8

Competition and Niche Theory

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8.1 Introduction: Definitions and Theoretical Background

8.1.1 *Competition*

By definition, competition occurs when two or more organisms, or other organismic units such as populations, interfere with or inhibit one another. The organisms concerned typically use some common resource which is in short supply. Moreover, the presence of each organismic unit reduces the fitness and/or equilibrium population size of the other. Competition is sometimes quite direct, as in the case of interspecific territoriality, and is then termed *interference competition*. More indirect competition also occurs, such as that arising through the joint use of the same limited resources, which is termed *exploitation competition*. Because it is always advantageous for either party in a competitive interaction to avoid the other whenever possible, competition presumably promotes the use of different resources and hence generates ecological diversity. The mechanisms by which members of a community of organisms partition resources among themselves and reduce interspecific competition shapes community structure, and may often influence species diversity profoundly (see Schoener, 1974, for a review).

Ecologists are, however, divided in their attitudes concerning the probable importance of competition in structuring natural communities. Some, myself included, either tacitly or explicitly assume that self-replication in a finite environment must eventually lead to some competition. Other ecologists, particularly those that study small organisms and/or organisms at lower trophic levels, tend to be much more skeptical about the impact of competition upon organisms in nature. Still others have begrudgingly elevated competition to the status of a dogma—this school in turn emphasizes the importance of predation in structuring natural communities. While the persistence of this dispute over the strength of competition in natural communities could conceivably reflect a natural dichotomy, it might well be more realistic and more profitable not to view competition as an all-or-none phenomenon. An emerging conceptual framework envisions a gradient in the intensity of competition, varying continuously between the end-points of a complete competitive vacuum (no competition) to a fully saturated environment with demand equal to supply ('over-saturated' environments are also possible, with demand temporarily exceeding supply).

Competition lends itself readily to mathematical models, and an extensive body of theory exists, most of which assumes saturated communities at equilibrium with their resources, sometimes referred to as 'competitive' communities. Much of this theory is built upon the overworked Lotka–Volterra competition equations:

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \sum_{j \neq i}^{n} \alpha_{ij} N_j}{K_i} \right) \tag{8.1}$$

Here n is number of species (subscripted by i and j), r_i is the intrinsic rate of increase of species i, K_i is its 'carrying capacity,' N_i is its population density, and α_{ij} is the 'competition coefficient' which measures the inhibitory effects of an individual of species j upon species i. At equilibrium, all dN_i/dt must be equal to zero, giving the equilibrium population densities:

$$N_i^* = K_i - \sum_{j \neq i}^{n} \alpha_{ij} N_j^*, \tag{8.2}$$

for all i from 1 to n.

The Lotka–Volterra competition equations greatly oversimplify the process of interspecific competition (for examples, see Hairston *et al.*, 1968; Wilbur, 1972; and Neill, 1974). Indeed, the alphas in these equations could be illusory and may often obscure the real *mechanisms* of competitive interactions. Nevertheless, whatever flaws the Lotka–Volterra equations may have, they have clearly contributed much to current ecological thinking. Not only do they provide a conceptual framework, but they have helped to give rise to many exceedingly useful ecological concepts in addition to competition coefficients, including equilibrial population densities, the community matrix, diffuse competition, r and K selection, as well as non-linear isoclines (see, for example, Ayala *et al.*, 1973a; Schoener, 1974; Gilpin and Ayala, 1973). Some important papers, books and/or major reviews in the voluminous literature on competition include Crombie (1947), Birch (1957), Milne (1961), Milthorpe (1961), DeBach (1966), Miller (1967), MacArthur (1972), Grant (1972a), Stern and Roche (1974), Schoener (1974, 1976a, 1977) and Connell (1975).

8.1.2 *Niche theory*

Among the first to use the term niche was Grinnell (1917, 1924, 1928), who viewed it as the ultimate distributional unit, thus stressing a spatial concept of the niche. Elton (1927) emphasized more ethological aspects, and defined the ecological niche as the functional role and position of the organism in its community, stressing especially its trophic relationships with other species. Although the term niche has been used in a wide variety of ways by subsequent workers, the idea of a niche gradually became linked with competition. Empirical studies of Gause (1934) and others (see below) showed that ecologically similar species were seldom able to coexist in simple laboratory systems; hence species living together must each have their own unique niche. The one species per niche concept became accepted as ecological dogma, although a few dissenters urged otherwise (Ross, 1957, 1958). Because the term 'niche' has been used in a wide variety of different contexts and is rather vaguely defined, some ecologists prefer not to use the word [see, for example, commentaries on niche in Williamson (1972) and Emlen (1973)]. The ecological niche has, however, become increasingly identified with resource utilization spectra (Fig. 8.1), through both theoretical and empirical work of a growing school of population biologists (Levins, 1968; MacArthur, 1968, 1970, 1972; Schoener and Gorman, 1968; Pianka, 1969, 1973, 1974, 1975; Colwell and Futuyma, 1971; Inger and Colwell, 1977; Roughgarden, 1972, 1976, 1979; Vandermeer, 1972; Pielou, 1972; May and MacArthur, 1972; May, 1974d, 1975d; Cody, 1974; Schoener, 1968, 1975a, 1975b, 1977). Such an emphasis upon resource use is operationally tractable, although it largely neglects considerations of reproductive success (some earlier treatments of the niche such as the n-dimensional hypervolume concept of Hutchinson (1957) used fitness to define niche boundaries).

Although niche theory will ultimately have to include aspects of reproductive success as well as resource utilization phenomena, emphasis

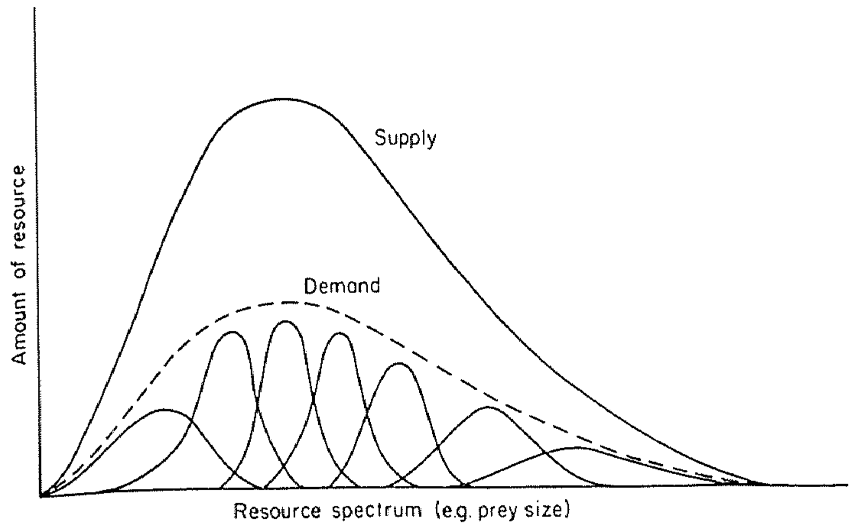


Fig. 8.1. Niche relationships among potentially competing species are often visualized and modelled with bell-shaped resource utilization curves. The uppermost bell-shaped curve represents the supply of resources along a resource continuum, such as prey size. The vertical axis measures the amount of resource available or used over some time interval. The lower small curves represent seven hypothetical species in a community, with those species that exploit the 'tails' of the resource spectrum using a broader range of resources (that is, they have broader niches) because their resources are less abundant. The sum of the component species' utilization curves (dashed line) reflects the total use or the overall demand along the resource gradient. Pressures leading to the avoidance of interspecific competition should result in a relatively constant ratio of demand/supply along the resource continuum, as shown. Discrete, rather than continuous, resource states can be handled in analogous ways.

must be on the latter here. Possibilities abound for significant further work, both theoretical and empirical, on the constraints and interactions between optimal foraging and optimal reproductive tactics (Pianka, 1976).

The concept of niche 'breadth' (niche 'width' or 'size' are frequent synonyms) has proven to be extremely useful. Niche breadth is simply the total variety of different resources exploited by an organismic unit. In the absence of any competitors or other enemies, the entire set of resources used is referred to as the 'fundamental' niche (Hutchinson, 1957) or the 'pre-interactive,' 'pre-competitive,' or 'virtual' niche. Any real organismic unit presumably does not exploit its entire fundamental niche since its activities are somewhat curtailed by its competitors as well as by its predators; hence its 'realized,' 'post-interactive,' or 'post-competitive' niche is usually a subset of the fundamental niche (Hutchinson, 1957; Vandermeer, 1972). The difference between the fundamental and the realized niche, or the niche change due to competitors, thus reflects the effects of interspecific competition (as well as predation).

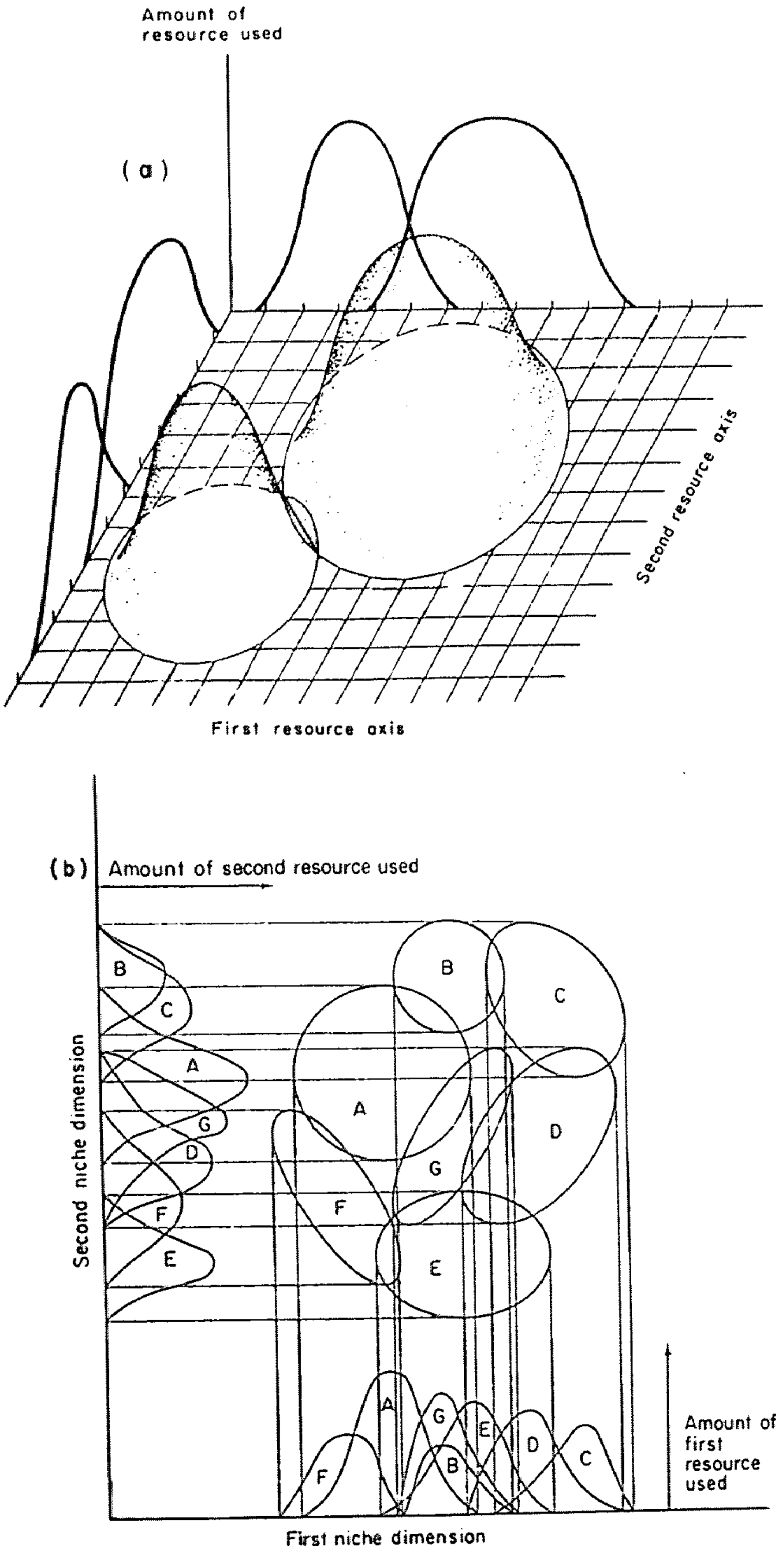
Consideration of the variety of factors influencing niche breadth leads into the problem of specialization versus generalization. A fairly substantial body of theory on optimal foraging predicts that niche breadth should generally increase as resource availability decreases (Emlen, 1966, 1968; MacArthur and Pianka, 1966; Schoener, 1971; MacArthur, 1972; Charnov, 1973, 1975). In an environment with a scant food supply, a consumer cannot afford to bypass many inferior prey items because mean search time per item encountered is long and expectation of prey encounter is low. In such an environment, a broad niche maximizes returns per unit expenditure, promoting generalization. In a food-rich environment, however, search time per item is low since a foraging animal encounters numerous potential prey items; under such circumstances substandard prey items can be bypassed because expectation of finding a superior item in the near future is high. Hence rich food supplies are expected to lead to selective foraging and narrow food niche breadths. A competitor can act either to compress or to expand the realized niche of another species, depending upon whether or not it reduces resource levels uniformly (which leads to niche expansion) or in a patchy manner (which should often result in a niche contraction, especially in the microhabitats used).

Two fundamental aspects of niche breadth have been distinguished—the so-called 'between-phenotype' versus 'within-phenotype' components (Van Valen, 1965; Roughgarden, 1972, 1974b, 1974c). A population with a niche breadth determined entirely by the between-phenotype component would be composed of specialized individuals with no overlap in resources used; in contrast, a population composed of pure generalists with each member exploiting the entire range of resources used by the total population would have a between-phenotype component of niche breadth of zero and a maximal within-phenotype component. Real populations clearly lie somewhere between these two extremes, with various mixtures of the two components of niche breadth.

Another central aspect of niche theory concerns the amount of resource sharing, or niche overlap. Ecologists have long been intrigued with the notion that there should be an upper limit on how similar the ecologies of two species can be and still allow coexistence. Concepts that have emerged from such thinking include the so-called 'principle' of competitive exclusion (below), character displacement, limiting similarity, species packing, and maximal tolerable niche overlap (for examples, see Hutchinson, 1959; Schoener, 1965, MacArthur and Levins, 1967; MacArthur, 1969, 1970; May and MacArthur, 1972; Pianka, 1972; Grant, 1972a). A number of models of niche overlap in competitive communities, typically built upon eq. (8.1), have generated several testable predictions (MacArthur and Levins, 1967; MacArthur, 1970, 1972; May and MacArthur, 1972; May, 1974d; Gilpin, 1974; Rappoldt and Hogeweg, 1980; Roughgarden, 1974a, 1975b, 1976). Some of these models suggest that maximal tolerable niche overlap should decrease as the number of competing species increases, with such decreases in overlap approximating a decaying exponential (cf. Fig. 8.12). Indeed, MacArthur (1972) coined the term 'diffuse competition' to describe the total competitive effects of a number of interspecific competitors, implying that a little competitive inhibition per species when summed over many other species can be equivalent to strong competitive inhibition by fewer competing species. One model, that of May and MacArthur (1972), predicts that maximal tolerable overlap should be relatively insensitive to environmental variability.

Most existing theory on niche overlap is framed in terms of a single niche dimension (but see May, 1974d, and Yoshiyama and Roughgarden, 1977). Real plants and animals, however, differ in their use of just one resource only infrequently (for such an example, see Fig. 8.9). Rather, pairs of species frequently show moderate niche overlap along two or more niche dimensions (Fig. 8.2). Ideally a multidimensional analysis of resource utilization and niche separation along more than a single niche dimension should proceed through estimation of proportional simultaneous utilization of all resources along each separate niche dimension (Pianka, 1974, 1975; May, 1975d). In practice however, it is extremely difficult to obtain such multidimensional

Fig. 8.2. (a) Diagrammatic representation of resource utilization of two hypothetical species along two niche dimensions, such as prey size and foraging height above the ground. Note that, although the shadows of the three dimensional peaks on each separate niche dimension overlap, true overlap in both dimensions is very slight. Adapted after Clapham (1973).
(b). A similar plot for seven species, showing that pairs with substantial or complete overlap along one dimension can avoid or reduce competition by niche separation along another dimension.


Amount of resource used
(a)
Second resource axis
First resource axis
(b)
Amount of second resource used
Second niche dimension
B
C
A
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D
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E
B
C
A
D
G
F
E
A
G
E
D
C
F
B
Amount of first resource used
First niche dimension

utilization data because animals move and integrate over both space and time. An individual animal would have to be followed, and its use of all resources recorded continually, in order to obtain accurate estimates of its true utilization of a multidimensional niche space. Since this is often very tedious or even impossible, one usually attempts to approximate from separate unidimensional utilization distributions (Fig. 8.3).

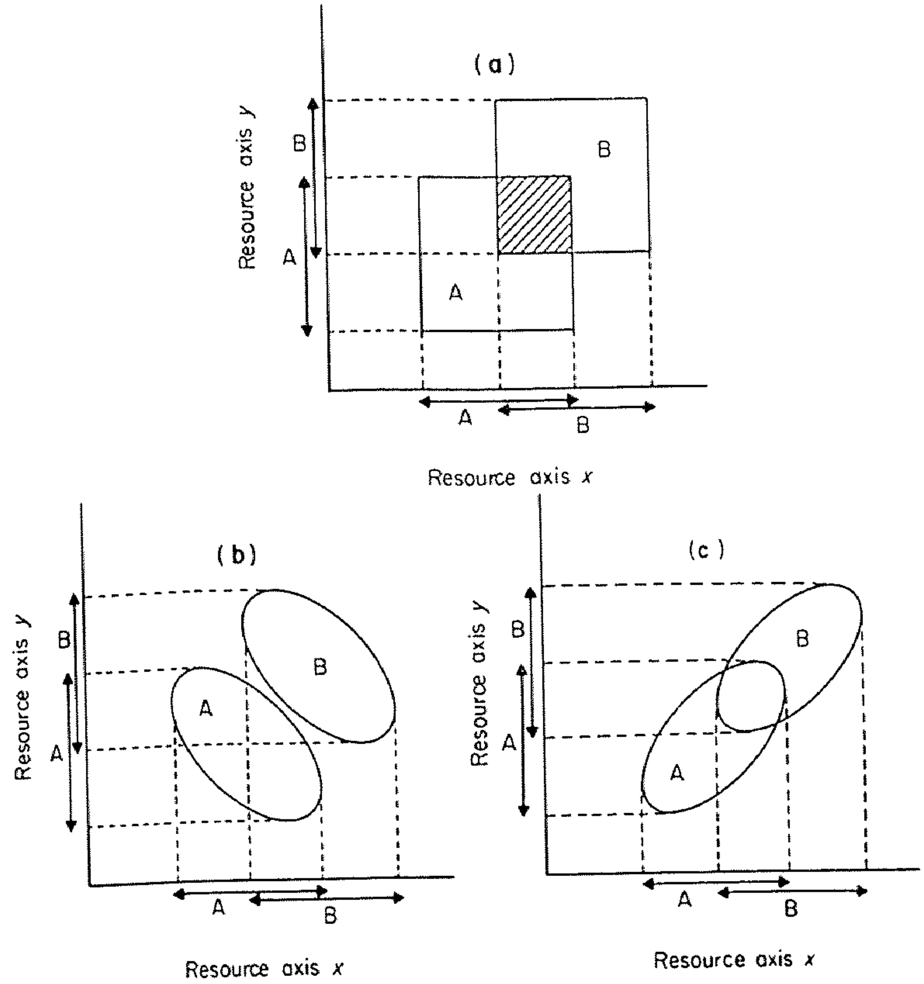

Fig. 8.3. Three possible cases for the use of two resource dimensions (assumed to be constant within boxes or ellipses) for two hypothetical species, A and B. Although unidimensional projections are identical in all three cases, true multidimensional overlap is zero in case (**b**). Case (a) illustrates truly independent niche dimensions, with any point along resource axis x being equally likely along the entire length of resource axis y; under such circumstances, niche dimensions are orthogonal and unidimensional projections accurately reflect multidimensional conditions. However, when niche dimensions are partially dependent upon one another (cases (**b**) and (**c**)), unidimensional projections can be severely misleading.

Provided that niche dimensions are truly independent, with for example any prey item being equally likely to be captured in any place, overall multidimensional utilization is simply the product of the separate unidimensional utilization functions (May, 1975d). Estimates of various niche parameters along component niche dimensions can then simply be multiplied to obtain multidimensional estimates. However, should niche dimensions be partially dependent upon one another (Fig. 8.3), there is no substitute for knowledge of the true multidimensional utilization functions. In the extreme case of complete dependence (with, for example, any given prey item being found only at a particular height above ground), appearances to the contrary, there is actually only a single niche dimension, and a simple average provides the best estimate of true utilization. Moreover the arithmetic average of estimates of unidimensional niche overlap obtained from two or more separate unidimensional patterns of resource use actually constitutes an *upper bound* on the true multidimensional overlap (May, 1975d). Certain pitfalls in the analysis of niche relationships along more than one dimension have been noted by May (1975d) and Pianka (1974, 1975).

An important aspect of niche dimensionality concerns the notion of the number of immediately adjacent species in niche space (MacArthur, 1972). An increased number of niche dimensions results in a greater potential for adjacent species in niche space (see Fig. 8.2) and hence may intensify diffuse competition (MacArthur, 1972; Pianka, 1974, 1975).

8.1.3 *Niche overlap and competition*

Because competition coefficients are exceedingly difficult to estimate directly except by population removal experiments (below), measures of niche overlap have often been used as estimates of the alphas in eqs. (8.1) and (8.2) (Pico *et al.*, 1965; Schoener, 1968; Levins, 1968; Orians and Horn, 1969; Pianka, 1969; Culver, 1970; Brown and Lieberman, 1973; May, 1975d). However, tempting though it may be, equating overlap with competition can be dubious and misleading (Colwell and Futuyma, 1971). Although niche overlap is clearly a prerequisite to exploitative competition, overlap need not necessarily lead to competition unless resources are in short supply. (In a competitive vacuum with a surplus of resources available, niches could presumably overlap completely without detriment to the organisms concerned.) Moreover, interference competition is unlikely to evolve unless there is a potential for overlap in use of limited resources (i.e., exploitation competition must be *potentially* possible). Avoidance of competition can lead to entirely non-overlapping patterns of resource utilization (disjunct niches), as for example occurs in interspecific territoriality. In the parlance of the mathematician, niche overlap in itself is neither a necessary nor a sufficient condition for interference competition; moreover, overlap is only a necessary but not sufficient condition for exploitation competition.

Indeed, the preceeding arguments suggest that there may often be an inverse relationship between competition and niche overlap. If so, extensive overlap might actually be correlated with reduced competition. Such reasoning led me to propose the 'niche overlap hypothesis', which asserts that maximal tolerable overlap should be lower in intensely competitive situations than in environments with lower demand/supply ratios (Pianka, 1972; see also Roughgarden and Feldman, 1975). The impact of predators on competition is poorly understood, but they may often reduce its intensity and hence facilitate coexistence (Paine, 1966; Connell, 1975).

8.1.4 *Temporal variability and fugitive species*

Most existing theory on both interspecific competition and niche relationships assumes that component populations have reached an equilibrium with their resources and differ enough in their use of these resources to coexist. Hutchinson (1951) formulated a somewhat more dynamic and perhaps more realistic concept of a 'fugitive' species, which he envisioned as predictably inferior, always excluded locally under interspecific competition, but which persists in newly disturbed regions merely by virtue of its high dispersal ability. Hutchinson's mechanism for persistence of a colonizing species by means of high dispersal ability in a continually disturbed and changing patchy environment, in spite of pressures from competitively superior species, has been modelled analytically (Skellam, 1951; Levins and Culver, 1971; Horn and MacArthur, 1972; Slatkin, 1974; Levin, 1974). This view of competitive pressures and processes varying in time and space is appealing and doubtlessly realistic, although perhaps operationally intractable in many instances. In a later attempt to explain the apparent 'paradox' of the plankton (that is, the coexistence of members of a diverse community in a relatively homogeneous physical environment with few possibilities for niche separation), Hutchinson (1961) suggested that temporally-changing environments may promote diversity by periodically altering the relative competitive abilities of component species, hence allowing their coexistence (Weins, 1977, recently revived this idea).

8.2 Empirical studies

Competitive effects can be measured in two ways: (1) by perturbation experiments in which rates of population growth of competitors are monitored as they approach equilibrium, and (2) by addition and/or removal experiments, in which the equilibrium population density of a species, N_i^* in eq. (8.2), is monitored at equilibrium both in the presence and in the absence of its competitor, in an otherwise unchanged environment. Either slowed rates of population growth, or an observed reduction in population density, or a niche shift in response to the presence of a competitor constitute direct evidence of interspecific competition.

Most experimental studies of competition have been performed under relatively homogeneous and constant laboratory conditions. Such studies, briefly considered below, led to the so-called 'principle' of competitive exclusion of Gause (1934) (see also Cole, 1960; Hardin, 1960; Patten, 1961; DeBach, 1966), which asserts that some ecological difference must exist between coexisting species.

Although competition is the conceptual backbone of much current ecological thought, it has proven exceedingly difficult to study in natural communities, probably partially because reduction or avoidance of competition is always advantageous when possible. Also, the great spatial and temporal variability characteristic of most natural communities demands a dynamic approach to the investigation of competitive interactions. Existing evidence of competition in nature is largely circumstantial (see below) and unequivocal removal experiments hold considerable promise (Connell, 1975). Indeed, because competition lies at the heart of so many ecological processes but has been studied so inadequately, carefully designed and well executed empirical investigations into the precise mechanisms and results of competitive interactions seem virtually certain to be of central importance to the future of ecology.

8.2.1 *Laboratory experiments*

Gause (1934) performed some of the earliest competition experiments with several species of *Paramecium*, using laboratory culture media, renewed at regular intervals. Population growth and population densities were monitored both in single-species cultures and in mixtures of two competing species grown together (Fig. 8.4). One experiment clearly demonstrated competitive exclusion of *P. caudatum* by *P. aurelia*. In another experiment with *P. caudatum* and *P. bursaria*, this pair of *Paramecium* species coexisted in a mixed culture, although at lower population densities than when grown in pure cultures of a single species (Fig. 8.4). Competition coefficients, reflecting the intensity of the competitive interaction, are readily calculated from such data.

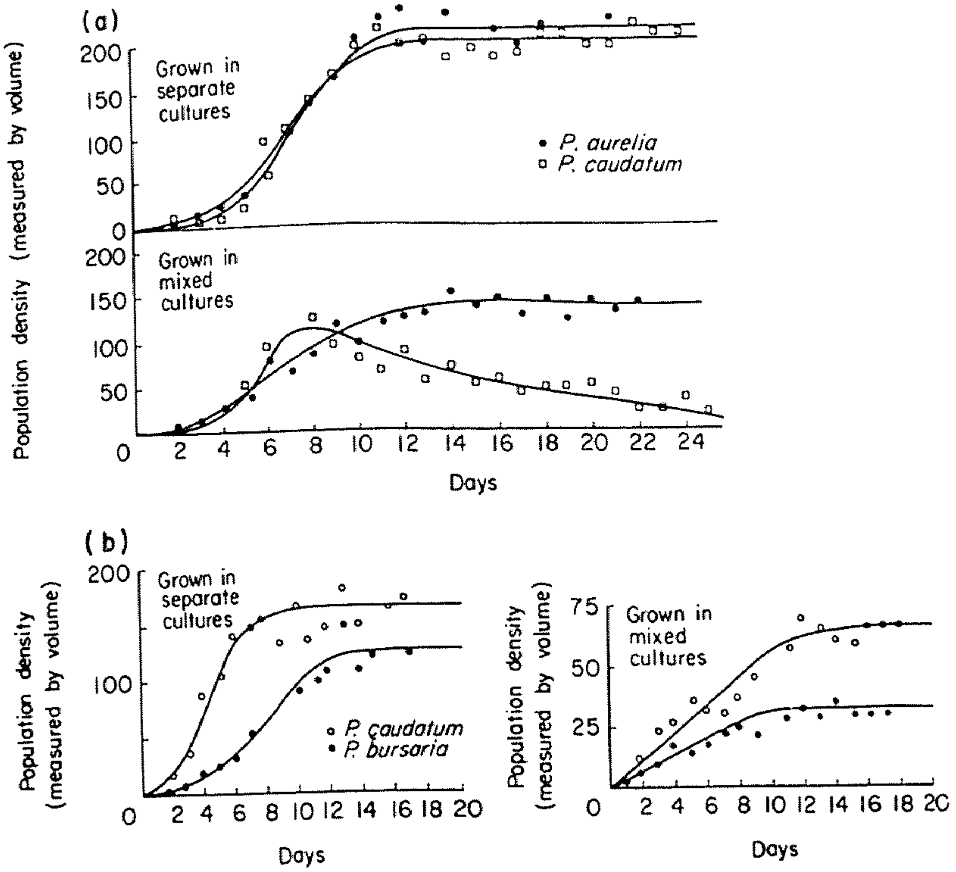

Fig. 8.4. (a) When *Paramecium aurelia* and *P. caudatum* are grown together in mixed laboratory cultures, *P. aurelia* excludes *P. caudatum*. Modified from Gause (1934) after Clapham (1973). (b) Laboratory competition experiments with two more dissimilar *Paramecium* species, *P. caudatum* and *P. bursaria*, result in coexistence at lower population densities than in pure cultures. From data of Gause, modified from Clapham (1973).

By far the most exhaustive laboratory studies of competition are those of Park (1948, 1954, 1962) and his associates, who worked with flour beetles, especially of the genus *Tribolium*. While Park's studies are much too extensive to review here, they also convincingly demonstrated competitive exclusion. In addition, a series of experiments showed that the outcome of interspecific competition depends upon (a) initial population densities (Neyman *et al.*, 1956), (b) environmental conditions of temperature and humidity (Park, 1954), and (c) on the genetic constitution of the strains of competing species (Park *et al.*, 1964).

Among the numerous other laboratory experiments on competition that have been undertaken since Gause's and Park's pioneering efforts, perhaps one of the more informative is the elegant work of Neill (1972, 1974, 1975). Using aquatic laboratory microcosms containing communities of four species of micro-crustaceans along with associated bacteria and algae under equilibrium conditions, Neill performed a series of replicated removal experiments and allowed the resulting systems to return to equilibrium. Each species of microcrustacean, as well as each possible pair of species, were removed and estimates of population densities of the various species were made under nearly all possible competitive regimes. Competition coefficients estimated from these equilibrium population densities varied with community composition. In both Neill's microcosms and in an amphibian community studied by Wilbur (1972), the joint effects of two species upon a third in a 3-species system cannot always be predicted from the separate interactions in the three component 2-species systems. Such results indicate that, if eq. (8.1) is to reflect reality, it must somehow be expanded to include 'interactive' competition coefficients reflecting the joint effects of two species upon a third, as suggested by Hairston *et al.* (1968) and Wilbur (1972).

8.2.2 *Field observations*

Removal experiments under field conditions are usually next to impossible, and have seldom been attempted (but see below). Instead, field studies of competition tend to rely heavily on 'natural' experiments, in which aspects of the ecology of a species are compared between areas where it occurs alone (allopatry) with other areas where it occurs with another competing species (sympatry). Provided that the two areas are otherwise basically similar, niche shifts observed in sympatry should reflect the response to interspecific competition. However, as pointed out by Grant (1972) and Connell (1975) among others, such observations often lack a suitable 'control', since other factors probably differ between allopatry and sympatry.

Niche shifts and character displacement

Such a situation occurs among two species of flatworms along temperature gradients in streams (Beauchamp and Ullyett, 1932). Figure 8.5 depicts the distributions of these two species of *Planaria* in streams

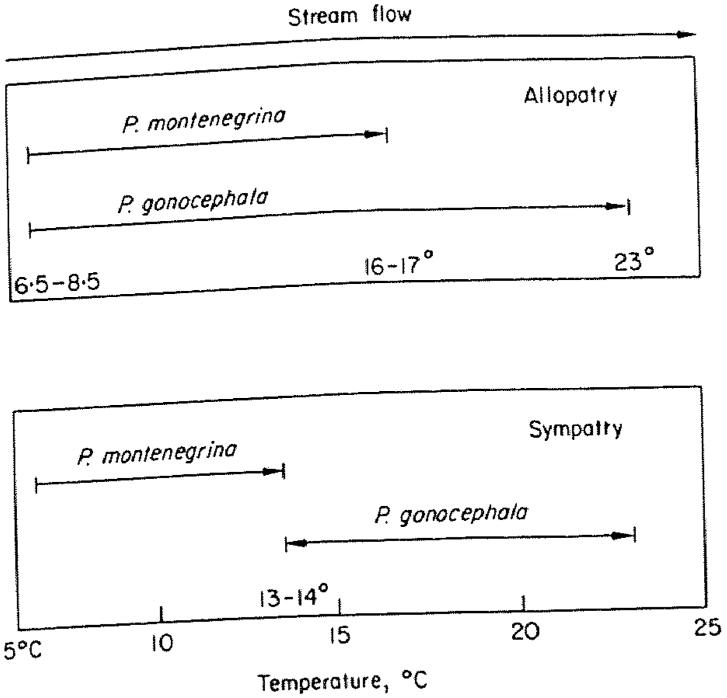

Fig. 8.5. Distributions of *Planaria montenegrina* and *P. gonocephala* along temperature gradients in streams when they occur separately (above) and together (below). Each species is restricted to a smaller range of thermal conditions when in competition with the other. From Beauchamp and Ullyett (1932) after Miller (1967).

where each occurs separately and where both exist together. Neither species occupies as broad a range in temperature when the two occur together as it does when it is the only species in the stream (Fig. 8.5). Similar observations of niche shifts in 'incomplete' faunas include studies on salamanders (Hairston, 1951) and birds (Crowell, 1962).

A related phenomenon, termed 'character displacement' by Brown and Wilson (1956), sometimes occurs when two wide-ranging species have partially overlapping geographic distributions, with a zone of sympatry and two zones where each species occurs alone in allopatry. Such species pairs are often very similar to one another where they occur in allopatry, but they typically diverge when they coexist (Fig. 8.6).

Hutchinson (1959) first commented on the apparent constancy in the magnitude of morphological character displacement, reporting ratios of

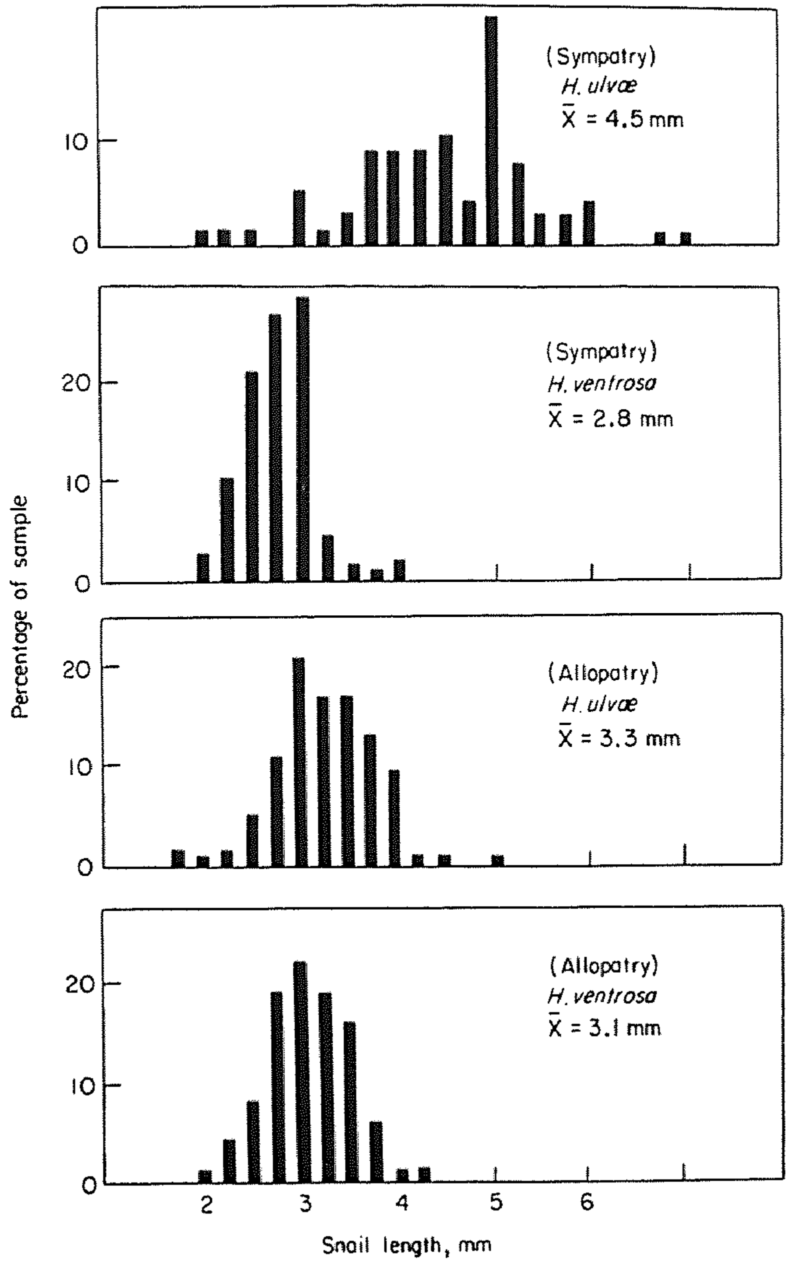

Fig. 8.6. Length-frequency distributions of the shells of two species of snails, *Hydrobia ulvae* and *H. ventrosa*, at a locality where they coexist (top two boxes) and at two localities where they occur in allopatry (bottom two boxes). From Fenchel (1975).

mouthpart sizes among coexisting congeneric species of insects, birds and mammals ranging only from about 1·2 to 1·4. Schoener (1965), Grant (1968) and Diamond (1973) found similar ratios of bill lengths among coexisting pairs of bird species, while Fenchel (1975) obtained comparable but slightly larger character displacement ratios in body sizes of two species of small marine snails (Fig. 8.6). Pulliam (1975) reports very constant, although slightly smaller (about 1·1), bill length ratios among seed-eating sparrows. However, sympatric *Anolis* lizards in the Caribbean often differ by considerably greater ratios, particularly on small islands where the ratio of sizes approaches 2 (Schoener, 1970). Indeed, Schoener (1977) suggests that niche variance along the food-size dimension and the between-phenotype component of niche breadth may be generally greater among lizards than in birds due both to lack of parental care in lizards and their slower indeterminate growth, which results in greater variation in size among individuals within a population. For an irreverent review of the Hutchinsonian 1·3 ratio, showing that it turns up in many contexts (including kitchen implements, children's bicycles, and ensembles of musical instruments), see Horn and May (1977) and Maiorana (1978).

Under circumstances in which there is a potential for intense exploitation competition, niche overlap may be reduced by interference competition leading to interspecific territoriality (Orians and Wilson, 1964), which could conceivably select for an actual convergence in phenotypic characteristics involved in recognition and territorial defence (Cody, 1969, 1974). In a critical review, Grant (1972a) evaluated existing evidence for and against both character convergence and divergent character displacement; he concludes that not only is the evidence for the ecological bases of character displacement (differential resource use) quite weak, but also that many putative examples of divergent character displacement (including the 'classic' *Sitta* nuthatch case!) could easily represent merely gradual clinal variation associated with various environmental gradients.

Two reasonably strong cases for ecological character displacement have appeared since Grant's review. In one study by Fenchel (1975), mentioned above, two small species of deposit-feeding marine snails, *Hydrobia ulvae* and *H. ventrosa*, have nearly identical size frequency distributions where each occurs in allopatry under different conditions of salinity and hydrography, However, in relatively narrow (and probably quite recent) zones of sympatry along certain salinity gradients, the two species appear to coexist in a stable equilibrium with the more widespread *H. ulvae* becoming conspicuously larger than in allopatry while the other species gets noticeably smaller (Fig. 8.6). Fenchel (1975 and unpublished) has expanded these studies and shown particle size selection by snails of different sizes, providing an ecological basis for differential resource utilization arising from the size difference.

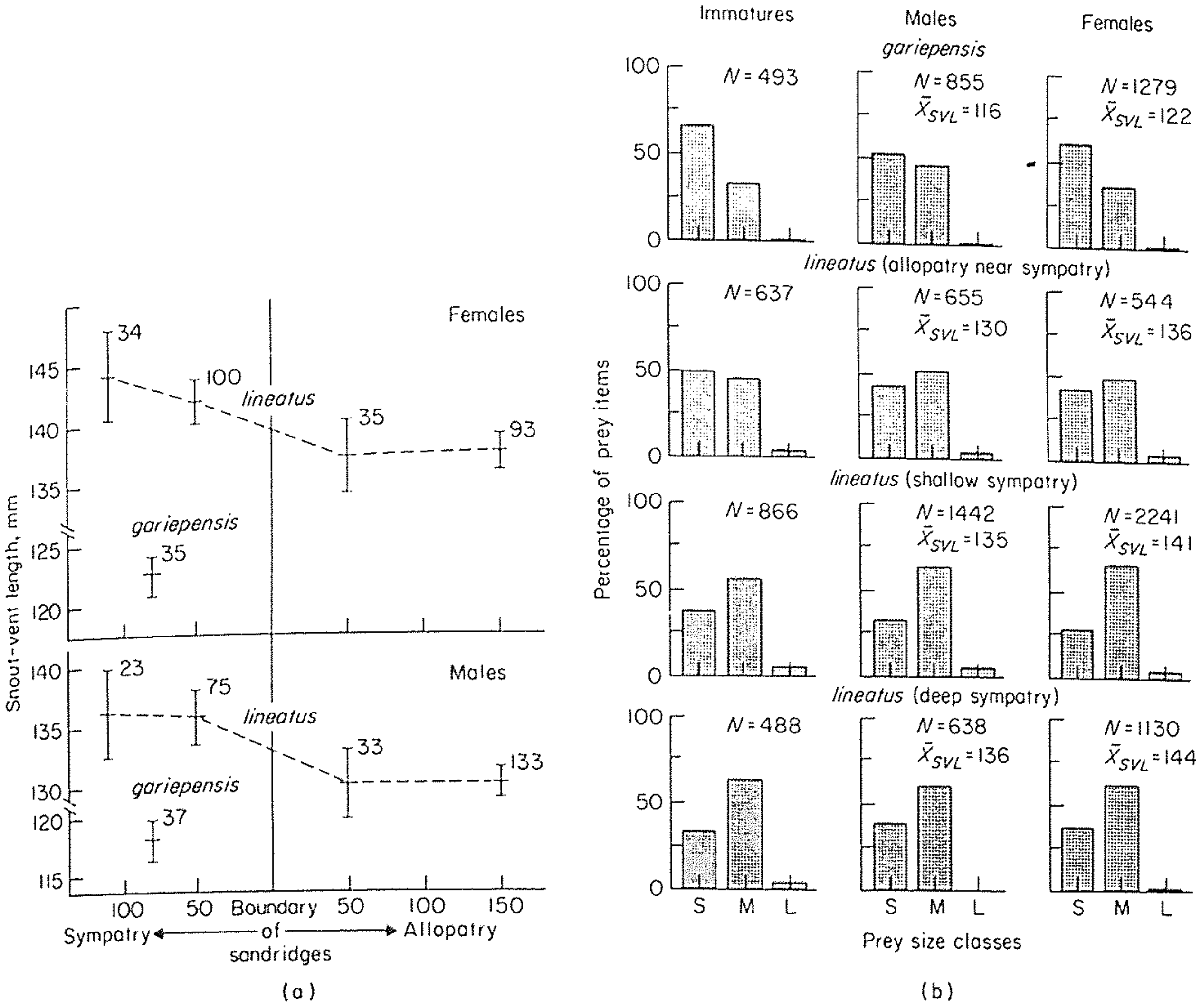

Fig. 8.7. (a) Step clines in mean snout-vent lengths of subterranean legless lizards (Scincidae: *Typhlosaurus lineatus*) associated with the presence of a smaller congeneric species *T. gariepensis*. Head proportions also change with proportionately larger heads occurring in sympatry.
(b) Distributions of prey sizes eaten by *Typhlosaurus* immatures, adult males, and adult females under various conditions of allopatryand sympatry. Sympatric *T. lineatus* eat more larger prey items than do allopatric *T. lineatus*. Both figures from Huey *et al.* (1974).

The second study of character displacement involves two species of subterranean skinks (genus *Typhlosaurus*), which occur in sympatry throughout the sandridge regions of the southern part of the Kalahari semidesert (Huey *et al.*, 1974; Huey and Pianka, 1974). Both lizard species eat almost nothing but termites, largely the same few species. Although the smaller of the two species (*T. gariepensis*) is known only from sympatry, the larger species (*T. lineatus*) also occurs in allopatry on adjacent flat sandveld areas. Snout-vent lengths of *lineatus* increase abruptly at the boundary of the sandridges (Fig. 8.7a), suggesting divergent ecological character displacement in sympatry (although the possibility that sandridge habitats differ fundamentally from sandveld ones cannot be entirely discounted—see Pianka, Huey and Lawlor, 1979). Moreover, heads become *proportionately* larger in sympatry. Correlated with this increase in body size and head proportions is a dietary shift to larger castes and species of termites (Fig. 8.7b), which reduces overlap and probably competition with *T. gariepensis*. Ratios

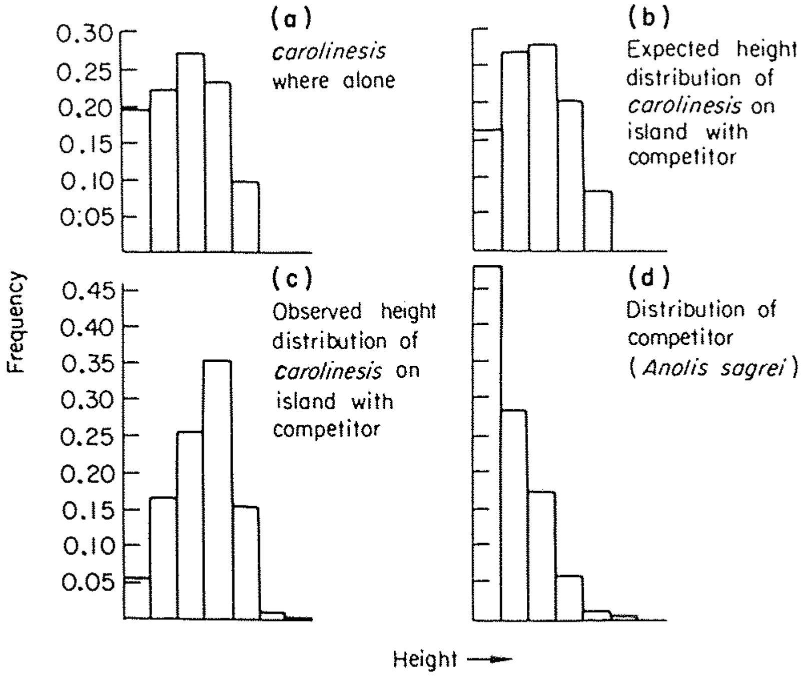

Fig. 8.8. Expected and observed frequency distributions of perch heights of *Anolis* lizards. (a) Observed height distribution of *A. carolinensis* where it occurs alone without competitors. (b) Expected distribution of perch heights of *A. carolinensis* on another island with different availabilities of various perch heights, assuming no niche shift. (c) Observed distribution of *Anolis carolinensis* on the second island with a competitor (compare with b). (d) Height distribution of the competing species, *A. sagrei*. From Schoener (1975a).

of snout-vent lengths of the two species in sympatry are about 1·17, while head length ratios are around 1·5.

Interpreting such niche shifts between allopatry and sympatry is often difficult due to geographical variation in various environmental aspects, such as resource availability (Schoener, 1969; Grant, 1972a; Connell, 1975). Schoener (1975a, 1975b) devised a technique to correct for such changes in resource availability and used it to demonstrate niche shifts in response to competition among *Anolis* lizards (Fig. 8.8).

Overdispersion of niches

Several different approaches to the theory of limiting similarity predict an upper limit on tolerable niche overlap (MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1975a; Lawlor and Maynard Smith, 1976; Fenchel and Christiansen, 1976). Schoener (1974) suggests that such limits on niche similarity of coexisting species, coupled with interspecific competition, should result in regular (as opposed to random) spacing of species in niche space (but see next section

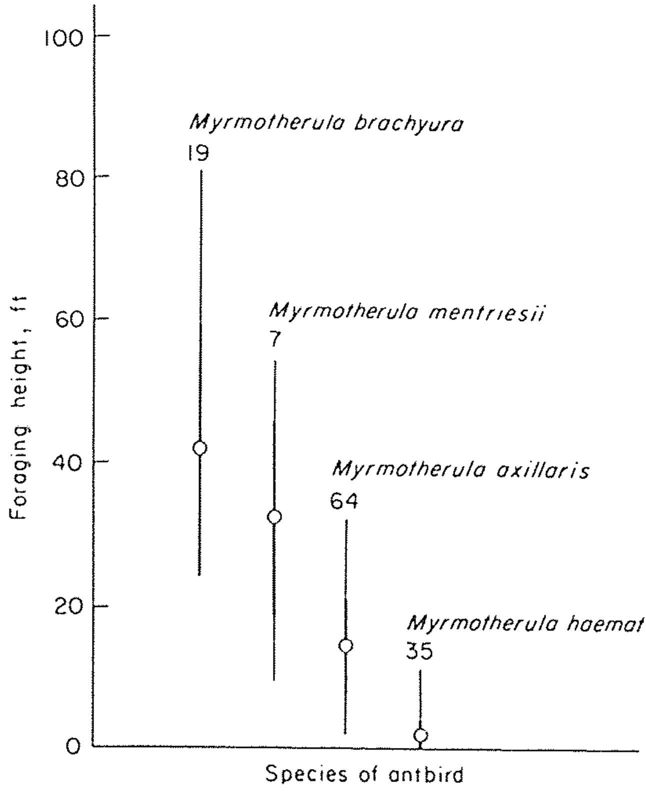

Fig. 8.9. Foraging heights of four species of sympatric antbirds (genus *Myrmotherula*). Means shown with dots and standard deviations by thickened bars. From MacArthur (1972) after data of Terborgh.

for an alternative). A number of sets of species that differ primarily along a single niche dimension do indeed appear to be separated by rather constant amounts (see, for example, Orians and Horn, 1969; MacArthur, 1972). One celebrated example is Terborgh's observation that various species of antbirds forage at different heights above the ground (Fig. 8.9).

However, as indicated above, ecologies of most potential competitors probably differ along several niche dimensions simultaneously. Thus, Schoener (1968, 1974) demonstrated that pairs of species of *Anolis* lizards with high dietary overlap tend to separate out in their use of microhabitats, while pairs using similar microhabitats overlap relatively little in prey sizes eaten (Fig. 8.10). Comparable inverse relationships between dietary and microhabitat overlap occur among many pairs of species of nocturnal gekkonid lizards in Australian deserts (Pianka and Pianka, 1976). In a similar vein, Cody (1968) found that grassland birds partition resources along at least three distinct niche dimensions, with the relative importance of various dimensions in separating species

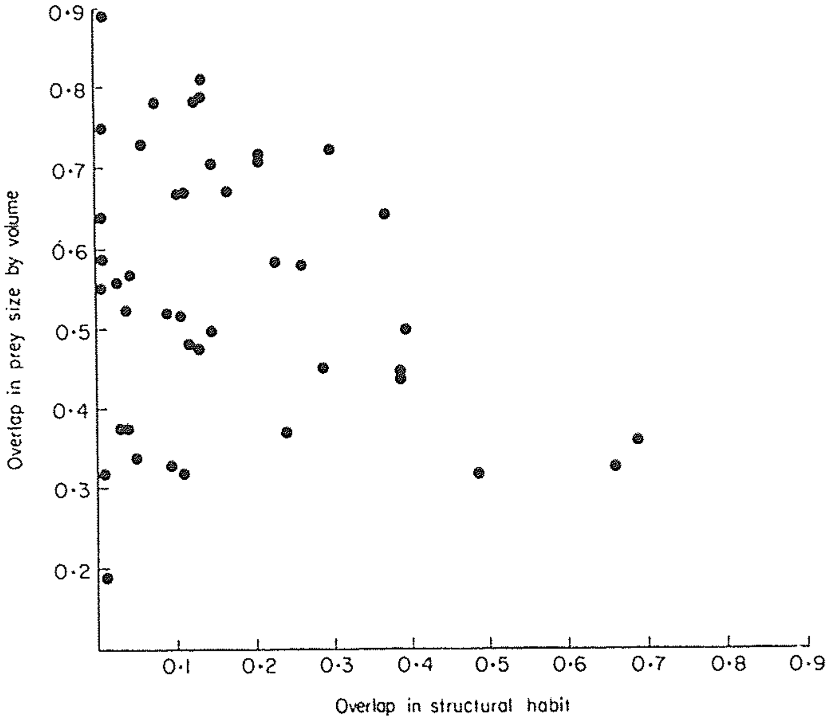

Fig. 8.10. Overlap in prey size plotted against overlap in structural microhabitat among various species of *Anolis* lizards on the island of Bimini. Pairs with high dietary overlap tend to exploit different structural microhabitats; conversely, those with high spatial overlap overlap relatively little in prey sizes eaten. From Schoener (1968).

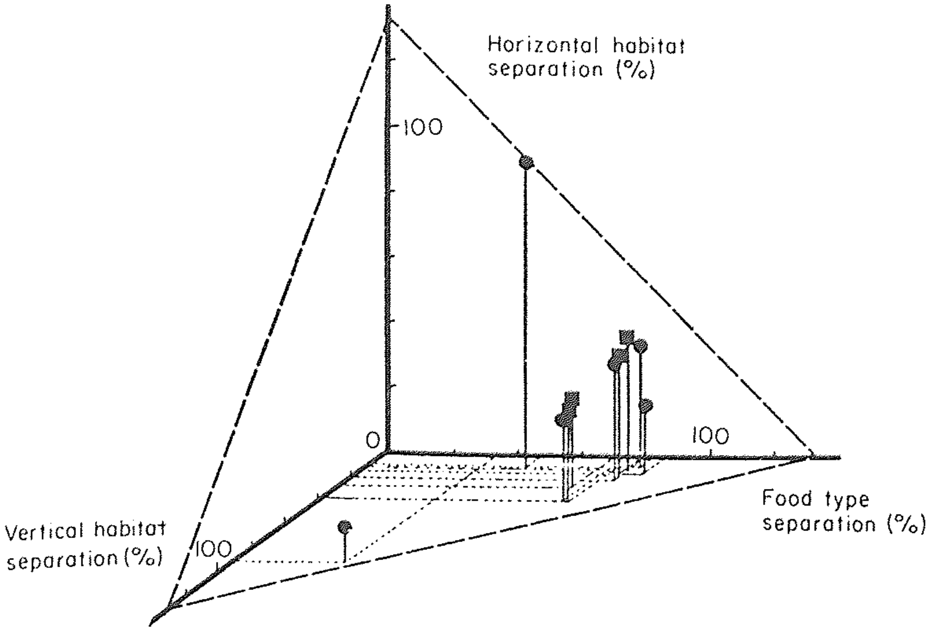

Fig. 8.11. Average niche separation along three dimensions in ten grassland bird communities, suggesting a relatively constant overall amount of separation. From Cody (1968).

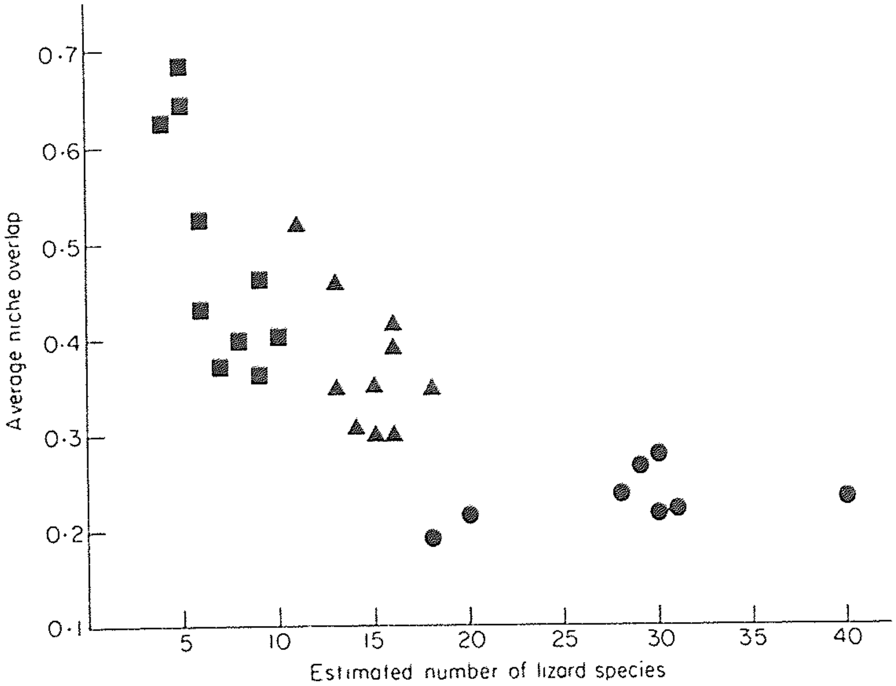

Fig. 8.12. Mean niche overlap plotted against the number of lizard species for 28 study areas on three continents. Squares represent North American sites (Great Basin, Mojave, and Sonoran deserts), triangles are areas in Kalahari semidesert of southern Africa, while dots indicate sites in the Great Victoria desert of Western Australia. This inverse correlation is highly significant statistically ($r = -0{\cdot}73$, $p < 0{\cdot}001$). Several estimates of maximal niche overlap are also inversely correlated with the number of lizard species. From Pianka (1974).

differing in various communities (Fig. 8.11). An intriguing degree of constancy in the overall niche separation along all three dimensions suggests that avian niches in these communities are both overdispersed in niche space and that bird species within the communities may have reached some sort of limiting similarity.

My own studies on the niche relationships of desert lizards along three dimensions also suggest overdispersion of niches (Pianka, 1973, 1974, 1975); however, niche separation among these lizard communities is not constant, but both average and maximal overlap vary inversely with the number of lizard species (Fig. 8.12). A decrease in overlap with increasing numbers of species is predicted by several theoretical formulations of limiting similarity and may be due to diffuse competition among coexisting species (see also below).

Guild structure

Another aspect of the pattern in which species are spread out in niche space concerns the extent to which functionally similar species exist in clusters of high overlap pairs. Members of such guilds (Root, 1967) would interact strongly with each other but weakly with other members of their community (see also section 9.5). In competitive communities, guilds would thus represent arenas of relatively intense interspecific competition.

Using the 'single-linkage' criterion of cluster analysis, a guild may be objectively defined as a group of species separated from all other such clusters by a distance greater than the greatest distance between the two most disparate members of the guild concerned. This definition allows complex hierarchical patterns of nesting of smaller guilds in the large ones (Pianka, 1978). Although techniques of measuring guild structure are embryonic, the concept has begun to attract increasing interest (Feinsinger, 1976; Inger and Colwell, 1977; Holmes *et al.*, 1979; Pianka *et al.*, 1979). Numerous intriguing questions can be raised about guilds, but very few answers can yet be supplied. For example, do guilds simply reflect gaps in resource space or can they be evolved when resources are continuously distributed? What are the effects of guilds on diffuse competition, community structure, and organization? What are components of guild structure (spacing, nesting, size, gaps, etc.) and how can they be measured? Some speculations about the effects of guild structure upon overall community stability are in section 9.5.

Experimental manipulations

Both Colwell and Fuentes (1975) and Connell (1975) have recently pointed out various limitations and shortcomings of natural experiments, especially the lack of a suitable control, and they make a strong case for experimental manipulation of densities in the field. Introduction and/or removal of species with concomitant monitoring of changes in population densities and/or niche shifts before, during, and/or after the experimental manipulation is potentially a fruitful avenue to studying competition in the field. Not all such experiments can be expected to produce results, however, because niche shifts and/or changes in population densities associated with the presence or absence of potential competitors need not necessarily occur in ecological time unless the populations concerned are periodically released from interspecific competition under natural conditions. A species that experiences strong interspecific competition pressures continually would not be expected to retain the capacity to use many of the resources and much of the niche space that is regularly exploited by its competitor; such a species might show only a slight niche shift in ecological time with removal of its competitor. Various such manipulative studies on competition have been undertaken with ants (Brian, 1952; Pontin, 1969), numerous marine invertebrates (Connell, 1961; Paine, 1966; Dayton, 1971; Menge, 1972; Vance, 1972; Stimson, 1970, 1973; Black, 1976; Haven, 1973), salamanders (Jaeger, 1970, 1971), lizards (Nevo *et al.*, 1972; Dunham, 1980), birds (Davis, 1973), as well as with many rodents (DeLong, 1966; Koplin and Hoffman, 1968; Grant, 1972b; Joule and Jameson, 1972; Joule and Cameron, 1975; Rosenzweig, 1971, 1973; Schroder and Rosenzweig, 1975). Many of these experiments are reviewed by Connell (1975).

Some removal experiments have documented competitive exclusion in pairs of species too similar to coexist. For example, Connell (1961) demonstrated that the barnacle *Chthamalus* was able to persist in the intertidal rocky zone normally occupied only by larger *Balanus* barnacles when the larger barnacle species was removed. Noting that two lizards *Lacerta sicula* and *L. melisellensis* have mutually exclusive geographic distributions on small islands in the Adriatic, Nevo *et al.* (1972) report on the experimental introduction of small populations of each species to islands that supported only the other species; in two of three such experiments, the introduced species went extinct, while on a third island the introduced species appeared to be replacing the native form. These authors also performed a reciprocal transplant introduction experiment with the two species on two small but similar islands for future workers to monitor.

Field experiments on naturally coexisting species have also been informative. Vance (1972) studied competition for empty gastropod shells within and among three sympatric species of intertidal hermit crabs by measuring shell preferences and by manipulating the availability of empty shells. An index of 'shell adequacy' was generated by offering crabs a choice of empty uncontested shells; given such a selection, most crabs moved into larger shells than those in which they were found in nature. Under natural conditions, unoccupied shells tended to be in the smallest shell size categories. Very small hermit crabs tended to have shells close to their preferred size, while shell adequacy generally decreased with increasing crab size. Addition of empty shells to the natural environment resulted in increased crab densities, indicating that shells were indeed a limiting resource in short supply. Vance suggested that habitat specificity differences among the three species of hermit crabs could allow the observed coexistence in spite of considerable overlap in their utilization of a limiting resource (shells).

Dunham (1980) studied interspecific competition between two coexisting species of iguanid lizards in Texas by experimentally manipulating densities. During this four-year study, two years were below average in precipitation (and, presumably, in productivity) whereas the other two years were wetter than average. In the two dry years, removal of the larger lizard species (*Scelaporus merriami*) had numerous significant effects on the smaller species (*Urosaurus ornatus*), including increase in density, feeding success, growth rates, lipid levels and prehibernation body weights. In the two wet years, however, treatments did not differ from controls. Removal experiments demonstrated only one effect of the smaller species on the larger one: survival was significantly higher in one of the two dry years. Competition between these two lizard species is clearly not reciprocal and varies in intensity from year to year.

In another field experiment on competition between two broadly sympatric species of sea stars, *Pisaster ochraceus* and *Leptasterias hexactis*, Menge (1972) removed all individuals of the larger *Pisaster* from one small island-reef and added them to another similar reef; a third undisturbed nearby reef supporting both species was monitored as a control (the reciprocal experiment involving removal and addition of *Lep-*

tasterias was not done). Although these two species of sea stars differ greatly in size and reproductive tactics, their diets do overlap broadly (Menge and Menge, 1974). Average weight of individual *Leptasterias* increased significantly with removal of *Pisaster* and decreased with its addition, while the size of control *Leptasterias* did not change (Fig. 8.13a). Moreover, estimated standing crops (biomass/m^2) of the two species varied

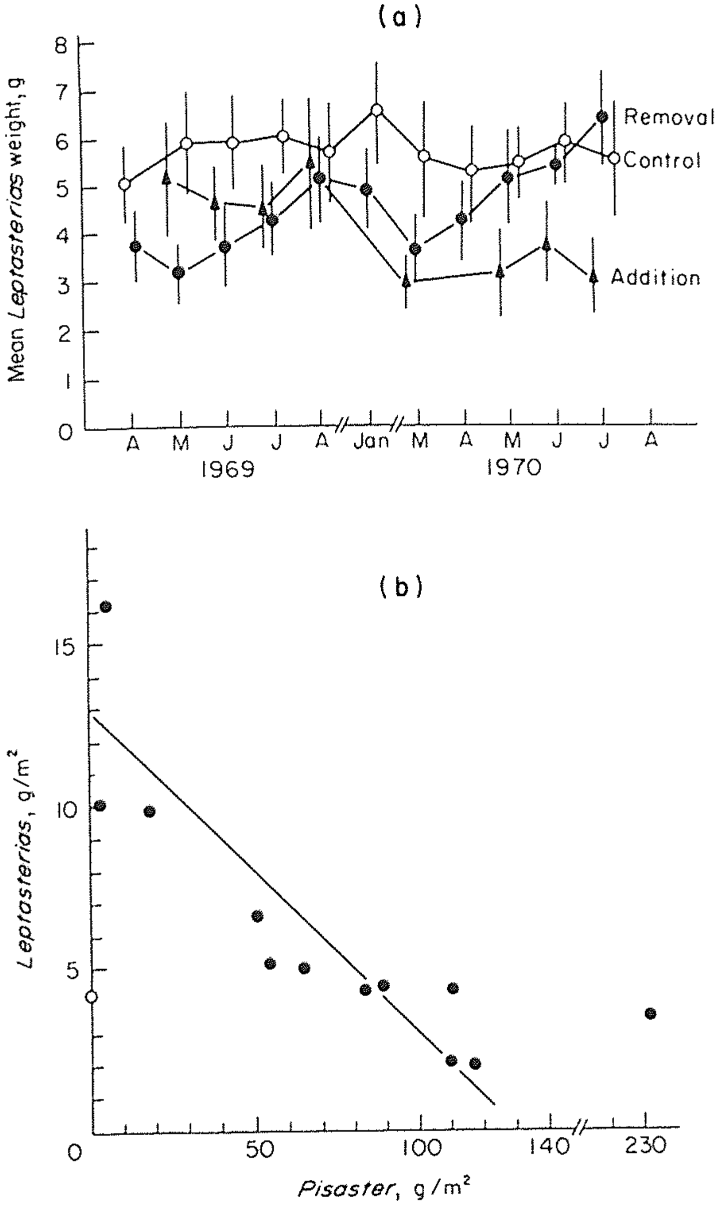

Fig. 8.13. (a) Changes in average wet weight of individual *Leptasterias* with removal of *Pisaster* (●), addition of *Pisaster* (▲), and in controls with no change in *Pisaster* densities (○). (Vertical lines represent 95 per cent confidence intervals of means.) (b) Plot showing the inverse correlation between the biomass per m^2 of two species of sea stars, *Leptasterias hexactis* and *Pisaster ochraceus* ($r = -0{\cdot}64$, $p < 0{\cdot}01$). From Menge (1972).

inversely over the areas sampled (Fig. 8.13b). Competition coefficients cannot be calculated from these data, but interspecific competition is clearly implicated. As indicated above, somewhat similar removal experiments have been undertaken with many other marine invertebrates and with small rodents (see Connell, 1974, 1975, for reviews of some of this work).

8.3 Neutral models of community structure

Until fairly recently, students of resource partitioning and community structure have been unable to accomplish much more than merely describe existing patterns of resource partitioning among various coexisting consumer species. Even such descriptive efforts seldom allow very useful comparisons with other studies of communities partially because there is 'no . . . standard protocol for community analysis' (Inger and Colwell, 1977). In some cases with low niche dimensionality, observed estimates of overlap have been compared with values of limiting similarity generated from various theoretical arguments such as those of MacArthur and Levins (1967) or May and MacArthur (1972). (For examples, see Orians and Horn, 1969 and/or May, 1974d.) But such comparisons may not be particularly revealing since values of limiting similarity depend strongly on the specific assumptions of models concerned (Abrams, 1975); this point was discussed more fully in section 5.3.

Sale (1974) responded to this dire need for null hypotheses by suggesting that communities might be compared to randomized versions of themselves. Overlap in observed communities of grasshoppers did not differ markedly from that in such randomized analogues, leading Sale (1974) to conclude that competition had not been a force in reducing overlap among or otherwise organizing these communities of insects. In a similar analysis using desert lizard communities, however, Lawlor (1980) found that average overlap was substantially lower in observed communities than in randomized replicates, suggesting that competition has shaped the organization of these lizard communities. This rather promising 'neutral model' approach has now been exploited in a number of studies of community structure (Caswell, 1976; Inger and Colwell, 1977; Pianka, Huey and Lawlor, 1979; Taylor, 1979; Joern and Lawlor, 1980; Connor and Simberloff, 1980).

8.4 Indirect effects of competition: competitive 'mutualists'

The traditional approach* to interspecific competitive interactions is strictly pairwise: only the *direct* effects of each species on any other target species are modelled. Indirect interactions, mediated through other members of the community, must also occur (Levine, 1976). Thus, two species with non-overlapping diets preyed upon by a common predator may nevertheless have a net negative effect on each other's population density. Similarly, two predatory consumer species with little or no dietary overlap can benefit each other indirectly if their prey species compete: an increase in either predator population depresses the density of its own resource population, hence ameliorating conditions for the other predator's major resource (for details, see Vandermeer, 1980). Under certain conditions, pairs of potential competitors can actually act to *increase* one another's densities if both

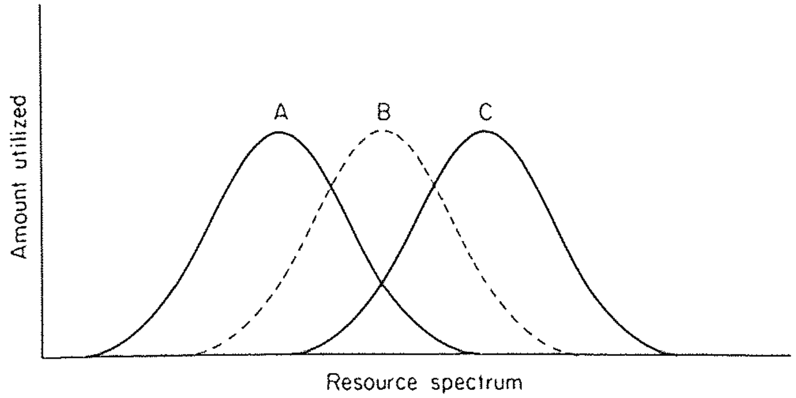

Fig. 8.14. Hypothetical illustration of the conditions leading to competitive mutualism between species A and C (here considered from the view of species C as the 'target' species—entirely analogous arguments can be made for species A). This example involves only a single resource dimension, but the phenomenon can also occur in cases of higher niche dimensionality. Resource requirements of species A and C overlap moderately, so that, in isolation, these two species are competitors. Both species A and C overlap more extensively with species B. When all three species coexist, the direct competitive effects of A on B are stronger than those between A and C; because these strong negative effects of A on B decrease the density of B, the negative impact of B on C is reduced by the presence of A. If this indirect effect mediated through species B is greater than the direct effect, A and C are in effect 'mutualists' in the context of the presence of species B. The arguments are easily extended to situations with more species.

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* As for example in the 'alpha matrix' of competition coefficients for a community (Levins, 1968).

share other competitors (Lawlor, 1980). Such a competitive mutualism may arise when two weak to moderate competitors have a common strong competitor: because both species inhibit this third species markedly, each has a beneficial net effect on the other even though their direct pairwise interaction is detrimental (Fig. 8.14). Lawlor (1979) extends this approach to n-species communities, stressing that pairs of species with the potential for high overlap and strong interspecific competition might in fact interact only weakly in the context of an entire community. Further, he relates such indirect competitive mutualism to community assembly, noting that the addition of one of a pair of such species may make it easier for the other to invade a community. Members of different guilds may often be competitive mutualists (Pianka, 1980).

8.5 Some prospects and problems

Many possibilities still remain for important theoretical work on competitive interactions. Innovative new ways of modelling competition that depart from the traditional Lotka–Volterra equations and the concept of constant competition coefficients will be of great interest. Such approaches should provide fruitful insights into the actual *mechanisms* of competition. Even within the framework of the Lotka–Volterra equations, competition coefficients badly need to be treated as *variables* in both ecological and evolutionary time (see, for example, Leon, 1974, and Lawlor and Maynard Smith, 1976). As explained above, competitive effects between two species may frequently vary with the presence or absence of a third species; theory on interactive competition coefficients is virtually nonexistent. An attractive alternative to competition coefficients is to quantify species' interactions with partial derivatives that reflect the 'sensitivity' of each species' own density to changes in the density of the other ($\partial N_i/\partial N_j$ and $\partial N_j/\partial N_i$ terms measure the dynamics rather than the statics of competition). Alphas could also profitably be made density dependent; the actual *shapes* of resource utilization functions might be allowed to change (with an appropriate constraint such as holding the area under the curves constant) either in ecological time due to ethological release or in evolutionary time via directional selection conferring advantages on individual genotypes that deviate from the mean. Roughgarden (1974a, 1974b, 1974c, 1979) has made a start on such theoretical work. Niche overlap theory could be profitably expanded to incorporate effects of diffuse competition (Pianka, 1974, 1975); moreover, the theory of limiting similarity needs to be extended to many species and to multidimensional resource space.

Fundamental questions emerge from such theoretical considerations. Consider, for example, two competitive communities with similar numbers of species, one of which is composed of several distinct clusters of competitors with strong competitive interactions among themselves but very weak or nonexistent interactions between members of different clusters. Compare this community with another with the same number of species, but one in which all members interact moderately with all others (i.e., greater diffuse competition). Such a difference in guild structure between two communities might arise with a difference in niche dimensionality, for instance. What, if any, differences will there be between the two communities in community-level properties, such as stability? Will maximal tolerable overlap between pairs of species differ? One might find, for instance, stronger competitive interactions and greater niche overlap between *pairs* of competing species in the first community with fewer immediate neighbours in niche space, but *total* niche overlap summed over all interspecific competitors might well be greater in the second community with greater diffuse competition (see, for example, Pianka, 1974). Further work on indirect effects and competitive mutualism will obviously be of great interest.

Niche breadth theory could profitably be expanded to include age-specific phenotypic changes in resource use. Under such a selection regime, will population structure evolve to make most efficient use of available resources? What selective forces determine the optimal degree of within-phenotype versus between-phenotype components of niche breadth?

The neutral model approach has considerable promise. Algorithms for constructing various randomized analogues of real communities are by no means exhaustive. Families of such randomized communities with differing degrees of semblance to observed communities should help to elucidate the structure of the latter (see Lawlor, 1980, for the beginnings of such an approach). A major virtue of this methodology is that samples of analogue communities can be generated that are adequate for statistical comparisons with observed communities. The approach essentially allows 'experimentation' with real communities and is limited only by the imaginative powers of ecologists. A promising but as yet unexploited variant on these techniques is the artificial 'removal' and/or 'addition' of species to existing communities.

Numerous possibilities also exist for important empirical work, of course. For example, the within-phenotype and between-phenotype components of niche breadth have seldom been separated (but see Roughgarden, 1974b). As pointed out repeatedly earlier, field experiments clearly hold great promise, although their precise nature is not easily foreseen. Incomplete removal or addition experiments may well allow quantification of competition by monitoring rates of return to equilibrium densities, thereby measuring the dynamics of population growth (see Hallet and Pimm, 1979). Indeed, gathering useful new data on competition and niche relationships is probably far more challenging (and likely to be more significant) than adding to its existing theoretical foundation.