. There is much to be gained by identifying possible linkages between these two approaches.

Abrams' frustration with the sensitivity of competitive coexistence models to the structure of the competition coefficient led him to remark, "...it would seem to be more useful to explain the differences in niche overlap in different commu-

nities rather than to look for universal patterns."
(Abrams 1975). Although made by a theoreti-
cian, this statement appears to rationalize an
exclusively empirical approach to the coexist-
ence problem, devoid of general theoretical ex-
planation. However, such an approach would
not allow us to understand the mechanisms and
processes that underlie empirical patterns. Eco-
logical theories are a necessary complement to
empirical studies of ecological coexistence, yet
resource partitioning studies have frequently
ignored coexistence theoretical literature. Our
understanding of ecological coexistence would
be enhanced if resource partitioning studies were
more informed by coexistence theory. Such
theory can profitably be used to develop hypoth-
eses and predictions for resource partitioning
studies, and to interpret the meaning of empiri-
cal results.

Mathematical models must make simplifying
assumptions to achieve any level of tractability
and generality, yet ecological dynamics are nota-
bly complex relative to systems in other scientific
disciplines. The hope for mathematical approaches
to ecological coexistence rests on the tendency
for ecological systems to sometimes exhibit low-
dimensional dynamics. This result is produced
when one or a few ecological parameters exert
such a strong influence on system dynamics at a
particular scale, or in a particular region of phase
space, that the effects of the myriad variables and
parameters that influence ecological dynamics at
other spatio-temporal scales or in other regions
are swamped out. These other sources of varia-
tion can then be ignored without sacrificing too
much accuracy. Mathematical models of eco-
logical coexistence have proliferated despite the
often complex and high-dimensional behavior of
ecological communities. One possible explana-
tion for this is, "...the dubious but nonetheless
popular cachet of legitimacy provided by math-
ematics to an idea..." (Salt 1983) which may have
permitted serious consideration of many models
with little relevance to actual ecological dynam-
ics. For whatever reason, theoretical ecologists
have often treated the connection between their
models and the dynamics of actual communities
carelessly. Finding low-dimensional behavior in
ecological systems is a difficult challenge and
must be taken seriously by theoreticians in order
to design models that offer realistic theoretical
explanations of ecological coexistence. This is
where empirical studies of coexistence have much
to contribute. In essence, empirical pattern can
inform theory about which simplifying assump-
tions can be made without sacrificing too much
biological accuracy.

Biological trade-offs as coexistence mechanisms

In recent studies of ecological coexistence, trade-
offs have increasingly been cited as "coexistence
mechanisms" (Shmida & Ellner 1984, Brown
1989, Chesson 1991, Tilman 1994, Rosenzweig
1995, McPeek 1996). Rosenzweig (1995) de-
scribed the essence of trade-offs in the "trade-off
principle" which states that, "...phenotypes excel
at most functions by losing the ability to perform
other functions well." Earlier, regional coexist-
ence was explained based on a trade-off between
competitive ability and dispersal. This particular
trade-off is best represented by the notion of a
weed. Weedy, or pioneer species have sacrificed
competitive ability in order to become more mo-
bile (Connell & Slatyer 1977, Shmida & Ellner
1984). The reason for this trade-off is that physi-
ological investments in dispersal (e.g., seed pro-
duction) usually come at the cost of investment in
structures for local exploitation (e.g., roots) and
vice versa (See Tilman 1994 for an example from
prairie grasses). This trade-off ensures that the
species who are the best at one thing (e.g., disper-
sal) will be the worst at the other (e.g., in-patch
exploitation). The result is that the trade-off
functions as a niche axis or coexistence mecha-
nism that presents opportunities for resource par-
titioning among competitors.

The dispersal-exploitation relationship is only
one example of how a biological trade-off can
serve as a coexistence mechanism. Brown sug-
gested three other trade-offs that functioned as
coexistence mechanisms in his desert rodent as-
semblages (Brown 1989). Each of these trade-
offs promoted the coexistence of one or more
rodent species by ensuring that there was a part of
niche space in which each species was the most
efficient forager.

Trade-offs are evident in mechanistic models
of competitive coexistence. In such models, co-
existence requires that ZNGI's cross, which is
equivalent to the species with the lower intercept
having the shallower slope. In the case of food-
web models, this means that the species that is the
better resource exploiter is also more vulnerable
to the predator. In essence, coexistence in these
models requires that there be a trade-off between
resource exploitation ability and predator avoid-
ance. The general importance of trade-offs as
coexistence mechanisms in communities has led
to the view that trade-offs not only facilitate
coexistence, but are required for it (Brown 1989,
Chesson 1991, Kotler et al. 1994, Tilman 1994,
Schluter 1995, McPeek 1996, Vincent et al. 1996).
Biological trade-offs function as coexistence
mechanisms in ecological communities because

they cause niche space to be divided among multiple species. In the words of McPeek (1996), "Trade-offs force species to differentiate among niche dimensions...". The result is that each species can ensure its coexistence in a community by mastering its own, singular trade. In the absence of trade-offs, communities would be dominated by single, jack-of-all-trade, super-species (Rosenzweig 1995).

Competition, resource saturation and ecological coexistence

The research paradigms of coexistence theory and resource partitioning both make the assumption that communities are competitively structured. Why should species segregate according to trade-offs unless competition forces them to do so? In coexistence theory (often referred to as "competitive coexistence" theory), this assumption is the very fabric of the Lotka-Volterra model and its analogues. Competition coefficients largely govern interspecific dynamics, producing either coexistence or exclusion. Resource partitioning studies measure ecological differences among species in coexisting assemblages. This does not assume competitive structure in itself. However, when observed niche differences are interpreted as mechanisms by which species have partitioned niche space, the notions of competitive exclusion and competitive structuring of niches are implicitly invoked. A number of ecologists have attacked the assumption that niches are competitively structured within communities, suggesting alternative processes which may explain the coexistence of species in ecological communities.

These alternative explanations commonly cite the argument for individualistic-natured communities (Strong 1983, den Boer 1986). They claim that the distributions and abundances of species are governed not by pressure from adjacent species in niche space, but by the independent tolerances, preferences, and limits of each species with respect to environmental gradients (Gleason 1926, Whittaker 1956). Ecologically-similar species may, therefore, have *increased* chances of coexisting because their shared ecological attributes lead them to wind up in the same places at the same times (den Boer 1980, 1986).

The attacks on the importance of interspecific competition in communities came from three principal directions. The first was a laboratory experiment with two species of *Drosophila* that purported to refute Gause's principle (Ayala 1969, 1971). This experiment claimed to show that competitors could coexist even if all of the conditions for Lotka-Volterra competitive exclusion were met (i.e., homogeneous, unvarying environment, closed population). However, this claim was largely dismissed when several different authors concluded that Ayala's result was produced by the overriding effect of intraspecific competition relative to interspecific competition in the experiment (Ayala 1971, Borowsky 1971, Gilpin & Justice 1972).

The second line of attack was a series of papers that challenged the logical structure of the argument for competitively structured communities (Connor & Simberloff 1979, Simberloff 1983). Proponents of this idea suggested that competitive structure in communities had been treated simultaneously as a prediction and as a foregone conclusion by many. They suggested that the hypothesis of competitive structuring of communities was in need of rigorous, hypothetico-deductive testing, particularly against the null hypothesis that communities are assembled at random from among the species in a regional pool. Various authors introduced statistical methodology to this end, especially in a series of papers that tested whether congeners (presumed to be ecologically-similar) coexisted in communities more or less frequently than would be expected by chance (Simberloff 1970, den Boer 1980, 1986, Azovsky 1996). These studies concluded that congeners were *more* likely to coexist in natural communities than expected by chance (but see scale-dependent result of Azovsky, 1996). On this basis, den Boer (1980) went as far as to replace the competitive exclusion principle with "the coexistence principle", which stated that, "Species that are ecologically closely related will more often than not be found coexisting in the same habitats".

The third attack on the idea of competitively structured communities was a number of papers that reviewed extensive field evidence and concluded that interspecific competition was rare in natural communities (Connell 1975, 1983, Wiens 1977, Birch 1979, Strong 1983). These studies concluded that factors other than interspecific competition, such as predation, parasites, environmental variability, and environmental heterogeneity, set more important limits to the growth of natural populations. These limits depress natural populations below carrying capacity such that available resources are not exhausted, and interspecific competition for these resources is not significant. This conclusion directly parallels the results of coexistence modeling studies (see earlier section) that have incorporated the effects of predation (e.g.,

Roughgarden & Feldman 1975), parasites (e.g., Yan 1996), environmental variability (e.g., Abrams 1976, Turelli 1981, Chesson & Warner 1981), and/or environmental heterogeneity (e.g., Levins & Culver 1971, Horn & MacArthur 1972, Tilman 1994). These, and other factors have all been shown to promote coexistence essentially by creating non-equilibrium conditions in which the consumers do not competitively exclude each other because they do not use up the resources completely (Abrams 1988, Huston & DeAngelis 1994).

Has all of this literature succeeded in refuting the idea that communities are competitively-structured? The continuing popularity of the resource partitioning paradigm (see references in Wishieu 1998) and mathematical studies of competitive coexistence (see earlier sections) suggest that this idea is not dead. The notion that communities exhibit competitive structuring is still widespread in recent community ecological literature (Rosenzweig 1995, Holt et al. 1994, Tilman et al. 1994). But what evidence is this based on? Are these ecologists blindly accepting the competition dogma and ignoring contrary evidence as some have suggested (Simberloff 1983)?

There do exist examples in which interspecific competition has been shown to be an important factor in extant, natural communities (Schoener 1974, 1983, Connell 1983, Denno et al. 1995). Nonetheless, the empirical evidence that predation is at least an equally important limiting factor is convincing. However, the prevalence of predation does not contradict the assumptions of competitively-structured communities. Holt (1977) first described how predation pressure could produce niche segregation patterns identical to those produced by competition. He described this phenomenon as "apparent competition". Other food web and keystone predator modelers have since shown that even if predators limit consumers well below resource saturation, ecologically identical species still can't coexist. There is still "competitive" pressure to diverge, and for coexisting species to subdivide niche space according to trade-offs. In the words of Vance (1978), "...observed resource partitioning between similar species implies nothing about the relative roles of competition for resources and predation in structuring the community.". Therefore, the prevalence of predation pressure does not mean that competitive pressures among coexisting species are unimportant. Whether you call it "competitively-structured", or "apparent-competitively structured", the result is the same. Evidence that predation is an important limiting factor in extant communities does not, therefore,

invalidate the assumption that niches should exhibit competitive structuring.

However, one might still suggest that environmental variability or other factors create non-equilibrium conditions, which prevent competition (or apparent competition) from having a strong effect on community structure (Hutchinson 1961, McNally 1995). Perhaps niches are still distributed randomly or individualistically in communities. However, evidence of non-equilibrial conditions in many extant ecological communities does not automatically refute the idea the competition is an important influence on the niche structure of communities. Competition could still be a major influence on niche structure even if it only occurs during rare and brief intervals in time (Wiens 1977). Consider the process of speciation. This is a phenomenon that has rarely, if ever, been observed in extant communities, yet no one would question its importance as a biological process governing diversity.

Disentangling the effects of competition from among the other factors that may shape the niche structure of extant communities is a difficult challenge. Winston (1995) did just this in an analysis of morphological differences among sympatric freshwater minnows in the southeastern USA. He concluded that interspecific competition explained observed patterns of community structure better than random or phylogenetic hypotheses. However, few studies of extant communities have produced evidence germane to this issue. Similar to speciation, the most compelling evidence for the importance of competition in structuring communities comes from the fossil record

Three well-documented paleontological patterns suggest that communities should exhibit competitive structuring. The first is the rapid bursts in species diversity that follow in the wake of mass extinctions (Webb 1989, Kauffman & Fagerstrom 1993, Rosenzweig in press). Such bursts have occurred after all of the major mass extinctions, and typically last 3-10 million years before diversity levels off. This is not a function of the idiosyncratic behavior of particular taxa, but is a cumulative effect over whole communities. Why should such bursts be associated with mass extinctions? It must be something about the very absence of species, which promotes the proliferation of many new forms. It suggests that when many niches are empty, there is a sort of evolutionary vacuum, which causes niche space to be filled rapidly.

The second pattern is comprised of long-term diversity steady-states. This pattern has been observed in many different communities and geologic periods when care has been taken to factor-

out sampling effects (e.g., Rosenzweig & Taylor 1980, Miller & Foote 1996, Rosenzweig in press). Several paleontologists have recently described a phenomenon known as "coordinated stasis", in which such periods of steady-state diversity are associated with little taxonomic turnover (Brett & Baird 1995). These steady states are the flipside of the previous pattern. Once niche space is generally full, there must be some kind of competitive suppression of new forms by the existing forms. At this stage, a new species can only survive by outcompeting, and replacing an existing one.

The third pattern consists of taxonomic replacement series in geological time. The most well-known example being therapsids, dinosaurs, and eutherian mammals as the dominant large, terrestrial quadrupeds in the Paleozoic, Mesozoic, and Cenozoic eras, respectively. This, and other examples (marine invertebrates: Kauffman & Fagerstrom 1993) are essentially the taxonomic signature of the two previous patterns. The forms that dominate particular ecological niches in particular time periods suppress the evolution of new forms until they are wiped out. Then they are rapidly replaced with ecological analogues, which may originate from completely different taxa.

These patterns imply that the function of change in diversity through time exhibits density-, or species richness-dependence. In other words, the number of species in a province exerts a negative feedback on the slope of the species accumulation curve. What processes other than competition can explain this negative feedback? The incorporation of new species must either be repressed by preexisting ones (reduced speciation/invasion) or must be balanced by losses of preexisting species (increased extinction). These processes represent a sort of evolutionary competitive exclusion. Thus, communities at or near diversity steady-states (which may be termed evolutionary equilibria) should exhibit competitively-structured niches. When the community is far from equilibrium (i.e., immediately following a mass extinction), the number of species is well below the plateau that it may eventually reach, and diversity is rapidly rising. Species should not yet have been squeezed by interspecific competition. Niches should broad, species should be poor competitors, and communities should not be competitively structured. Coexistence is easy. When the province approaches a plateau in species diversity, competitive pressures are exerting their limit on diversity. As a result, niches should be relatively small (specialized), species should be good competitors, and the niches should exhibit competitive structuring. Coexistence is harder. Even

during one of these long-term steady states, however, competition is only partially responsible for structuring communities. This is suggested by the modern day ecological data discussed earlier, as 65 million years have passed since the last major mass-extinction.

What does this mean for coexistence studies? If competition is only partially responsible for community structure, then competitive coexistence theory is only partially applicable as an explanation for the coexistence of species in real biological communities. Niche space has been partitioned among species according to trade-offs only partially. Species should be masters of their own trades to some extent, but their niches should be broader than is theoretically possible. Communities should have some vacancies. A productive direction for future coexistence studies would be to frame the extent of niche partitioning within the context of historical factors and non-equilibrium dynamics in particular systems, thereby assessing both the competitive, and the non-competitive components of coexistence.

Some investigators have developed useful and innovative ways of framing coexistence patterns within the context of competitive pressures in particular communities. Pianka (1974) conceptualized the relationship between competition intensity and resource limitation in the form of the demand/supply ratio. He noted that competitive pressure is high when this ratio is high, and that in such situations, niches should exhibit low interspecific overlap. He also noted that communities with high levels of niche overlap may therefore correspond to cases in which resources are not saturated (low demand/supply ratios). This is consistent with Wiens' (1977) description of episodic competition, and with Pulliam's (1985) suggestion that grassland sparrows in Arizona experience strong interspecific competition and discrete microhabitat partitioning only during infrequent years of extreme food scarcity.

Coexistence at a finer scale: habitat selection dynamics

In studies of coexistence at the ecological scale, the niche characteristics of organisms are assumed to be fixed. At the scale of the behavioral decisions of individual organisms, these characteristics may be fluid (Rosenzweig 1987a). Imagine the niche in the former sense as a mean, and in the latter sense as including the variation about the mean. Coexistence at this finer scale occurs before Gause's paramecia have had a chance to drive one another to extinction.

Multi-species habitat selection models such as isoleg theory, developed by Rosenzweig and associates (1981, 1987a, Pimm et al. 1985), are essentially studies of coexistence at this finer scale. Isoleg theory reflects the general phenomenon that intraspecific competition causes species to broaden their use of resources or habitats, while interspecific competition causes them to restrict the number of resources or habitats they use (Rosenzweig 1991, Mehrhoff & Turkington 1995). In isoleg theory, interspecific competition tends to cause species to segregate into different habitat types but allows for coexistence in some cases. Patterns of species' occupancy of habitats depend on the densities of the interacting species, the competitive hierarchy among them, the presence of detectable intra-type variation in patch quality, and on their fundamental habitat preferences (Rosenzweig 1981, 1991, Brown & Rosenzweig 1986).

Danielson (1991) took a very different approach to multi-species habitat selection modeling by assuming that species had distinct habitat preferences, and that individuals occupying a patch preempted all other individuals from that patch. His result was that one species can exert either a positive or a negative effect on the other depending on the densities of two species, the proportions of different habitat patches in the landscape, and the amount of patch sampling by individuals.

Habitat selection modelers have sometimes framed their studies in the context of the competitive exclusion principle, describing observed results as "coexistence mechanisms" (Brown 1989, Morris 1996, Vincent et al. 1996). Coexistence at the scale of habitat selection processes is not, in fact, identical to Gauseian coexistence, however. The relationship between habitat selection-mediated coexistence and ecological-scale coexistence is an important frontier for community ecology.

Birch (1979) described one possible linkage between coexistence at these two different scales. He noted that environmental and population fluctuations may cause species to be temporarily pushed into marginal habitats by density-dependent processes. The tolerance of competitively inferior species for suboptimal habitats is a way for these species to persist despite temporary exclusions from their preferred habitats. In this case, density dependent habitat selection dynamics act as a buffer to competitive exclusion, permitting the long-term coexistence of ecologically similar species. Wolff (1996) provided another example, showing that the competitive relationships between deer mice and white footed mice in the Appalachian Mountains flip-flop depending

on the food availability in a given year. He suggested that the long-term coexistence of these species was dependent on a competitive balance produced by the year to year variation in food production.

Other authors have conceptualized the between-scale transition of coexistence as a function of realized vs. fundamental niche evolution. Wishieu (1998) suggested that shared preference community organization should evolve into distinct preference organization over time. Her rationale was that in shared preference communities, density dependent dynamics are forcing some species into a portion of niche space that doesn't correspond to their preference. Over evolutionary time, natural selection should favor mutations that enhance species' efficiency at utilizing their realized niches, such that eventually each species' fundamental niche coincides with its realized niche. Species that initially shared preferences for certain portions of niche space eventually prefer their own distinct portion of niche space. This is essentially the idea of the "ghost of competition past" (Connell 1980).

Rosenzweig (1987b) suggested that the above scenario requires environmental stability through evolutionary time. In variable environments, the evolution of species' fundamental niches cannot keep up with the variation in their actual niches. This would favor broad fundamental niches and the maintenance of shared-preference community organization. Indeed, the prevalence of shared preference scenarios in extant communities is testament to the fact that the transition from shared- to distinct-preference community organization does not always occur (Wishieu 1998).

Coexistence at the largest scale: species diversity patterns

Take Gause's test tubes and let them go so far that the equilibrium reached by the initial competitors is insignificant. How many species of paramecia would ultimately be able to coexist within a particular test tube given unlimited time for speciation? What factors would affect the number of species that would ultimately be reached? The size of the tube? The amount of nutrient? Heterogeneous conditions within the tube? When we relax the assumptions of fixed numbers of species, niches, and habitats, we are extending the classical ecological coexistence problem to a new level and asking new questions. What determines how many species can potentially coexist in particular communities? To what extent is that potential filled in actual communities?

These questions are the fodder for studies of global and evolutionary species diversity patterns. The species diversity literature has rarely been incorporated into studies of ecological coexistence. Nonetheless, a brief review of several species diversity concepts is warranted here since these larger scale patterns and processes provide an important context for interpreting coexistence at the ecological scale.

Schluter & Ricklefs (1993) divided the various determinants of species diversity into local and regional factors. Local factors are so called because they are attributes of a point locality. These include habitat complexity (MacArthur & MacArthur 1961), disturbance frequency (Connell 1978), and others (see references in Wright et al. 1993). The most important of these is productivity, defined as a rate of energy flow through the biological component of an ecosystem (see reviews by Wright et al. 1993 and Rosenzweig & Abramsky 1993).

The function of species diversity with increasing productivity is either always increasing or unimodal (Wright et al. 1993, Rosenzweig & Abramsky 1993). The increasing phase of the diversity-productivity relationship has most often been explained based on the resources required to sustain minimum viable populations.

Given two communities with identical abundance distributions of species, the minimum viable population size limit will be reached for a species with a higher abundance rank in the less productive environment (Rosenzweig 1995). Each species needs a certain amount of the resource pie to survive, and so a smaller pie can support fewer species.

The consequences of the productivity-diversity relationship for ecological coexistence are profound. The minimum portion of the resource "pie" required for a sustainable population can be represented as the area occupied by one species under a resource availability curve (Fig. 1). If the productivity of the ecosystem is increased, this raises the overall amount of resources, and species can obtain the same quantity of resource from a narrower portion of the niche axis (Fig. 1b). This means that niches in highly productive habitats may, in effect, be just as large as niches in less-productive habitats even though they appear narrower or more specialized. We should therefore expect that coexisting species may appear to be more ecologically-similar in more productive habitats than in less productive habitats even in the absence of all other differences.

Regional determinants of species diversity are so called because they are attributes of the larger

Environmental gradient or niche axis
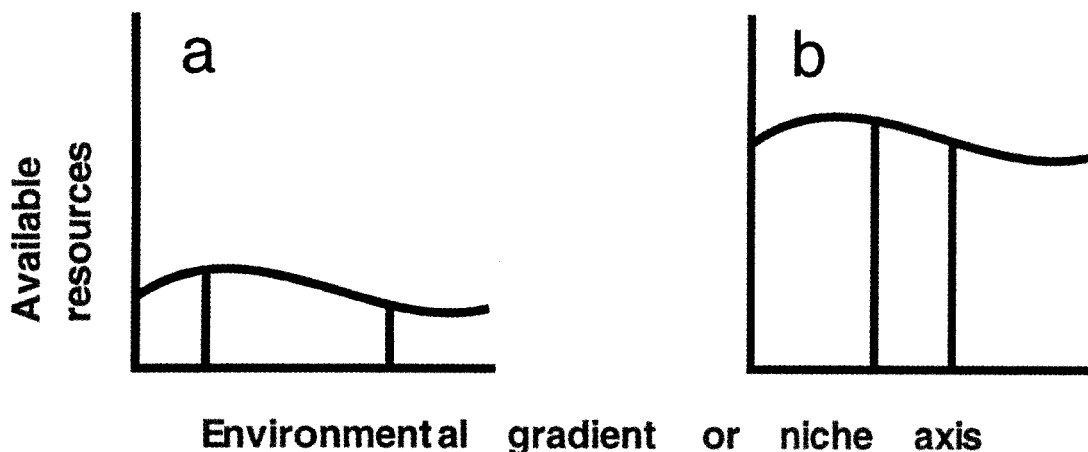
Fig. 1. Minimum niche breadth (the horizontal distance between the two vertical lines under each curve) as a function of ecosystem productivity (the amount of available resources) in a less (1a) and more (1b) productive ecosystem. The amount of resources included in a niche is represented as the area in between the lines under the curve. While the niche in figure 1a is broader than the niche in figure 1b, the two contain identical resource levels and can therefore be considered to be equally sized. Narrower niches, and hence increased opportunities for the coexistence of similar species, are possible in the more productive environment.

Anchos mínimos de nichos (la distancia horizontal entre las dos líneas verticales bajo cada curva) en relación a la productividad del ecosistema (la cantidad de recursos disponibles) en ecosistemas menos (1a) y más (1b) productivos. La cantidad de recursos dentro de un nicho está representada como el área dentro de las dos líneas bajo la curva. Aunque el nicho en la figura 1a es más amplio que el nicho en la figura 1b, los dos tienen la misma cantidad de recursos, por lo que se puede considerar que los dos nichos tienen el mismo tamaño. Nichos más angostos son posibles en el ecosistema más productivo, entonces tiene alta potencial para la coexistencia de especies similares.

spatial context of a particular locality (Schluter & Ricklefs 1993). The most important of these for explaining patterns of species diversity in natural communities is province size. Rosenzweig (1995) defined a biological province as, "...a self-contained region whose species originate entirely by speciation within the region." Larger provinces are more diverse than smaller provinces of equal productivity (Rosenzweig 1995). This relationship between province-size and diversity is a broadly general pattern, which has been noted by ecologists dating back at least to Hutchinson (1959) and recently reviewed by Rosenzweig (1995). Rosenzweig admitted that technically, under his definition, the only truly discrete biological province (that we know of) is the earth. However, the notion of a biological province as an evolutionarily-isolated spatial unit is a highly useful concept for understanding patterns of species diversity.

In general, the effective size of a biological province is a function not only of geography, but also of the spatial scale of movements of organisms. A province is functionally bigger for sedentary organisms than for highly mobile organisms (Kotliar & Wiens 1990, Holt 1993, Rosenzweig 1995). Additionally, the notion of a biological province is not just limited to discrete land areas separated by water. Major habitat-types within geographic areas can function as biological provinces since species may perceive them as islands of acceptable habitat in a sea of inhospitable surroundings (Terborgh 1973, Rosenzweig 1995). A classic example emerged from the data of Ralph (1985). He showed that bird communities in Patagonia, Argentina were least diverse in the most structurally-diverse habitat type (beech forests), contradicting the well-known correlation between bird species diversity and foliage height diversity (MacArthur & MacArthur 1961, MacArthur 1964). Ecologists have explained this result based on province size effects. South American temperate beech forests have low bird diversity despite their structural complexity because of a limited areal extent relative to other habitat types in the region, such as shrub desert (Schluter & Ricklefs 1993, Rosenzweig 1995).

In summary, larger provinces have higher diversities but provinces are not completely discrete entities in nature. They roughly correspond to isolated geographic areas or major habitat-types within those areas. They can only be precisely defined, however, with respect to specific taxa because the effective size and the strength of the boundaries of a province varies according to the movements and habitat tolerances of particu-lar organisms. Regions can be expected to behave more or less like provinces for given taxa to the extent that within-region speciation is significant.

The province-size effect on species diversity has two important implications for ecological coexistence. Firstly, since provinces are defined by speciation from within, similar species that coexist within a province should often share common ancestry. This provides an explanation for the frequent coexistence of congeners within ecological communities (den Boer 1980, 1986). Contrary to den Boer's interpretation of this pattern, it may be purely a result of within-province radiation and is not contradictory to the notion of competitively-structured communities.

Secondly, the effect of province size on species diversity has implications for the competitive structuring of communities and hence, the competitive coexistence of species within communities. Province size, and other regional diversity determinants do not affect the size of the resource pie within communities as do local determinants of species diversity. Rather, they appear to affect how small a piece species can get away with and still persist through evolutionary time. Consider two communities of equal local conditions (i.e., productivity, habitat structure); one a small island, the other, a vast continent. If species on the island subdivide niche space as finely as they do on the continent, the chances are that many will go extinct. The smaller size of island populations would make them more vulnerable to the "extinction vortex" of demographic stochasticity (Frankel & Soulé 1981). The smaller areal extent occupied by the island populations would also make them more vulnerable to being extinguished by singular, localized catastrophic events. The only species that persist in evolutionary time on the island are those that maintain dense populations and broad niches. Even though their piece of pie is big enough so that it could normally be split up, they need to maintain an oversized niche to ensure survival through local environmental fluctuations, and to maintain large population sizes. This pattern was described for island birds by MacArthur et al. (1972) who referred to the increased population sizes on islands as "density compensation" and to the habitat breadth of island species as "ecological release".

This provides an explanation for the invasibility of ecological communities on small provinces such as oceanic islands. If species typically occupy wide niches relative to the productivity level, this implies underused resources. There is less pressure for species to become efficient at what they do. It really *is* paradise, that is, until a

scrappy continental species comes along who's used to fighting for its niche.

It also leads to a prediction about community structure and coexistence. Communities of large provinces should be more competitively-structured, and should contain more opportunities for ecologically-similar species to coexist than communities of similar environments on small provinces.

How full are communities?

Factors such as productivity and province size affect how many species *can* coexist in particular communities. In essence, they determine a sort of niche carrying capacity. But we may also ask what proportion of the carrying capacity is actually full. This question can be addressed by examining the dynamic factors that affect the accumulation of species diversity in time.

The amount of time required for a community to fill its niche carrying capacity can be roughly inferred from the paleontological patterns discussed earlier (see competition section). Immediately following mass-extinctions, species diversity rises sharply, leveling off after 3-10 million years, at which time levels of diversity are roughly equal to those prior to the mass extinction (Kauffman & Fagerstrom 1993, Rosenzweig in press). The process that leads to this replacement of diversity can be conceptualized as a rough coevolution of all species in the community. Ultimately, a diversity steady state is reached, which corresponds to a sort of evolutionary equilibrium.

Major mass extinction events have generally occurred less frequently than this, roughly once every 35 million years (Raup & Sepkoski 1984). Therefore, there has typically been adequate time for communities to reach equilibrial diversities in-between such episodes. Indeed, major disturbances in diversity are interspersed with long periods of relatively little change in diversity levels (Rosenzweig & Taylor 1980, Miller & Foote 1996, Rosenzweig in press).

However, the determinants of niche carrying capacities are shifting on a much faster time scale. Glacial cycles have occurred roughly every 10,000 years in the Pleistocene. These cycles are associated with major shifts in climatic conditions worldwide. This can either be conceptualized as drastic shifts in productivity within provinces, or as latitudinal migrations of constant-productivity provinces, with consequential shifts in province size and shape. Such climate oscillations correspond with astronomical Milankovitch cycles

(Valentine & Jablonski 1993). Though the geological imprints of glacial cycles are best documented in the Pleistocene, Milankovitch cycles are believed to have occurred throughout the Phanerozoic (Valentine & Jablonski 1993).

Indeed, some paleontologists have noted drastic changes in community composition at the time scale of glacial oscillations (southwest USA deserts: Van Devender & Spaulding 1979; eastern USA deciduous forests: Davis 1983; west coast USA marine invertebrates: Valentine & Jablonski 1993). This has led some to conclude that communities are generally non-equilibrial, randomly assembled, and invasible, with non-competitively structured niches (Simberloff 1981, Johnson & Mayeux 1992, Valentine & Jablonski 1993). Indeed, this evidence suggests that niche space in communities is not, and most-likely has never been completely full. Therefore, the evolutionary equilibria that we see in the fossil record do not represent the process of community coevolution taken to its maximum diversity endpoint. Even when we have seen diversity steady-states in the fossil record, such communities could not have achieved the maximum possible niche partitioning, specialization and diversification. The 3-10 million year process of community coevolution is trying to hit a target that is constantly moving on the scale of 10,000 year oscillations.

The interpretation of the evolutionary dynamics of communities parallels the debate over the role of competition in communities. Valentine and Jablonski (1993) suggested that the observed pattern of unsaturated communities was consistent with neontological evidence for unsaturated communities (e.g., Wiens 1974, Rotenberry & Wiens 1980, Strong 1983, Cornell & Lawton 1992, Shorrocks & Sevenster 1995, MacNally 1995). If communities are not full, then species either must have oversized niches, or there are unoccupied portions of niche space. The consequence is that interspecific competition should be weak and niches should not be competitively structured within communities, rendering them highly invasible (Simberloff 1981, Connell 1983, Strong 1983). Communities are not highly coadapted webs but are ephemeral, unsaturated combinations of species (Connor & Simberloff 1979, Valentine & Jablonski 1993, Holt 1993).

On the other hand, Coope (1987) arrived at a different conclusion from his data set on the species composition of Pleistocene beetle assemblages in Great Britain. He observed some changes in species composition through Plesitocene glacial oscillations but highlighted the rough compositional constancy of particular species

assemblages in the face of these geographic shifts. Many species underwent drastic latitudinal shifts in tracking specific climatic zones and their corresponding beetle assemblages through these cycles.

Again, the truth lies on neither extreme of the spectrum but somewhere in between. Communities are neither full and completely coevolved, nor are they completely unsaturated. But can we get any more specific about how full they are?

One way to begin to address this question more precisely is to look at the overlaps between fundamental and realized niches in communities. Consider the evolution of the ghost of competition past (Connell 1980, Rosenzweig 1987b, Wishieu 1998). In this model, species with initially overlapping preferences or fundamental niches are segregated in niche space by competition. If this segregation remains stable through time, species' fundamental niches should eventually approach their realized niches (see earlier discussion). Therefore, if the process of community coevolution was ever allowed to proceed until the niche carrying capacity were completely full (an evolutionary climax), all species' fundamental niches would equal their realized niches. All species would fully play to their strengths. Preferences that were initially shared would all have become distinct. Therefore, the prevalence of shared preferences vs. distinct preferences may be viewed as an index of the fullness of particular communities. Wishieu (1998) concluded that among resource partitioning studies in general, these two types of community organization were equally common. Perhaps a best first approximation therefore, would be that communities are, on average, half full.

At the very least, Wishieu's data suggest that both scenarios are common in natural communities. This provides another independent line of evidence for the partial competitive structuring of communities. Distinct -preference organization in extant communities is consistent with competitively-structured niches, and with long-term diversity steady states in the fossil record. Shared-preference community organization in nature is consistent with randomly, or non-competitively-structured niches, and with the haphazard and ephemeral coexistence of species in finer-scale studies of fossil communities. Species partition niche space competitively amongst themselves to some degree, but they retain enough ecological flexibility and oversized fundamental niches to roll with the 10,000 year punches. Communities are continually being pushed towards the climax by community coevolution, and away from it by shifting climate.

It should finally be noted that with a sufficiently long-term perspective, there is no climax level of species diversity. The overall trend of increasing diversity of life through time testifies to this conclusion. Given enough time, certain lineages will invade new provinces (e.g., land), or develop important biological innovations (e.g., seeds) that radically change the ways in which organisms fill up niche space. The biological trade-offs themselves are plastic at this level and the ultimate potential for species' coexistence cannot be predicted.

CONCLUSION

Despite the simplicity of the competitive exclusion principle, the current state of knowledge about how and when species may coexist reveals a highly complex and heterogeneous problem. Studies of coexistence published in the ecological literature span an impressive range of mechanisms, techniques, scales, concepts, and patterns. One way to increase our understanding of species' coexistence will be to clearly define different types of coexistence problems, and then draw linkages between them.

A primary example is the linkage of patterns and processes across scales. Coexistence has been studied at time scales ranging from behavioral interactions between individuals to niches evolving toward optima, and everywhere in between. This paper provides a framework to divide coexistence into three distinct time scales. Coexistence at the finest scale incorporates density-dependent habitat selection dynamics and behavioral interactions among individuals. In studies of classical, Gauseian, or ecological-scale coexistence, smaller-scale interactions are integrated through time and community dynamics are studied at the point where populations have had enough time to achieve equilibrium. At the highest scale, the niches, habitats, and species pools of communities may themselves evolve, and coexistence is affected by the factors that control species diversity and coevolution. Various authors have begun to make linkages between coexistence at these different scales (Birch 1979, Connell 1980, Rosenzweig 1987b, Wolff 1996, Vincent & Vincent 1996). These, and other multiscale approaches hold great potential for enhancing our understanding of ecological coexistence.

Significant advances can also be made by developing better linkages between empirical and theoretical studies of ecological coexistence. Resource partitioning studies have provided

valuable empirical data on patterns of coexistence in nature. However, they have often ignored the theoretical ecological literature on coexistence. Ideas that have emerged from coexistence theory can suggest important variables to be measured in purely observational studies, and can be used to develop hypotheses in more experimental field studies. For example, metapopulation coexistence models would suggest that dispersal abilities and competitive relationships should be measured in coexisting sets of species. Increased measurement of competition among coexisting species would permit a better linkage to coexistence theory. Experimental determination of realized vs. fundamental niches of coexisting species would help address the question of competitive niche structuring in communities.

Conversely, coexistence theorists should develop models that are more firmly rooted in empirical patterns of species coexistence. Competition-based models of ecological coexistence have been a useful first step, but to accurately predict species coexistence in real communities, models should include both the competitive and non-competitive components of coexistence.

Explaining coexistence is an intrinsically difficult problem, yet the coexistence of species defines the very concept of an ecological community, and is thus of central importance in ecology. Our understanding of the patterns and processes of species' coexistence lies at the heart of our ability to understand and predict the dynamics of ecological communities.

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