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Chapter 9

Modelling competition

> . . . he was very sorry to part with his sheep, which he left with the Academy of Sciences of Bordeaux, which offered as the subject of the prize of that year the question why the wool of this sheep was red; and the prize was awarded to a scholar from the North, who demonstrated by A plus B, minus C, divided by Z, that the sheep must be red and die of scab.
>
> *Voltaire (1759)*

> To construct appropriate mathematical models of ecological processes, is, of course, only one half of an ecologist's labours. No less important is their testing, but the matter seems to get much less than half of most workers' attention.
>
> *E. C. Pielou (1972)*

> Of course there are good models of the world and bad ones, and even the good ones are only approximations.
>
> *R. Dawkins (1976)*

All scientific knowledge can be thought of as a model of reality, a model which is continually updated as new information accumulates. Generally the word model is used in a narrower sense to mean a mathematical or graphical description of some aspect of nature. There is a great deal of confusion surrounding the value and application of models, largely because models are constructed for different reasons, and a model constructed for one purpose cannot always be used for another.

This chapter explores some of the models that have been used to explore competition in populations and communities. These models are important not so much because of their mathematical rigour, but because models can shape the way in which questions are asked and determine the kind of experiments performed and data collected. The principal objective of this chapter is not to survey all the mathematical models of competition. Rather, the objective is to provide an overview of the role of models in the study of competition, and a perspective on the way in which these models have influenced experimental and descriptive studies of the real world. The practical examples of Chapter 2 and the theoretical framework presented here will provide the foundation for the remainder of the book.

Models can have positive roles in ecology by forcing us to state our assumptions clearly and by assisting us in exploring the logical outcomes of these assumptions. These and other virtues of models are explored below. However, models also have costs. Simberloff (1983a) writes of the 'bloated theoretical literature' when complaining that many models contribute little to the development of ecological theory. (In fairness, one could equally conclude, as I do in Chapter 4, that simply collecting another descriptive data set may be equally irrelevant to the long-term goals of ecology.) There can also be a tendency to assume that because mathematical models are strictly logical, or because they are explored with huge computers, that their conclusions correctly reflect biological reality. The basic thesis of this chapter is that models are tools. What we need to do is to sort them. There are at least three possible categories. Some may be demonstrably valuable and should be used and refined. Others are perhaps being kept only for sentimental value. Still others, new and untested, may seem to be sufficiently important that it is worthwhile testing their assumptions or predictions; given that it is often easier to spawn models than to test them, care will have to be taken about assigning models to this third category.

9.1 KINDS OF MODELS

Starfield and Bleloch (1986) provide an excellent introduction to the topic, and suggest five reasons for constructing models:

(1) to define problems;
(2) to organize thoughts;
(3) to understand data;
(4) to communicate and test understanding;
(5) to make predictions.

Models constructed for one purpose may be quite unsuitable for another. We use a simpler classification here, and recognize three purposes: prediction, exploration and description. Consider these in turn.

Predictive models are designed to predict the future states of systems based on relationships specified within the model between predictor (independent) variables and the predicted (dependent) variables. The dependent and independent variables must be measurable. Mechanistic relationships are not necessarily assumed. Success or failure of the model is easy to judge: the more accurate the prediction is, the better the model (Rigler, 1982).

Exploratory models can be derived from predictive models, but often have a completely independent origin. Such models allow the logical consequences of changes in assumptions or initial conditions to be explored systematically. The distinction is that the scientist is using the model to assist in a thought experiment rather than with the goal of simple prediction.

Descriptive models are used to summarize existing knowledge about the behaviour of a system. The picture may not be sufficiently complete to permit the model to be used to make predictions, but the summary can serve as a foundation for future work, or as a guide to possible experiments.

A variety of other classifications could be used. For example, Pielou (1977) proposes that mathematical models can be classified dichotomously using four criteria for a total of 16 possible styles of models. She uses the criteria:

(1) whether it treats time as continuous or discrete;
(2) whether it is an analytical or a simulation model;
(3) whether it is deterministic or stochastic;
(4) whether it is inductive (empirical) or deductive (theoretical).

However, this classification emphasizes the actual construction of the model rather than the objective for which it is used. Thus, the simpler division into three based upon modelling objectives will be used for examining models of competition.

Another useful classification of models comes from the realm of general systems theory (Weinberg, 1975), where one can recognize small, medium and large number systems. These have very different properties, and therefore generate different approaches to modelling. Small number systems have few components and few interactions, and these systems are amenable to precise mathematical description. Population ecology is an example, and while science has in general been successful with small number systems, in ecology these are usually inadequate because the small number systems can only be created by artificially removing populations from the many connections they have with other populations. At the other extreme are large number systems where there are so many components that the average behaviour becomes a useful description of the system. The ideal gas laws provide one example; the position and velocity of a particular gas molecule are not of interest, but the properties of volume, temperature and pressure are. These systems too have been scientifically analysed with some success.

The problem in ecology according to Lane (1985) is that ecosystems are neither large nor small number systems. These medium number systems contain too many components to be treated analytically, and too few for statistical analysis. Further a rhinoceros and a grass plant cannot be averaged like an ideal gas molecule, nor are their behaviours and population dynamics equivalent to random events. As the number of components increases arithmetically, the number of interactions increases geometrically. Thus some method of simplification is necessary in order to solve problems involving medium number systems (Lane, 1985; Starfield and Bleloch, 1986). This requires carefully preserving critical interactions and components while excising or ignoring others. The inherent difficulty in doing so wisely probably explains why, at present, medium number systems require modelling approaches that are as much an art as a science.

In designing models, an investigator is faced with many trade-offs. The more precise the model is made, the more it incorporates the details of a specific system, the greater the possibility that accurate prediction is possible. However, as the model is finely tuned to one situation, there is an inevitable loss of generality. The skill of the modeller determines the degree to which a model combines generality and accuracy. Empiricists are frequently criticized for not appreciating the importance of general models, whereas modellers are often criticized for their lack of attention to reality.

Starfield and Bleloch (1986) and Holling (1978) have suggested two axes along which models can be arranged: degree of understanding, and volume of data. When the degree of understanding is low but the volume of data is high, models may be used to search for patterns and test hypotheses about them. In contrast, the degree of understanding may be high (in the sense that there is some understanding of the structure of the problem), but there may be insufficient data with which to work. This is frequently the case with ecological problems, and in such cases ecologists and ecological models are presented with two daunting challenges. First, management decisions may have to be made despite the lack of data and understanding. How do we make good decisions under such circumstances? Secondly, how do we most efficiently collect the information necessary to improve our understanding and predictive ability? Starfield and Bleloch (1986) address both of these problems.

Let us now consider some of the specific models which have shaped research on competition. The first, the Lotka–Volterra models, have been extensively covered in introductory textbooks. They are included here for completeness, but can be skipped by those familiar with them.

9.2 THE LOTKA–VOLTERRA MODELS

The Lotka–Volterra models are so popular in the study of ecology that the study of the equations themselves is frequently recognized as ecological research (Simberloff, 1983a; Fagerstrom, 1987). They can be classified as exploratory models since they assist us in thinking about how competing organisms might change in population size as a function of time and population sizes of competitors.

In introducing the use of these equations for the study of competition, Lotka (1932) begins with the concept of exponential growth. That is, in the absence of any restraining influences, the rate of growth of a population is assumed to be proportional to existing population size:

$$\mathrm{d}N/\mathrm{d}t = rN \tag{9.1}$$

Since this is clearly unrealistic, we assume that limitations in resource supply set an upper limit to population size, termed carrying capacity, K:

$$dN/dt = rN[(K - N)/K] \tag{9.2}$$

Note that when population size is very small (N near zero), the population growth rate is close to that of Equation (9.1) and the population is growing exponentially. When population size is very large (N near K), then population growth rate is nearly zero.

To explore competition, two equations must be examined simultaneously. What is needed for each population is a measure of how it is affected by the presence of the other. Consider population 1. The effect of each individual of population 2 upon population 1 can be measured by comparing the *per capita* effects of population 2 relative to those of population 1. This is done with an entity called a competition coefficient. If individuals of population 1 have the same effect on population 1 as individuals of population 2, then the competition coefficient equals unity – that is, the two populations are indistinguishable from the point of view of population 1. However, if individuals of population 2 have much greater effects upon individuals of population 1 than individuals of population 1 have upon each other, then the competition coefficient is greater than unity. Conversely, if the per capita effects of population 2 are much less that the effects of population 1, then the competition coefficient is less than unity. By proceeding with analogous arguments for population 2, one ends up with two differential equations. The growth rate of each population is then determined both by its own population size and that of the other population, with the effects of the latter weighted by its competition coefficient (a_{ij}) as follows:

$$dN_1/dt = r_1N_1[(K_1 - a_{11}N_1 - a_{12}N_2)/K_1] \tag{9.3}$$

$$dN_2/dt = r_2N_2[(K_2 - a_{22}N_2 - a_{21}N_1)/K_2] \tag{9.4}$$

By definition, each species' competition coefficient upon itself is unity. Since there are two competing populations, two outcomes are possible when these populations are allowed to grow, interact and reach equilibrium: (1) one species becomes extinct and the other climbs to its own carrying capacity; or (2) the species co-exist.

A principal objective of studying these equations has been to determine what controls whether the two species co-exist, and, if they fail to do so, which of the two will be the winner. Since the only parameters to work with are the values for r_1, r_2, N_1, N_2, K_1, K_2 and a_{12} and a_{21}, the solution is given in terms of these.

One way to picture this two-species interaction is using species isoclines. An isocline is simply all possible sets of conditions where the growth rate of a population is zero. In the case of this model it is all possible pairs of population densities where the growth rate of one population is zero. The isocline is derived by setting the population growth rate equal to zero:

$$dN_1/dt = r_1N_1[(K_1 - a_{11}N_1 - a_{12}N_2)/K_1] = 0 \tag{9.5}$$

For this population, the growth rate is zero when one of three conditions is satisfied:

$$r_1 = 0 \qquad N_1 = 0 \qquad K_1 - a_{11}N_1 - a_{12}N_2 = 0 \tag{9.6}$$

Obviously if r or N equals zero, the rate of population growth will be zero and thus these are trivial solutions. It is the third condition which is of interest. We can plot this isocline on a graph by solving for the intercepts of the axes and joining them with a straight line. The intercept with the N_1-axis is derived by setting N_2 equal to zero, in which case

$$\begin{aligned} K_1 - a_{11}N_1 - a_{12}0 &= 0 \\ K_1 - a_{11}N_1 &= 0 \\ K_1 &= a_{11}N_1 \\ N_1 &= K_1/a_{11} \end{aligned} \tag{9.7}$$

Similarly, the intercept with the N_2-axis is determined by setting N_1 equal to zero. What we are doing biologically is asking how many individuals of either population 1 (N_1) or population 2 (N_2) are required to produce a zero growth rate for population 1. These results can be plotted as in Fig. 9.1. Above this isocline population 1 has exceeded the carrying capacity, so the population size declines with time. Below the isocline the population size gradually increases. At any point along the isocline the growth rate is zero and the population size

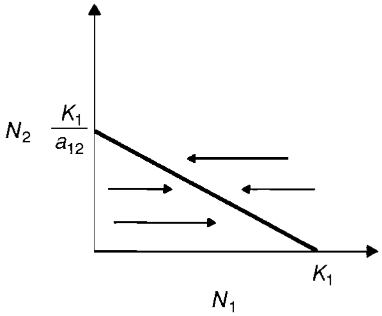


Fig. 9.1 The isocline for population 1 plotted in two-dimensional space, showing all possible combinations of N_1 and N_2 (that is, population sizes for populations 1 and 2) where the population growth rate of N_1 is zero. As the arrows show, above this line population size falls to the isocline, and below the line population size increases to it. A similar isocline can be drawn for population 2.

remains constant. This simple plot enables us to explore how the size of population 1 will change under all possible sets of conditions represented by different sizes of the two populations.

To explore the interaction of both populations simultaneously, we must go through the identical series of steps for population N_2, and plot its isocline in an identical manner. This is where things start to become interesting, and we can begin to talk about the behaviour of the model, for the two isoclines can be arranged in different ways. Figure 9.2 shows the four possibilities, and each of

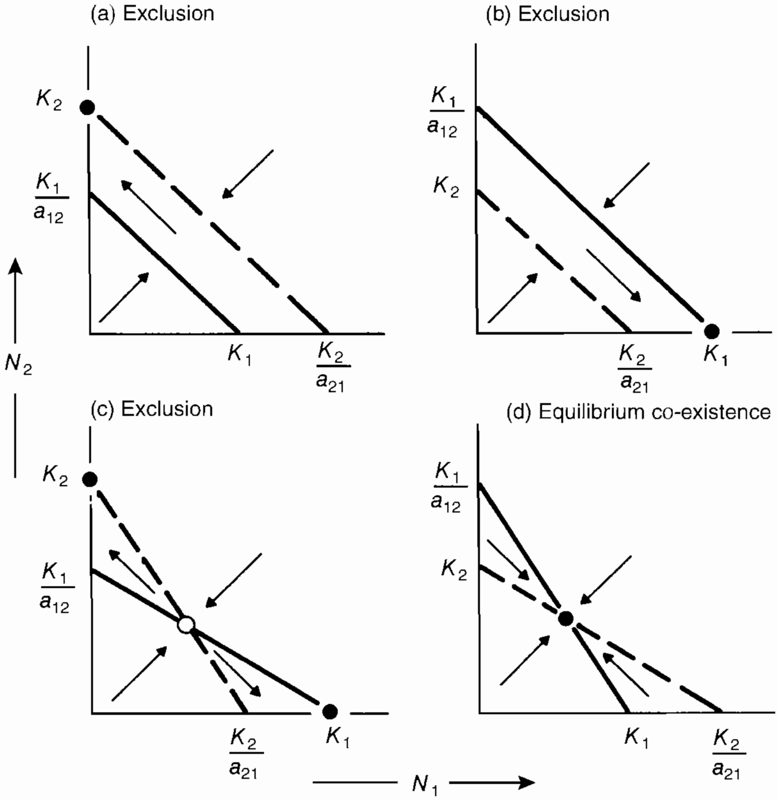


Fig. 9.2 Four possible arrangements for the isoclines of two competing populations. The arrows show, as in Fig. 9.1, changes in population size with time. The solid dots represent the equilibrium points (expected outcomes) of these pairwise interactions. Three of the four possible arrangements (a)–(c) result in competitive exclusion. (a) Exclusion; competitive dominance by population 2. (b) Exclusion; competitive dominance by population 1. (c) Exclusion; contingent competition (Yodzis, 1978). The winner depends upon the initial starting densities. The open circle is an unstable equilibrium point which is of greater mathematical than biological interest. (d) Equilibrium co-existence: *not* to be confused with 'co-existence' which includes many other mechanisms that prevent competitive exclusion (e.g. Fig. 7.1).

these arrangements of isoclines has different consequences for the mixture of the two species.

In the top two cases only one species survives at equilibrium; i.e. there is a competitive dominant and a subordinant, with the dominant being the species with the isocline furthest from the origin. We must specify at equilibrium because if we start at some arbitrary mixture of the two populations, both will co-occur until the trajectory collides with the axis of the dominant. Since ecologists frequently use these models to study co-existence under equilibrium conditions, the top two models often receive the least attention.

In the third case the two species co-exist. This is because each species is more negatively affected by intraspecific competition than by interspecific competition. It is regularly assumed that intraspecific competition is indeed higher than interspecific competition, based on the assumption that more similar individuals compete more intensely, with conspecifics being most similar to each other. Thus, this outcome has a certain appeal based on its assumed biological reality. Also, since many modellers are most comfortable with the assumption that nature is at equilibrium (even if we know that this is most certainly not the case), this outcome has a certain mathematical appeal. Thus, this outcome is frequently given more attention than the above two. Questions such as 'How many species can co-exist at equilibrium . . .?' can be explored using this model.

In the final situation, the winner of the two-species competition can be predicted only when starting population sizes are known. Yodzis (1978) calls this 'contingent' competition. The intensity of interspecific competition is such that, once a species begins to achieve numerical superiority, it damages the other so severely that the outcome becomes certain. Which population achieves this initial superiority depends solely on the assumed starting density. Gill (1974) emphasizes that this outcome is only possible if there is interference competition between the two species. We can again predict with certainty that only one of the populations will persist at equilibrium. Thus, the model is again unsatisfactory for the study of co-existence under equilibrium conditions. It is also unsatisfactory because it suggests that the resource harvesting characteristics of the two species do not allow us to determine their behaviour in mixture. Note that in theory co-existence is possible, in that there is an equilibrium point where the two isoclines intersect. This is an unstable equilibrium point, however, in that as soon as the populations diverge from this precise mixture of population sizes, they move inexorably towards exclusion. Thus, this equilibrium point is of limited mathematical or biological interest.

In a more rigorous manner, we may specify the above outcome in terms of the carrying capacities (K) and competition coefficients (α_{ij}) of the two populations. Since both may vary, it is easiest to picture this by assuming the carrying capacities of the two populations are identical ($K_1 = K_2$). In cases where they require the same resources, and we use an appropriate measure of carrying capacity such as biomass, this is not unreasonable. Under such circumstances we can specify the three outcomes as follows:

Exclusion (competitive dominance) (Fig. 9.2(a) and (b))

$$\begin{aligned} a_{11}/a_{21} < 1 \quad &\text{and} \quad a_{12}/a_{22} < 1 \\ a_{11}/a_{21} > 1 \quad &\text{and} \quad a_{12}/a_{22} > 1 \end{aligned} \tag{9.8}$$

Exclusion (contingent competition) (Fig. 9.2(c))

$$a_{12}/a_{22} > 1 > a_{11}/a_{21} \tag{9.9}$$

Equilibrium co-existence (Fig. 9.2(d))

$$a_{12}/a_{22} < 1 < a_{11}/a_{21} \tag{9.10}$$

Roughgarden (1979, Fig. 21.4) illustrates for each of the three above outcomes the actual trajectories which pairs of populations will follow given different starting population sizes.

Variation in carrying capacity can be superimposed on these relationships. For those who think graphically, Vandermeer (1970) has provided an elegant demonstration of these relationships (Fig. 9.3). In this figure the isoclines are plotted relative to different axes. Displacing the axes is equivalent to changing the carrying capacity and, as the figure shows, a situation with a stable equilibrium point (A) can be converted to one with competitive dominance (B) as carrying capacities are changed.

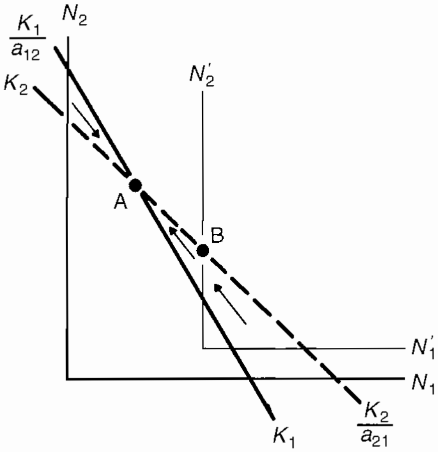


Fig. 9.3 The effect of changing carrying capacity on a two-species system. Using axes N_1 and N_2, stable equilibrium occurs at point A. Using axes N_1' and N_2' population 2 excludes the other and achieves dominance at point B. (After Vandermeer, 1970.)

9.2.1 The community matrix

The two-species situation can be expanded to n interacting species, in which case the equation for each species is expanded to include all other species. Thus, the equation for population 1 expands to

$$\mathrm{d}N_1/\mathrm{d}t = r_1 N_1[(K_1 - a_{11}N_1 - a_{12}N_2 - \cdots - a_{1n}N_n)/K_1] \qquad (9.11)$$

where the equation includes a competition coefficient for each of the n species with which it is possible to interact. For the case of three species, each isocline becomes an isoplane in three-dimensional space. The competitive dominant in such a three-species system would be the one with an isoplane farthest from the origin. If the planes were tipped such that they intersected, stable lines rather than stable points can be imagined. Situations with more dimensions are usually represented with a matrix of competition coefficients called a community matrix (Levins, 1968; Yodzis, 1978). In this matrix (Fig. 9.4) each row lists all of the competition coefficients determining the population growth rate of the species represented by that row. In the same way each column vector lists all of the impacts which that species has upon the growth rates of neighbouring populations. By considering rows or columns, one can think either in terms of the effects of all species upon a selected species of interest, or of the effects of a selected species upon all possible neighbours.

Such matrices appear to be powerful tools for comparing the different kinds of communities which exist in nature, and exploring how they may respond to perturbations. To date, much of the emphasis has been upon the mathematical stability of such systems. That is, are there stable points, and how do model communities respond when perturbed away from such stable points (Levins, 1968; May, 1974)? In this context, stability occurs when the net population

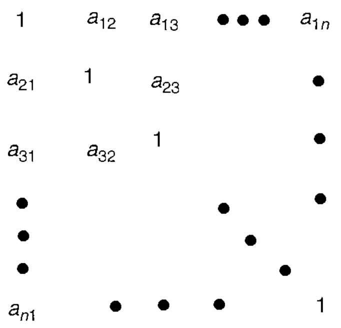


Fig. 9.4 A community matrix. Each competition coefficient a_{ij} measures the effect of an individual of population j upon an individual of population i. Each row describes how individuals of other populations reduce the population growth rate of the population represented by that row. Each column describes how one population reduces the growth rates of all other populations.

growth rates of all populations, dN_i/dt, equal zero. If such a system is perturbed, it may return to the stable point, it may continue to diverge from it or it may remain at the point to which it was perturbed. If it does change with time, it may do so monotonically or else through oscillations (May, 1974). Such questions assume either that nature is sufficiently near to equilibrium to make such questions relevant, or at least that stability is a useful reference point for studying real systems.

Since many natural communities are likely to be far from equilibrium, we may ask what other roles exist for community matrices. Yodzis (1978) has provided an exploration which places much less emphasis upon stability. Instead, he asks questions about the different kinds of community matrices which can exist, the sort of biological interactions which will exist in each, and finally (although it is not considered here) how each will respond to harvesting. Yodzis begins by contrasting competition for space with the competition for other kinds of resources. He proposes that although competition for many resources may be symmetric, competition for space is likely to involve interference competition and therefore be asymmetric. He emphasizes the importance of competition for space in ecological communities, noting that space will be particularly important as a resource for sessile organisms such as corals and plants, but also for the many kinds of animals which are territorial.

Yodzis then generates model communities using competition coefficients selected randomly according to certain constraints. He explores two basic types of communities. In the first kind, the competition coefficients are all greater than unity. This means that individuals of each population damage individuals of other populations more than themselves. As a consequence the first population to arrive and colonize a site holds it against all other populations. Thus, although competition is very definitely present in such communities, the distribution and abundance of populations is a consequence of their initial colonization patterns. Yodzis therefore calls these 'founder controlled' communities.

A second type of community matrix which Yodzis explored consisted of pairs of competition coefficients in which there are many asymmetric interactions. (Given that the competition coefficients were generated at random subject to certain constraints, such matrices also probably included co-existent interactions.) In this case, although initial colonization patterns initially determine the distribution and abundance of populations, competitive dominants gradually exclude their neighbours. Yodzis calls these communities 'dominance controlled'.

Several important points emerge. First, Yodzis draws our attention to the fact that matrices with different combinations of competition coefficients have different kinds of biological behaviour. This suggests the research strategy of asking what kinds of matrices occur in nature and what the consequences might be for the organization of such communities. Secondly, he notes that this may allow us to make predictions about how these communities will respond to natural perturbations such as harvesting. Lastly, he proposes that competition for space may be fundamentally different from competition for other kinds of resources, and encourages us to think about patterns of community organization that can be shared by very different kinds of organisms.

Although such matrices can be constructed artificially for exploratory modelling, producing actual community matrices is difficult. One procedure involves using measures of niche overlap to produce competition coefficients; this is invalid, as discussed below. An alternative is to use experimentally measured values from large competition experiments. This approach is considered in more detail in Chapter 6.

9.2.2 Relationship with biological reality

The Lotka–Volterra equations should be considered exploratory models with limited direct relationship to real ecosystems, and their popularity is probably at least partly attributable to sentimental attachment. Some obvious weaknesses are the unrealistic assumptions of the model, such as those that individuals are all equivalent, making age or size class structure irrelevant, and that individuals are thoroughly mixed so that they all influence each other directly and equally. The principal problem in applying these models to predict the behaviour of real communities lies in assigning meaningful values to the coefficients. This is so difficult as to be impossible for many systems. In the case of uniform environmental conditions (constant competition coefficients), the number of coefficients to be estimated is the square of the number of populations, so a comparatively simple community with 10 species requires the estimation of 100 competition coefficients. In nature the intensity of competition may vary with a range of environmental factors including climate, kind of resources, spatial distribution of resources and temporal variation in all of the foregoing. Thus, the coefficients themselves become variables.

In addition there is a second problem in estimating competition coefficients. Each competition coefficient for a row in a matrix is scaled relative to intraspecific competition for that species (for example, Begon and Mortimer, 1981). Intraspecific competition is assumed to be equal to unity for each species; i.e. in the community matrix it is assumed that the diagonal matrix consists of ones. However, with communities made up of very different species, there is no obvious reason why intraspecific competition should be the same for them all. In such cases we might expect intraspecific competition to be much more intense in some species than in others. If we then attempt to add up the effects of a species down a column vector, we are comparing competition coefficients each measured on a different scale. For a simple two-species system of very similar species, this assumption may not be far from biological reality, but the more we try to work with entire communities, the more biologically unrealistic the assumption seems.

These models can also misdirect research. For example, ecologists have been driven to understand the factors which determine the number of species which can co-exist in a given area (May, 1986). The Lotka–Volterra equations direct attention to the points of stable co-existence. However, there is an important distinction between co-existence and stable co-existence. In a world where the environment constantly fluctuates, non-equilibrium co-existence is more biologically plausible (for example, Huston, 1979; Grime, 1979; Pickett and White, 1985) even if it is less mathematically tidy. Reviews on competition such as Arthur (1987) still deal largely with stable co-existence. This illustrates the power that models can have in determining the sorts of questions that ecologists consider interesting.

Fisheries models and intraspecific competition

The misuse of models can have profound economic consequences. Models of oceanic fisheries are often build upon Lotka–Volterra type foundations. In studies of maximum sustained yield (MSY) a population is assumed to grow exponentially with a damping effect of interspecific competition leading to zero population growth at carrying capacity K. Carrying capacity is defined as maximum size of the fish population that can be supported by a given area of ocean, that is, the population size were intraspecific competition is high enough that birth matches death rates, producing no further increase in biomass. The maximum population growth rate then occurs half way between zero and K (Fig. 9.5(a)). If fishing effort is included in the model, then when the population remains unchanged with a given fishing effort, the annul catch is an equilibrium catch (Fig. 9.5(b)). The application of these models has had disastrous results, as illustrated most recently by the collapse of the North Atlantic cod fishery in Canada. Corkett (1997) argues that this has occurred because of an approach to models that is verificationist rather than falsificationist. Does the scatter in Figure 9.5(b) allow falsification of the model, or does one instead assume that if further data were collected, the model would indeed be confirmed? According to Corkett "*all* models of stock assessment are constructed according to the *verificationist's view of science*, cannot be falsified, and are of no more value for the management of the world's fisheries than the primitive magic spells of witch doctors" (italics his, p. 166). If, however, the possibility of diminishing returns with increasing effort are included, then the fishing effort curve (Fig. 9.5b) is no longer the mirror image of the logistic growth model (Fig. 9.5a), in which case, Corkett argues, falsifiable predictions are generated. It is essential, argues Corkett, that models show us what cannot be achieved, and in particular, what might be the unintended consequences of political decisions about stock management. "... pointing out what cannot be achieved is one of the most characteristic tasks for the development of an *understanding of the real-world*" (italics his, p. 166). Corkett draws extensively upon the writings of Popper, but it is instructive to see the degree to which his arguments converge with those of Peters (1980a, b). Peters agrees with Corkett that too many models persist because they lack falsifiability (Rigler and Peters, 1995), but argues that it is the

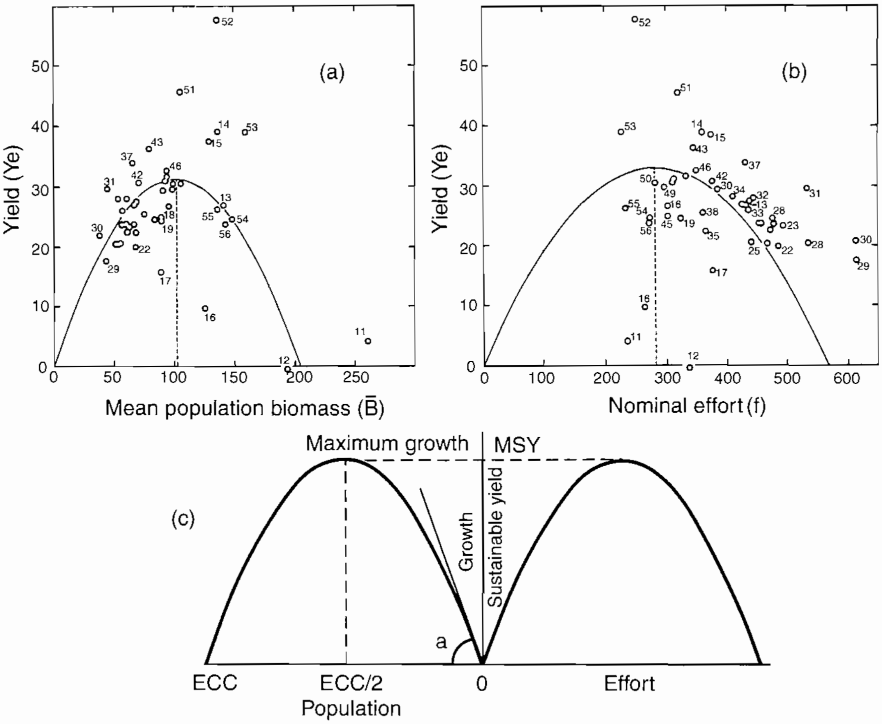


Fig. 9.5 Empirical (a, b) and theoretical (c) versions of the Graham–Schaefer model for fisheries. The parabolic curves assume intraspecific competition sets an upper limit on the number of fish which an area of ocean can support. Data points are for an exploited area of Pacific Halibut, with years marked 10, 11, . . . representing 1910, 1911, etc. In the lower panel, the maximum sustainable yield (MSY) curve on the right is the mirror image of the productivity curve on the left, which assumes intraspecific competition sets an upper limit upon fish population growth. The MSY model further ignores any effects of diminishing returns with increased fishing effort. (From Corkett, 1997.)

search for understanding rather than prediction which leads to the proliferation of unfalsifiable models.

9.3 THE MACARTHUR MODEL FOR RESOURCE SUBDIVISION

MacArthur (1972) explored the possible mechanisms underlying the a_{ij}'s of the Lotka–Volterra equations, and the implications of these for the way in which organisms might subdivide the resources available to them. How, he asked, are we to measure the value of a_{ij} in these equations? Picture, he said, the resources arranged along a line, say from smallest to largest, and consider two species that differ in the range of resources they eat. For each species he derived a resource utilization curve u that was normally distributed with a standard deviation of σ (Fig. 9.6). If the difference between the means of the two species is d, MacArthur showed that

$$\alpha = e^{-d^2/4\sigma^2}$$

That is, the smaller the value of d the closer the two species means along the resource continuum, the larger a_{ij}, which he designated by α, will be.

Is there some sort of natural disturbance that might be typical of species in this situation? We can explore this by plotting α, the competition coefficient, against the distance between the two species. More precisely, we can scale this distance by dividing it by the pooled standard deviation, which measures the breadth of the resource utilization curve (Fig. 9.7). The result? "As d grows from zero, α falls slowly at first and then more rapidly, most rapidly of all at $d = \sqrt{2}\sigma$,

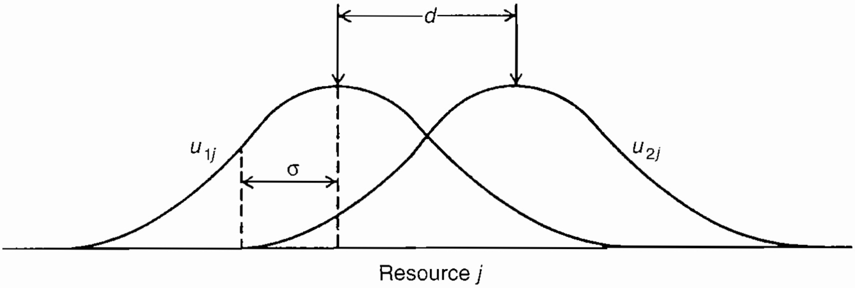


Fig. 9.6 Utilization u_{1j} and u_{2j} of two species along a resource axis. The distance between the means of the curves is d, and σ is the standard deviation of each. (From MacArthur, 1972.)

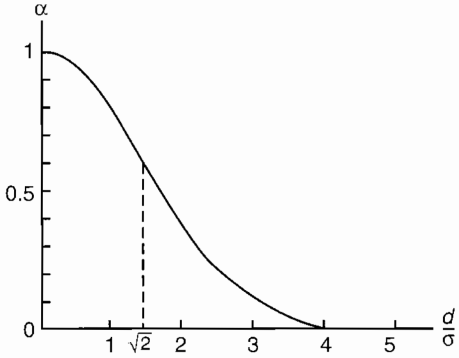


Fig. 9.7 The competition coefficient, α, plotted against the distance between mean utilization of two species as measured by α/σ.

and then more slowly again" (MacArthur, 1972, pp. 42–43). It is around $d = \sqrt{2}\sigma$ that α starts to become significant, and so, we might expect species in nature to be separated by approximately this distance.

These simple relationships form the foundation for what MacArthur called the economics of consumer choice. We can explore where an animal should feed to get the most food, and what items of food it should pursue. We can ask how many species can reasonably be expected to co-exist along a continuum of resources.

This simple model spawned several distinctive lineages of ecological research, including Pianka's work on desert lizards, and Brown's work on desert rodents (see Cody and Diamond, 1975), and many more elaborate models for species co-existence and co-evolution along gradients (e.g. Roughgarden, 1979; Pianka, 1981, 1983). Whether or not the formula for α is a reasonable measure of competition between two species, this formulation for the interaction between two species has had a powerful appeal to animal ecologists. It has become a way of seeing the world. The functions of theory, according to MacArthur, are to inspire experiments and inform us whether we have a coherent explanation with all the necessary ingredients. How has this model fulfilled his two criteria? At very least, many of the contemporary debates about pattern and assembly in ecological communities (see for example Schoener, 1974; Jackson, 1981; Strong et al., 1985; Diamond and Case, 1986) have their origin in this elegant formulation for the mechanisms of competition between two species. We will return to this model in section 9.13.

One of the most important questions about this widely used model is its degree of robustness. That is, how sensitive is the condition $d \geq \sigma$ to details in the underlying model (Yodzis, 1989)? If the curve shape is allowed to vary on kurtosis, that is, to range from platykurtic (broad peak, thin tails) to leptokurtic (narrow peak, thick tails), will the condition for limiting similarly change? Platykurtosis has no significant effect, but leptokurtosis can make quite a difference (Roughgarden, 1979; Yodzis, 1989). Since there is little reason to believe that resource utilization curves are exactly Gaussian, as in Figure 9.6 (Austin, 1976, 1990), there is little reason for confidence in the quantitative results of such an analysis. Yodzis concludes that "limiting similarity remains a valid and important *qualitative* insight into the structure of nature" (italics his) (p. 127), but ". . . a *quantitative* science of limiting similarity, while possible in principle (given unlimited grant support and vast armies of ecologists to carry out the necessary field and theoretical work), does not appear to be a practical goal at present" (p. 127).

9.4 LOOP ANALYSIS AND APPARENT COMPETITION

Recall that when a pair of species is emeshed within a large and complex food web, it is possible to generate interactions with third or fourth parties that create mutually negative effects for the pair under consideration. This phenomenon of 'apparent competition' was introduced in Chapter 1. It is not always possible to determine whether these are actual 'real' interference mechanisms (such as in ants and acacias) or simply fortuitous consequences ('apparent competition') arising from the particular network in which the allegedly competing species are found. A convenient framework for investigating this phenomenon comes from the realm of loop analysis, which allows for competitive interactions as well as other possible interactions among large networks of species. The objective of loop analysis is not to predict precise outcomes for the population sizes of particular species but rather to identify whether additions to or deletions from a single component (e.g. adding phosphorus to lake water) will produce increases or decreases in other elements of the network (e.g. an increase or decease in cyanobacteria or commercial fish species.) Loop analysis for biological systems was first popularized by Levins (1975), and has since been used for a broad range of studies from the physiology of disease to marine food webs (Lane, 1985).

We start with the (rather formidable) assumptions of linear system dynamics and a system near steady state. The interactions between pairs of species are then represented not by actual functions, but only by the slopes of those functions, that is, by plus or minus signs (Fig. 9.8). Where a system has n components (usually species), there will be an $n \times n$ matrix of signs summarized in a community matrix and a loop diagram (Fig. 9.8). As the number of components increases arithmetically, this matrix and the complexity of the loop diagram expand in size geometrically. Figure 9.9 shows a simple example going from 2 to 4 species with various connections to one another. The community effects matrix in the middle column shows the effects of increasing inputs to each component. At the far right the term F_n refers to the feedback of the entire system. If F_n is positive the system is unstable. There is insufficient space here to

Differential equations

$$\frac{dx_1}{dt} = b_1 - p_{12}x_2 - k_1x_1 - \theta$$

$$\frac{dx_2}{dt} = b_2x_2 + r_{12}p_{12}x_1x_2$$

Community matrix

$$\begin{array}{c|cc} & x_1 & x_2 \\ \hline x_1 & -1 & -1 \\ x_2 & +1 & 0 \end{array}$$

Loop diagram

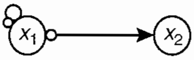
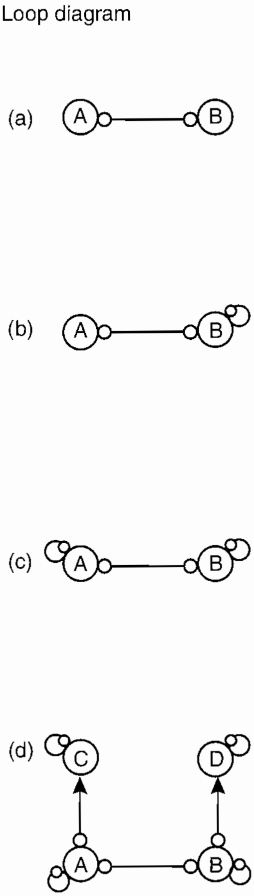


Fig. 9.8 Some essentials of loop analysis, as illustrated by a simple predator prey system. The differential equations governing the two populations are given at the top, followed by the community matrix and loop diagram. The prey is self-damped and enhances the predator. The predator decreases the prey. In the differential equations, b_1, b_2, p_{12}, k_1 and θ are parameters. (From Lane, 1985.)



Community effects matrix

(a)

Input	Effect on: A	B
+ A	0	+
+ B	+	0

Model characteristics

Variables = 2
Links = 2
Loops = 1
Valid paths = 2
Valid complements = 2
F_n (overall feedback) = +1

(b)

Input	Effect on: A	B
+ A	−	+
+ B	+	0

Variables = 2
Links = 3
Loops = 2
Valid paths = 3
Valid complements = 3
F_n (overall feedback) = +1

(c)

Input	Effect on: A	B
+ A	*	*
+ B	*	*

Variables = 2
Links = 4
Loops = 3
Valid paths = 4
Valid complements = 4
F_n (overall feedback) = 0

(d)

Input	Effect on: A	B	C	D
+ A	+	−	+	−
+ B	−	+	−	+
+ C	−	+	?	+
+ D	+	−	−	?

Variables = 4
Links = 10
Loops = 7
Valid paths = 16
Valid complements = 26
F_n (overall feedback) = −3

Fig. 9.9 Loop analysis of interference competition. A and B are competing species, C and D are predators. (From Lane, 1985.)

properly introduce the mathematical foundations of these analyses, and so the reader who lacks faith is referred to the original paper (Levins, 1975) and a later overview (Lane, 1985).

Effects upon each component are read across each row, with three possible outcomes, increase (+), decrease (−) or unknown (?). Unknowns can arise when two sets of interactions have opposite signs. Outcomes can often be counter-intuitive. Thus, at the top, increasing the amount of A produces no effect on A (in part because there is no negative feedback loop of A upon itself) but a positive effect on B. By way of explanation, Lane says "... a positive input to A results in an increase in B, not a decrease as might be expected, since the parameter input (+) times the path (−) must be multiplied by the feedback of the component (−) (negative by definition since the complement contains no variables) and this product is divided by the overall feedback (+)". Without the space to explore the mathematics further, we shall have to accept the results of the model as given. The essential point is that as negative food loops are added to species A or species B (that is, as intraspecific competition is added to the model) the nature of effects change. When new components are also added as species C or species D, the outcomes can generate all manner of possible cases of apparent competition. "These simple models are inadequate representations of interference competition since an increase in either species results in an increase in the other as result of overall positive feedback (F_n). Thus, as a result of community effects, the relationship is mutualistic (++) rather than competitive (−−) .... Thus even the simplest models of biological interactions can be erroneous and/or confusing if they are not checked first for total network effects" (p. 357).

9.5 COMPETITION ALONG GRADIENTS

The Lotka–Volterra equations explore competitive interactions within a single environment; only time and the number of individuals of the two species vary. Any changes that occur within the environment are assumed to be the effects of one species upon another, and therefore are included within the competition coefficient. Most species, however, occur in habitats with obvious spatial structure, quite often along gradients. Recall (section 2.2.3) that erosion and deposition are widespread processes that produce resource gradients in habitats ranging from mountainsides to wetlands. Further, recall the increasing reservoir of studies of competition along gradients (Chapter 7). Pielou had a long interest in such gradients, and she developed a number of valuable (but frequently overlooked) models to explore species responses to gradients. Here I summarize a model introduced in *Ecological Diversity* (Pielou, 1975, pp. 90–99).

Assume, says Pielou, that two species, A and B, colonize an environmental gradient. Assume that the equations describing population growth are functions of position along the gradient, G. Further, imagine a three-dimensional space with axes A, B and G, and assume that the isoclines for each species are planes. The isocline, recall, is the set of points in which the per capita growth rate of either species (e.g. $(1/A)\mathrm{d}A/\mathrm{d}t$) equals zero. Figure 9.10 shows the situation, in which case the population axes, A and B, are vertical and horizontal just as in Figures 9.1–9.3, and the gradient goes into the page. The curved arrows then indicate the trajectories of the two species for some value of G. In the top of Figure 9.10, there is an unstable equilibrium, so that at any point along the gradient, either species A or B wins. In this case, as G changes, there would be, at some point, an abrupt shift from species A to species B. This situation produces a crisp transition from dominance by one species to dominance by the other.

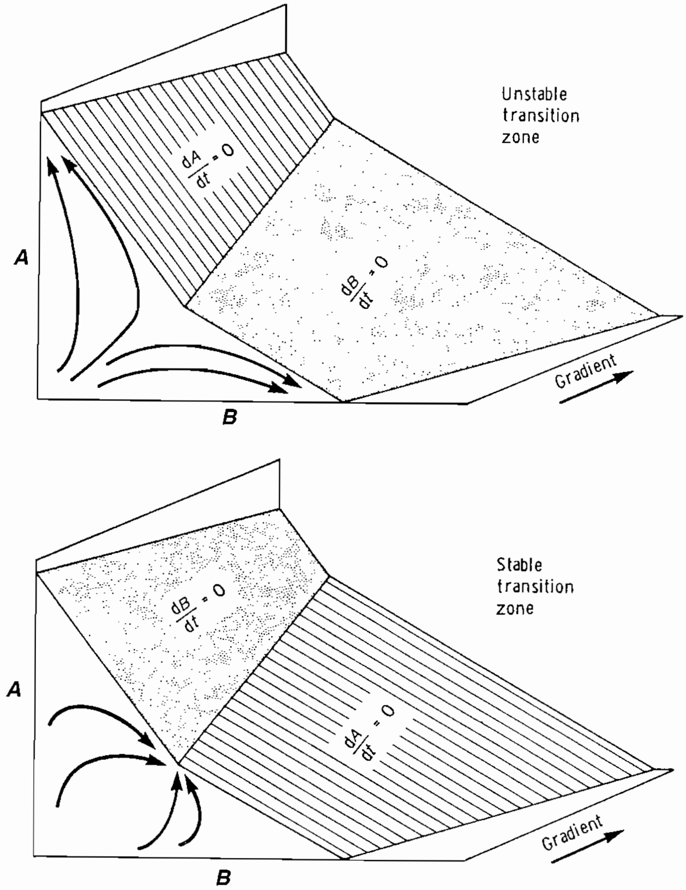


Fig. 9.10 Two-species competition on an environmental gradient. The isoclinal planes are $dA/dt = 0$ (hatched) and $dB/dt = 0$ (stippled). (From Pielou, 1975.)

Now instead assume that the equilibrium point is stable, so that at any point *G*, the population sizes converge upon a point with population sizes A, B, as shown in the lower diagram. In this case, as *G* changes, the relative abundances of A and B will slowly change, so that instead of an abrupt shift from one species to another, there will be a slow transition. This simple model, in which per capita growth is dependent upon *G*, is therefore capable of generating either abrupt or blended species boundaries.

The expectation of an abrupt boundary in the case of the unstable equilibrium goes somewhat beyond what the model actually predicts, says Pielou. The equations assume an enclosed space, and that the outcome of the interaction depends only upon the initial number of individuals of the two species present. In a real zoned community, the only uniform environments are vanishingly narrow strips and the strips are certainly not closed to immigration. An abrupt transition would only occur, therefore, if on one side of the boundary, A was always in a high enough proportion to ensure its dominance, and if on the other side, B was always present in a sufficiently high proportion to ensure its dominance.

In practice, then, there will usually be some spill-over, so that even if environmental conditions and initial population sizes would lead to dominance by one species, there would always be enough immigration from the other to maintain its population as well. In the field therefore, even if the populations had an unstable transition zone, one would be likely to find some individuals of each species occurring in the other's habitat, even if they were unable to reproduce.

Not satisfied with merely producing a model, Pielou then went on to explore methods of testing whether blended or blurred situations occurred. This was part of the reason for studying the zonation of *Cakile edentula* (Keddy, 1981, Chapter 3). The presence of the grass *Ammophila breviligulata* had strongly negative effects upon the annual *C. edentula*, but even though the population growth of *C. edentula* was demonstrably negative (death rate greater than reproductive rate) for long portions of its zone overlap with *A. breviligulata*, it none-the-less occurred mixed with *A. breviligulata* because of constant immigration (see also Watkinson, 1985b). Pielou also asked whether there were other means to distinguish between blending and blurring in the field, and suggested that comparing situations with steep slopes as opposed to narrow slopes might provide a means to do so. To the best of my knowledge, no one has taken this further.

What happens if one relaxes another assumption in the Lotka–Volterra model, and instead of assuming that species react instantaneously to one another, allows for a lag in response? This is done by making each species' growth rate a function not of the present population size of the other species, but a function of the population size of the other species at Δt units of time earlier. If species A and B are then allowed to colonize a gradient, simulations show that repeated zones, or stripes can appear, with alternating zones of dominance. These strips migrate down the gradient, producing a cyclical mosaic, as the population sizes of the two species oscillate. In the simulation Pielou ran, the oscillations were damped so that ultimately a steady state was reached with two discrete zones. It would, however, be possible to devise a more complicated model with a stable limit cycle and permanently migrating stripes. Thus, when one sees a series of vegetation bands on a gradient, it is possible that population dynamics may also be a causal agent.

Finally, Pielou adds, "It would also be easy, though perhaps unprofitable, to modify the original simple model . . . in many other ways" (p. 98). "The great merit of simple models" she continues, "is that they show what can happen, and what curious (or, at least non-obvious) phenomena are worth looking out for" (p. 99). The suggestion that some models may be unprofitable is a worthy contribution itself, and one well worth re-emphasizing. Just because one can make a model does not mean it is worth doing; restraint in the realm of model building may be as admirable as restraint in the realms of human reproduction.

Pennings and Callaway (1992) appear to have located an example of unstable transition in a southern California salt marsh. In this arid climate, flooding and salinity are uncoupled; that is, flooding decreases but salinity increases with elevation, so that higher elevations are hypersaline salt flats. Two common salt marsh plants both occupy an intermediate position on this gradient, and "biomass of both species was greatest immediately adjacent to their abrupt border." Transplant experiments showed that both species grew best in this intermediate region in the absence of neighbours, but co-occupy it in the field. Thus, Pennings and Calloway conclude: "since the border between *Salicornia* and *Arthrocnemum* occurs in prime habitat for both, the competitive interactions were not one sided but rather represented a standoff: each species excluded the other from the portion of the superior habitat in which it was the dominant competitor. Results of the competition experiment are mirrored by the patterns of standing biomass across the marsh. For each species, standing biomass was higher near their border than further away, corroborating our conclusion that the area near the border represents the best habitat for both species."

9.6 A RESOURCE COMPETITION MODEL

In the Lotka–Volterra model, the behaviour of two species was described using six constants: the inherent growth rates, carrying capacities and competition coefficients for each species. Six different constants are needed to explore a resource competition model proposed by Tilman (1982).

Only one of his models is considered here: the case of two species competing for two essential resources. Recall that essential resources were defined as non-substitutable resources in Chapter 1. A good example would be the requirement of plants for both light and nutrients, where one cannot be substituted for the other.

We begin by considering the growth rate of one species in two-dimensional space. However, in this case the two dimensions refer to the relative abundances of the two resources rather than to the abundance of the two species. As with the Lotka–Volterra model, we explore the behaviour of a single species by deriving its isocline, and then move to superimposing the isoclines of two species. A species' isocline is determined by specifying all possible sets of resource levels which produce zero net growth. In the case of essential resources, the isocline will look like that in Fig. 9.11. Below a critical level of either resource the population size declines. In this case the critical levels are marked as R_1' and R_2'. For all possible resource levels in the hatched area, growth is positive. If either resource is at the critical minimum level, growth is halted – thus the abrupt right angle in the isocline.

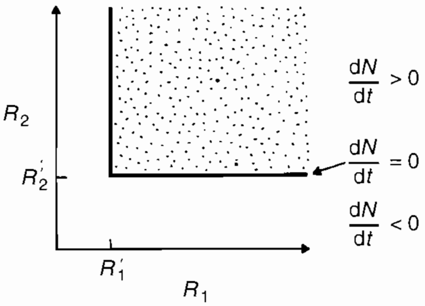


Fig. 9.11 The response of a population to two essential resources, R_1 and R_2 (recall Fig. 1.3). The thick line marks the zero net growth isocline where resource levels (R'_1 and R'_2) are just sufficient to maintain the existing population size. Above the critical levels R'_1 and R'_2 the population will grow (stippled area); below these resource levels the population size declines.

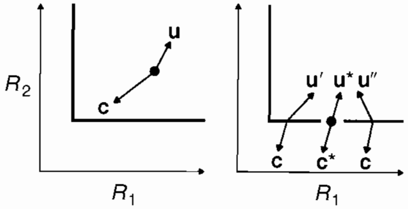


Fig. 9.12 (Left) The contrasting effects of resource supply rate (**u**) and resource consumption rate (**c**) on the resource levels in a habitat (R'_1, R'_2) indicated by the solid dot. The population can be pictured pulling the characteristics of the habitat (solid dot) towards the lower left by converting resources to biomass, whereas the supply rates pull it towards the upper right. The zero net growth isocline is also shown; in this case the population will continue to grow until the consumption vector (**c**) pulls the solid dot to the zero net growth isocline. (Right) The equilibrium point occurs when the environment (solid dot) has been pulled to the zero net growth isocline and the resource supply vector exactly balances the resource consumption vector (**u***, **c***).

Once the minimum necessary conditions for growth are specified, the rate of resource supply (or renewal) is considered. The biological argument here is that all habitats have a rate of resource renewal. In the case of plants it would be the rates of addition of elements like phosphorus through weathering and rainfall. In the case of scavenger beetles it would be the rate of death in small mammals. In the case of dung beetles it would be the rate of defecation in large mammals. In desert rodents it would be the rates of seed production by plants. In any habitat it should be possible to measure the supply rates of key resources. In a two-resource system we need to specify a supply vector, **u**, which specifies the rate of renewal for R_1 and R_2. This resource supply vector for the habitat is illustrated in Fig. 9.12 (left). The resource supply vector may vary with position along the two resource axes (Fig. 9.12, right). Obviously the resource supply vector, assuming it is positive, will gradually increase the resource levels above the isocline. Once this occurs the population will being to grow.

Once the population begins to grow, it begins to consume resources. This leads to the final constant which needs to be considered: the resource consumption vector, **c**. If a species is consuming two essential resources, one could measure the amount of resource consumed per unit time. A simple way of doing this might be to analyse the organism for the level of the two resources in 'its tissues. Alternatively, one might actually try to monitor the rates of resource depletion by determining rates at which dung beetles degrade dung or rodents consume seeds. If this is done, the result is the vector **c** called the resource consumption vector. Typical resource consumption vectors are illustrated in Fig. 9.12.

It should now be possible to picture intuitively the behaviour of this model. The current state of the environment is specified by the dot in Fig. 9.12 (left), and the resource consumption vector and resource supply vectors engage in a tug-of-war, pulling the environment around the two-dimensional space. If the rate of consumption exceeds the rate of supply, then the resource levels will gradually decline (i.e. the state of the environment will drift from upper right to lower left) until the isocline is intersected. At this point the growth of the population stops, halted by whichever resource is limiting at that isocline.

Where will it all end? It is obvious that equilibrium is possible if there is a point (or points) where the supply and consumption vectors are equal and opposite, i.e.

$$\mathbf{u} + \mathbf{c} = 0 \tag{9.12}$$

This equilibrium point must be on the isocline. Depending upon the size and direction of the supply and consumption vectors, it may also be a stable point, as illustrated in Fig. 9.12 (right, middle pair of vectors).

With these constants one can model the behaviour of a single population in this two-dimensional resource space. The next step is to pose questions about the behaviour of two species sharing this space. This is done by repeating the above steps for a second species. Note that although it is necessary to derive a new isocline and new consumption vector, the supply vector will remain the same, so that only four additional constants need to be specified for the second species. The possible outcomes are shown in Fig. 9.13. They are identical to the four possibilities identified with the Lotka–Volterra model: exclusion (competitive dominance by one of the species), unstable equilibrium (contingent competition) or equilibrium co-existence.

Consider these possibilities in turn. In the first case the isocline of species A is always inside that of species B. This means that species A requires less of both essential resources. At equilibrium it will have 'pulled' the resource state to a level outside the isocline of species B, and thus species B will decline to

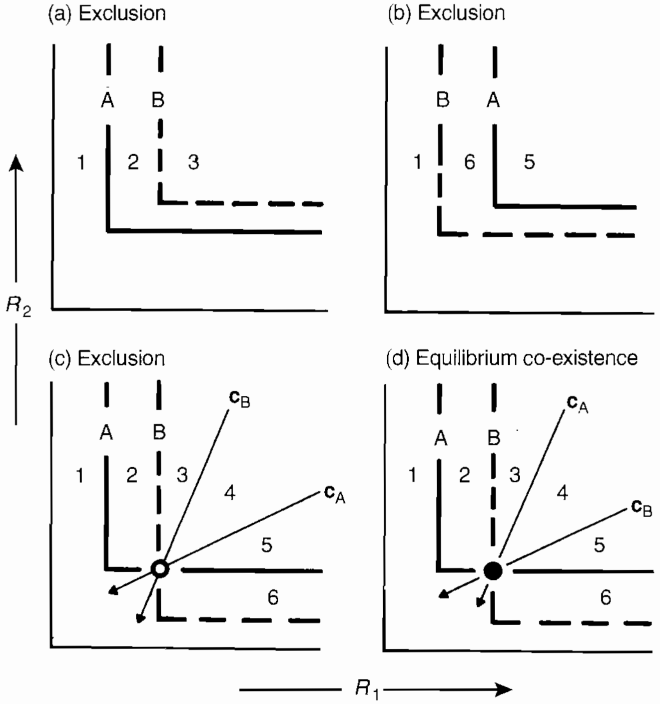


Fig. 9.13 The four possible outcomes of populations A and B interacting for resources R_1 and R_2 with consumption vectors $\mathbf{c}_A$ and $\mathbf{c}_B$. (a) Exclusion; competitive dominance by A. (b) Exclusion; competitive dominance by B. (c) Exclusion; contingent competition in region 4 (regions 1–6 are discussed in the text). (d) Equilibrium co-existence in region 4. (Regions 1–6 are discussed in the text.)

extinction. This is analogous to the situation in Fig. 9.2(a). A similar situation occurs in the second case, except that species B is dominant. In both of these cases, there is a shared requirement for the resources, and the dominant is the species that is capable of lowering resource levels to the point where the other is unable to survive.

The remaining two cases have isoclines which cross. Obviously, crossed isoclines produce an equilibrium point. In Fig. 9.13(c) the point is unstable, and in Fig. 9.13(d) it is stable. Up to this point the outcomes are little different from those of the Lotka–Volterra model. Where the behaviour deviates from the Lotka–Volterra model is the greater range of possibilities in the last two situations. In order to explore this, however, resource supply processes require more attention. For simplicity, consider the case of stable equilibrium (Fig. 9.13(d)). We must define another point, called the resource supply point, which specifies the maximum possible levels of the two resources. It has coordinates (S_1, S_2). Further assume that the rate of supply of a resource is dependent upon the distance which a point (R_1, R_2) is from it. That is, assume that rate of supply is proportional to $S_i - R_i$. If this is the case, then, for any arbitrary point (R_1, R_2) the resource supply vectors will point towards (S_1, S_2). Moreover, the length of the vector will vary with the distance from that point. The position of this resource supply point is then used to explore the co-existence models further. Now return to the numbered regions in Fig. 9.13(c) and (d). If the resource supply point is in region 1, then neither species can survive. If it is region 2, then only species A is capable of surviving and, in a symmetrical way, if it is in region 6, then only B is capable of surviving. Under these circumstances biological interactions are unimportant – the resource supply levels are simply outside the tolerance limits of one of the two species. When by themselves, either species can survive in regions 3, 4 and 5. When mixed, however, species A wins in region 3 and species B wins in region 5. In the case of situation (d), stable co-existence, the species will co-exist if the resource supply point is in region 4. This can be understood by picturing the trajectory that the species will follow in each of these regions. In regions 3 and 5 an isocline is intersected, whereas in region 4 they move towards the stable point. Exactly the same behaviour occurs in Fig. 9.13(c), except that in region 4 either species A or species B will win depending upon the initial conditions. In this case the equilibrium point is unstable, so that if there is the slightest departure from it one of the species will be driven to extinction; it is therefore only of mathematical interest. This is identical with the situation in Fig. 9.2(c). However, in the resource consumption model the critical factor which determines whether the equilibrium point is stable is the consumption vectors of the two species. If each species consumes relatively more of the resource that limits its own growth at equilibrium, then the point will be stable. If each species consumes more of the resource which limits the other's growth, then the point is unstable. This is exactly what occurred with the Lotka–Volterra model – there is stable co-existence only if intraspecific competition is greater than interspecific competition.

Tilman (1982) uses this model to explore questions of co-existence in plant communities, and readers are referred to his monograph for more details. The strength of this model is its emphasis upon mechanism. The picture of plants pulling the environment in different directions like stretching a piece of sheet rubber is a vivid one. A problem is that the amount of information needed to construct a predictive model is still excessive. Tilman (1982) writes "To test this theory thoroughly, it will be necessary to know the resource requirements and competitive interactions of the dominant species under controlled conditions, the correlations between the distributions of these species in the field and the distributions of limiting resources, and the effects of various enrichments on the species composition of natural communities". Since the model is relatively new, the verdict is not yet in on its utility. However, except for certain specific sets of conditions, it too may be exploratory rather than predictive. Applications to freshwater phytoplankton are discussed in Sell et al. (1984) and Tilman et al. (1984). Tilman (1988) has since presented a more elaborate model which considers plant responses to different resource ratios by including allocation to foraging. The inclusion of within-plant allocation is another attempt to include more mechanistic elements in competition models.

9.7 A BIOMECHANICAL MODEL

9.7.1 The effect of height upon relative competitive ability

Givnish (1982) has drawn upon game theory to provide an entirely different model of plant competition. He begins with the relationship between two properties: the carbon gain by plants, and the effects of canopy height upon light interception. How can we model the relationships between carbon gain, competition for light, and plant height? Consider, begins Givnish, a typical herbaceous plant with vegetative reproduction. To keep the model simple, let us assume that (1) photosynthetic characteristics do not vary appreciably with leaf height. Further, (2) assume that a clone of this herb has Z grams of carbon with which to construct a photosynthetic system consisting of n individual shoots. Let each shoot contain carbon as P of photosynthetic tissue, S of stem tissue, and V of leaf veins and petioles, so that:

$$Z = n(P, h) \cdot [P + S(P, h) + V(P)].$$

That is, the Z grams of carbon are allocated among n shoots (the first term) each with P, S and V carbon components (the second term). For single shoots, the challenge is to maximize allocation to resource trapping (the P component), while recognizing that as allocations to S and V decrease, the shoot becomes weaker until it cannot remain erect. There is thus a trade off between biomechanical rigidity and photosynthetic surface area. Further, the proportion of a plant's resource diverted into support tissue as opposed to synthetic tissue must decrease with increasing leaf height. Therefore, he concludes "herbs having similar photosynthetic responses and growing together under similar conditions should be selected to develop greater capacities for height growth until the photosynthetic gain each would make by being slightly taller than an opponent just balances the cost implied by a decreased proportional allocation to leaves".

Without exploring the eight pages of calculations in Givnish, we can conclude that for plants of a given height h, the biomass of photosynthetic tissue per ramet that maximizes the total annual amount of photosynthetic tissue is given by:

$$1 = P\frac{\partial\{\ln[S(P, h) + V(P)]\}}{\partial P}$$

Consider the simple case of intraspecific competition between two genotypes having different mean heights of h_1 and h_2. We know that as leaf height

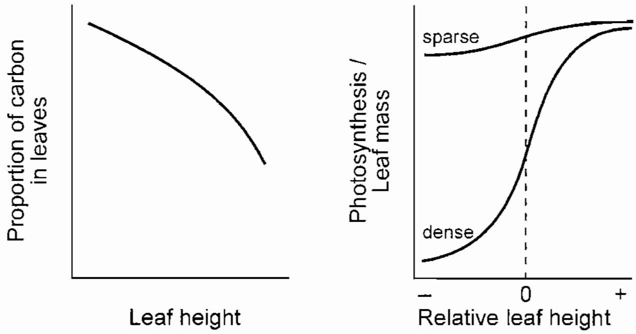


Fig. 9.14 Trade-offs associated with the evolution of leaf height in herbs. Left, taller plants must divert more resources into support tissue to remain mechanically stable, and so should display a lower proportional allocation to foliage. Right, balanced against this structural cost of greater leaf height is the expected photosynthetic advantage, averaged over many ramets, of holding leaves higher than a competitor. This advantage should be small in areas with sparse herbaceous cover, and larger where cover is more dense.

increases, allocation to P must decrease for biomechanical reasons (Fig. 9.14, left). Further, the photosynthetic rate per gram of leaf carbon will depend upon the difference in relative leaf heights, say as $g(h_1 - h_2)$. The height at which neither competitor could gain a further advantage by growing taller would be given by solving the following pair of equations, where each equation represents a genotype.

$$\left.\frac{\partial}{\partial h_1}[f(h_1)\cdot g(h_1 - h_2)]\right|_{n1=n2} = 0$$

$$\left.\frac{\partial}{\partial h_2}[f(h_2)\cdot g(h_2 - h_1)]\right|_{n1=n2} = 0$$

The evolutionarily stable strategy for leaf height (h^*) is given by:

$$-\frac{f'(h^*)}{f(h^*)} = \frac{g'(0)}{g(0)}$$

As the density of neighbours increases (Fig. 9.14), the relative competitive benefits of taller shoots should outweigh their higher biomechanical costs. This analysis does not include any additional benefits which may arise from suppression of neighbours. It follows, concludes Givnish, that the greater the plant density in a habitat, the taller the plants should be.

9.7.2 Adding in herbivory

Oksanen (1990) has provided a useful re-working of the above model, as well as an exploration of the effects of grazing upon it. He observes "the foliage height

ESS [evolutionary stable strategy] of herbs represents a balance between two factors. On one hand, it is always advantageous to be slightly taller than the neighbours. On the other hand, the taller the herb, the greater the fraction of available resources [that] must be allocated to support structures". It is this balance which the Givnish model examines. The point about marginal costs is particularly important "even if the plant cover is sparse and, consequently, $g'(0)/g(0)$ has a low value, prostrateness will not easily be an ESS for herbs in a purely competitive situation, because of low marginal costs of raising leaves slightly above the ground."

A built in assumption of Givnish (1982) is that tissue losses either do not occur, or that they are independent of shoot height. Oksanen therefore adds a mortality rate, **m**, due to grazing, a rate which increases with height, since the higher the shoot, the easier it will be for a grazer to reach. (This assumption is designed primarily for herbaceous vegetation; in fact, **m** would be likely to reach a maximum near the mean height of grazing and then decline again with height; the apex of, say, a sequoia may have a grazing mortality not dissimilar from a rosette plant. But for herbaceous vegetation, Oksanen's assumptions seems reasonable). Assume, then, that $\mathbf{m}(h)$, has a sigmoidal shape, reaching a constant maximum once a certain height is attained. The contribution of leaves to the energy balance of the plant is a function of their effective lifetime, **T**, which, if leaves are lost in a negative exponential manner, can be shown to be $\mathbf{T} = 1/\mathbf{m}(h)$. The structure of the equation clearly shows that the greater the grazing rate, the lower the leaf life span. Letting $z(h) = f(h)/\mathbf{m}(h)$, where, recall, $f(h)$ is the amount of resources available for foliage, one can determine that a given foliage height is an ESS if it satisfies the equation

$$-z'(h)/z(h) = g'(h)/g(0)$$

Plotting $z(h)$ as a function of height for different grazing intensities shows that "in most cases, weak or moderate grazing pressure has no impact on the foliage height ESS. When grazing pressure becomes high enough to have any impact at all, the impact is drastic . . ." and ESS jumps from high to very low.

This all or nothing response may be especially interesting in situations were grazing intensity fluctuates. Even if grazing intensity is usually high, prostrate plants might go extinct in years of low grazing intensity. Conversely, even if erect woody plants are favoured on average, the occasional outbreak of herbivores might prevent them from escaping to a 'safe size' before being killed (note Oksanen's view here that a sufficiently large height indeed reduces **m**). Graminoids, Oksanen notes, represent ideal growth form for dealing with such conflicting pressures: during years of high grazing pressure their basal leaves allow them to function like rosette plants, but during periods of low grazing pressure they can produce higher shoots to compete for light. In any case, the all important meristems are safely protected at the base of the plant (of course, this nice piece of natural history tells us a good deal about grasses, but rather little about the utility of the model). The actual trade-offs between grazing resistance and competition are still unknown, but both Oksanen (1990) and Louda et al. (1990) provide useful reminders that competition is not the only factor influencing ecological communities and evolutionary strategies.

This model has the appeal of being based upon simple biomechanical factors. We could further imagine that very similar analyses could be applied to a wide range of attributes that may be associated with competitive ability, ranging from long bills to large bodies to enlarged teeth. We will return to this topic in a later chapter. We may note in passing, as well, the comparisons with competition among human societies: there are certain benefits associated with a large military, but there is also the cost associated with allocating too large a proportion of a societies resources to military hardware. It has been argued that the collapse of the Soviet Union was the result of losing a race with the American economy to see which could sustain a greater allocation to military matters.

A strength of the model is a straight forward prediction about two easily measured attributes: leaf height and plant density. A problem is that while the analysis itself may increase our understanding of mechanisms of plant competition, and trade-offs in leaf design, the prediction is not a novel one. We have known for many years that infertile habitats usually have sparse plants, low biomass, and low canopies. Indeed, since biomass is a function of the volume of a plant community, it may be argued that the relationship between biomass and height (the latter being the third dimension of volume) is therefore a geometrical certainty. This may be because Givnish presents his model in terms of plant density rather than plant biomass, although in practice these are closely related. The outcome of the model may not be novel, but it is useful to see that biomechanical constraints and trade-offs can explain a commonly observed pattern in nature.

9.8 A SPATIAL MODEL

None of the three foregoing models address the reality of species distribution in space. Yet the different spatial distributions of organisms is the sort of thing easily observed by any naturalist. There is a frequently overlooked model that considers space, and that predates the latter two models by some 30 years. Skellam (1951) used it to explore how weak competitors might survive by escaping from superior competitors. His model is quite dramatic, because he begins with a crisp assumption: wherever the two species interact, the same one always wins. But we are getting ahead of ourselves.

The argument begins more or less like this (Pielou, 1975). Imagine two competing species that reproduce once a year. Let A be the stronger competitor and B the weaker competitor. Wherever they co-exist, A invariably wins. Therefore, the only habitat in which B can reproduce is those sites in which it occurs alone (Fig. 9.15). Assume that the region contains N sites, or islands of habitat, and

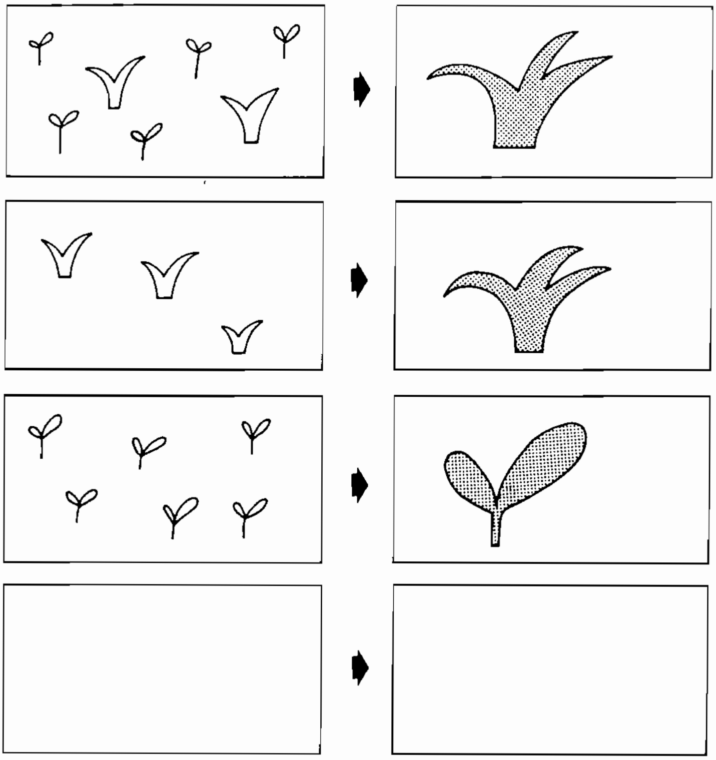


Fig. 9.15 Weak competitors can survive by escaping to habitat patches that are not occupied by stronger species. Four possible combinations of seedlings are shown on the left, and the outcome of adults is given on the right. (From Pielou, 1975; after Skellam, 1951.)

that at equilibrium the proportion of sites with a single A individual at the end of the growing season is Q. Since this means that NQ of the islands are dominated by species A, only $N(1 - Q)$ remain available for B to occupy. If we call this remaining portion of islands q, then q must be greater than zero for the competitive subordinate to survive. We want to know how much better dispersal of B must be for this to occur. Therefore, let F and f be the number of seeds produced by species A and B respectively. For species B to persist, f/F must be great enough to ensure that $q > 0$. It can be shown that for this to occur, f/F must exceed $-Q/(1 - Q)\ln(1 - Q)$. Provided this condition is met, species B will continue to occur in the landscape in spite of its explicitly poorer competitive ability.

Part of the elegance of this model is its simplicity. In spite of a most extreme assumption – complete competitive asymmetry – the weaker species can persist. Further, the model incorporates some realistic assumptions. Many habitats do occur in patches and organisms do have vastly different reproductive outputs. It is now possible to create elaborate computer simulations with vast numbers of cells and neighbouring species to examine further subtleties in models of spatially explicit competition. One gains the impression, however, that some models of competition (e.g. Tilman, 1982; Chesson, 1990, 1991), and some field experiments, have overlooked Skellam's contribution. Two sets of real observations also draw our attention back to this model for a second look. The first is the realisation that many species use escape in space or time to avoid competitors. The concept of 'fugitive species' is frequently encountered in studies of island biogeography, and the examples of species depending upon dispersal in time and space continue to accumulate. The second set of observations suggest that asymmetric competition is indeed a wide spread phenomenon (Chapter 5).

Consider one example. Bertness et al. (1992) divided salt marsh plants into two groups: competitive dominants and fugitive species. The fugitive species such as *Salicornia europa* colonize temporary high-salinity patches created by floating plant debris. Unlike the competitive dominants, they are little affected by salinities as high as 30 g/kg. The fugitive species are therefore able to escape competitors such as *Spartina patens* by constantly dispersing into these temporary patches.

9.8.1 Extensions and validity of the Skellam model

Armstrong (1976) experimentally explored some aspects of Skellam's model, and extended its theoretical basis. His experimental material consisted of two species of fungi, an *Aspergillus* and a *Penicillium*. He was able to show that the *Aspergillus* was competitively dominant, both overgrowing and infiltrating colonies of the subordinate. *Penicillium*, however, produced a greater number of daughter colonies, and so was a better colonizer of new patches. If all the patches became empty at the same time, and the $(n + 1)$th generation was initiated with spores from the nth generation, co-existence did not occur. If however, only a fraction of the patches became empty at any one time and newly emptied patches were inoculated from patches of several different ages, co-existence occurred.

The style of generation of new patches appears to be an important consideration for the survival of the subordinate. Skellam's model made the assumption that all patches become empty at the same time. Later models of 'fugitive species' (e.g. Levins and Culver, 1971; Horn and MacArthur, 1972) generated empty patches (empty 'cells') randomly. Although, says Armstrong, such models show unequivocally that fugitive species can co-exist with dominant competitors in a landscape (this should not, by the way, be confused with co-existence in single patches/cells), they do not consider the effects of different patch regeneration regimes.

Armstrong introduces a model, following Levins and Culver, where two species interact, S_2 can never capture a patch occupied by S_1, but a variable (and specified) proportion of sites occupied by S_2 will be captured by S_1. This introduces the inherent asymmetry of relative competitive abilities. Let the number of propagules produced by a patch of S_1 per unit time be a constant m_1 and the number of patches occupied by that species be N_1. On average, then, m_1N_1 viable propagules of S_1 will be produced per unit time. (In this case, viable means that it would successfully establish a patch if it were the only propagule to land there.) Assume further that the propagules are scattered randomly, with a fraction σ_1 actually landing in patches, the fraction $1 - \sigma_1$ being lost in dispersal. The rate at which new colonies are founded is then calculated by multiplying the rate at which viable propagules reach patches $(m_1\sigma_1N_1)$ by the fraction of patches that are available for colonization at that time. If X_i represents the fraction of the patches occupied by species i, then the number of patches available to the better competitor, S_1, is $(1 - X_1 - X_2)$ plus some fraction of the cells already containing S_2 which it will wrest away.

We are interested in the rate of generation of new patches. If colonies of S_1 become extinct at a rate ε, then $\varepsilon N_1\,dt$ extinctions occur per unit of time dt. It can be shown that the ratio of the largest and smallest values where co-existence occurs is

$$\mathbf{B}_\varepsilon = \varepsilon_{\max}/\varepsilon_{\min} = \sigma_2 m_2/\sigma_1 m_1$$

If the actual value of ε is less than $\varepsilon_{\min}$, the fugitive species will be eliminated by the competitive dominant. If ε is greater than $\varepsilon_{\max}$, then the competitive dominant will be lost. Armstrong suggests that this ratio be termed the ε-coexistence bandwidth. It is proportional to the ratio of potential colonization rates, and is independent of individual colonisation rates and the degree of dominance.

Other modifications of this approach are possible. Hubbell (1980) explored the possible effects of a host-specific insect which prevented trees from regenerating near existing adults. Atkinson and Shorrocks (1981) have examined the effects of patch size and the aggregation of the competitors. Newman (1982) explored the possible effects of having different kinds of patches, each patch favouring (but not ensuring) regeneration of a particular species. If a particular patch type becomes sufficiently rare, the species occupying it may disappear because the patch is swamped by seeds from species in adjoining patches. That is, unlike the simple deterministic case in Figure 1.12, Newman assumed that establishment in any patch would be in some way proportional to the relative abundances of propagules arriving there. "Coexistence of species", he says, "is likely to occur only if each habitat state has more than a certain minimum abundance".

When the models from Skellam (1951) to Armstrong (1976) were introduced and explored, there were two biological factors (patch regeneration, competitive hierarchies) that were assumptions of the models, and much of the value of the models depended upon the degree to which these assumptions were met in the real world. Three thorough and important reviews appeared within the next three years that independently confirmed the importance regeneration in patches, at least for plants (Grubb, 1977; Pickett, 1980; White, 1979). The second assumption, competitive hierarchies, has received less attention, but as Chapter 5 illustrated with a wide range of taxa, competitive hierarchies are also widespread. This class of models may therefore deserve more attention in future years.

9.9 A MODEL OF BEHAVIOUR AND HABITAT USE

The above models describe the effects of competition on population sizes and resource levels. Another possible dependent variable would be the behaviour of the competing species. We know from the many examples of resource partitioning that different species use different resources, but there are many unresolved issues in the study of trade-offs in foraging (Pyke, 1984), and it is not at all clear how patterns of resource use might change under different intensities of inter- and intraspecific competition. Pimm and Rosenzweig (1981) and Rosenzweig (1981) have presented such a model.

Envisage the following situation. There are two species that occupy a region which has two resource patches (or two resources). Each species 'prefers' one patch type – that is, each is specialized to exploit one patch type more efficiently than another. However, each species can exploit both patch types when population densities are low. The model explores how the foraging behaviour of one species responds to all possible population sizes of the two species. Under which conditions will a species use both habitats, and under which conditions will it use only the one upon which it is specialized? Under which conditions will it be a generalist, and under which will it be a specialist? (The words generalist and specialist are being used in a narrowly defined sense to describe variation in behaviour or variation in realized niche width, and not variation in fundamental niche width.)

Consider the habitat from the point of view of species 1 in the absence of species 2. In Figure 9.16 this is represented by the horizontal axis. If the population size of species 1 is small, then it will clearly be advantageous for species 1 to forage in the habitat upon which it is specialized. Now allow population density to grow by slowly moving to the right along this axis. As this happens, population densities in the preferred patch are increasing, as is intraspecific competition. Eventually a point is reached where intraspecific competition in the preferred patch is so intense that resources are depleted to the point where the two patches become equally preferable. If population size increases any more, the unoccupied patch type offers a better return per unit of foraging effort. This point on the axis is then marked with a dot. To the left, species 1 forages in one patch, to the right it forages in both. Now imagine that the other patch is occupied with a small number of individuals of species 2. This means that there is interspecific competition which species 1 encounters when foraging in that

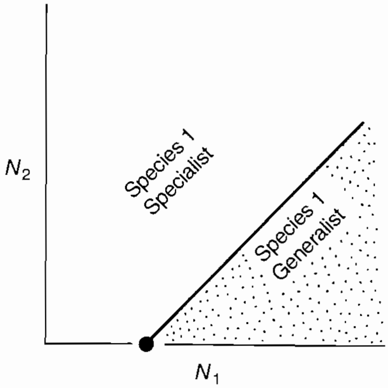


Fig. 9.16 The changes in foraging behaviour of species 1 as a function of all possible population sizes of species 1 and 2. In the absence of species 2 ($N_2 = 0$, consider only the horizontal axis) and at low levels of species 1 (left-hand end of axis), species 1 is a specialist upon its preferred resource. As the population size increases (moving right along the horizontal axis), intraspecific competition for the preferred resource becomes more intense. At some point (dot) individuals begin foraging for a less preferred resource in order to avoid intense intraspecific competition; at this point the species becomes a generalist. If we allow the population size of species 2 to increase (moving up the page), the point at which individuals of species 1 expand diet or habitat to include the less preferred resource also changes, since there is now interspecific competition for this resource. Higher levels of intraspecific competition are necessary to induce the switch in foraging from specialist to generalist. This logic marks out two regions for a species – a region where it is a specialist, and a region in which it becomes a generalist (stippled).

patch, which renders that patch even less suitable. That is, because it is already occupied by another species, its apparent quality to species 1 has declined. Now consider again how the behaviour of species 1 will change in response to increased size of its own population. Clearly the point at which intraspecific competition makes the other patch type attractive must be higher, since the other patch type is now less desirable. Thus, species 1 does not begin foraging in both habitats until its population size is somewhat higher. Following such logic, one can construct a line with positive slope which represents where the two behaviours produce equivalent returns. A decrease in the population size of species 1 favours specialist foraging: a slight increase favours generalist foraging. By analogy with the idea of population size isoclines, this line is referred to as an isoleg. Figure 9.16 shows the resulting behaviour of species 1 under all densities of the two species. The isoleg of species 2 can be derived in exactly the same manner.

As with the examples above, the interesting results for two-species interactions are derived by superimposing the two graphs. Figure 9.17 shows the situation for two species with non-intersecting isolegs. Three regions can be

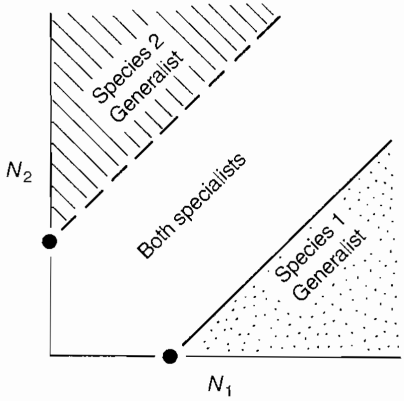


Fig. 9.17 One possible foraging behaviour for two species as a function of their population densities. This is obtained by superimposing the results of Fig. 9.16 for two species. At low population densities both species forage in their own preferred patches, but as the population sizes increase, intraspecific competition forces each to forage in the other's patch. Species 1 is therefore a generalist in the stippled area ($N_1 \gg N_2$) and species 2 is a generalist in the hatched area ($N_2 \gg N_1$).

recognized, corresponding to three of the four possible combinations of behaviours.

1. Both species have low population sizes and each therefore behaves as a specialist;
2. Species 1 is a generalist due to high intraspecific competition, but species 2 is still a specialist;
3. Species 2 is a generalist due to high intraspecific competition, but species 1 is still a specialist.

Pimm and Rosenzweig (1981) explore the four possible combinations of isolegs in two-dimensional space. The next interesting step is to superimpose these isoleg plots upon plots of isoclines, and Rosenzweig (1981) provides an introduction to this procedure.

It is therefore possible to explore how the behaviour of two species ought to change in response to varying degrees of inter- and intraspecific competition. This illustrates the difficulty of measuring competition coefficients from measures of realized niche overlap, because depending upon where one measures in Figure 9.17, one could find no niche overlap or high niche overlap.

The model is primarily exploratory, but could be made predictive for pairs of species if it were important to predict their foraging behaviour. This would require simultaneous measures of both the range of resources consumed and the population size of both species. The isoleg would be mapped by determining the region where behaviour shifts abruptly. Whether it is worth this much effort to predict the foraging behaviour of two species is open to discussion. It is not clear to what degree one could extrapolate from one pair of species to another, in which case this approach becomes a complicated method of describing the interactions of pairs of species on a case-by-case basis. We must ask at some point what the priority dependent variables (or state variables) for community ecology are, a theme which is returned to in later chapters. Perhaps the foraging behaviour of two species would not qualify for a high priority.

Rosenzweig (1981) summarizes the model's testable predictions. He concludes with some general observations on the testability of quantitative ecological models. "There is so much noise in ecosystems that it is always possible to wonder if the measurement failed to fit the theory because of the noise and not because of the inadequacy of the theory. On the other hand, theories which make qualitative predictions are often too easily fit. Most qualitative predictions simply state the existence and direction of a pattern.... All too often, even these are discovered before the theory is advanced and no further predictions from the theory are made to allow the pattern to be tested."

9.9.1 Foraging effort and competition

We have seen above that the abundance of neighbours might be reasonably expected to change foraging behaviour, but just how it might change is unclear. Mitchell et al. (1990) consider the consequences for time allocated to foraging and observe that the response depends "on whether an increase in competition reduces the marginal cost of foraging". Increases, decreases or no change in foraging effort may occur depending upon specific costs and benefits of foraging. Since it seems reasonable to assume that competition will simply decrease food supplies and increase foraging time, what other possibilities might occur?

The energy expended per unit time in maintenance can be considered a fixed cost (FC) whereas foraging is a variable cost (VC) so that total energy expenditure $= T * \mathrm{FC} + t_f\mathrm{VC}$ where t_f is the length of time T spent on foraging activities. The issue, then, is how t_f changes as a function of the number of neighbours also foraging (M) where the resource is depleted at the rate of

$$\frac{\mathrm{d}n}{\mathrm{d}t_f} = -Mf(n)$$

Mitchell et al. suggest that there are two possible kinds of responses, 'time minimizers' and 'fitness maximizers'.

A species that forages until a specific energy requirement is met is termed a time minimizer. Each unit of time they spend foraging costs the fixed cost (FC) + the variable cost (VC) and returns to them the rate of resource harvest, f, multiplied by the value of the resource (v). An increase in M must therefore be accompanied by an increase in t_f.

It is also possible to imagine a fitness maximizer which continues to forage until the marginal benefits equal the marginal costs. However, the marginal costs are difficult to quantify since they depend upon the marginal benefits of other activities such as burrow maintenance or grooming. It seems likely, however, that as animals become energy-stressed, the variable cost (VC) is likely to become increasingly important, so that energy-stressed animals may reduce foraging efforts. This yields results contrary to the assumption that competition by neighbours will automatically lead to increased foraging time (t_f).

As with any modelling effort, such work helps us think about the kinds of constraints which influence animals. The usefulness of the models beyond this value depends critically on the ability to measure costs and benefits in the field – by no means an easy exercise.

9.10 COMPETITIVE NEIGHBOURHOOD MODELS

We have seen that the presence of neighbours can impose costs on individuals, and as the density of neighbours increases, so do the costs of competition. The result is that there is a negative relationship between performance and the abundance of neighbours. For some purposes, we can assume that performance declines in a linear function with density. While this may be a reasonable first approximation, the actual pattern is curvilinear; at first the presence of neighbours may be barely detectable, but as the numbers of neighbours increase, a threshold is reached when performance declines sharply. We have already seen that once performance drops to a certain level, reproduction is inhibited, and when it drops further still, survival is at risk. Now let us back up, and ask not about these extreme effects, but about the effects that occur at very low density. First we can consider the limiting case – no neighbours at all – in which case performance is solely determined by the physical conditions of the site (for argument's sake, we assume the effects of herbivores to be negligible, although it is easy to factor them in at a later stage). In the absence of competition, that is, at zero density, performance is estimated by the y intercept of the performance–density curve. As we add neighbours (that is, move to the right), performance is at first entirely unaffected. As the number of neighbours increases, eventually performance declines to a detectable level. Another way to think about this is to consider just two individuals, say trees. When they are widely separated, neither is affected by the other. If, in our mind, we slowly push them toward one another, eventually their roots and or leaves begin to interfere with one another. The distance between these two individuals when one can just begin to measure competition between them is known as the competitive neighbourhood.

In practice, this neighbourhood of an individual will often contain more than one neighbour so that it is the mean distance to a set of neighbours which will be of interest. For example, Hickman (1979) found that the mean distance of a *Polygonum* plant to its four nearest neighbours could account for more than half of the variation in biomass of *Polygonum* plants.

Weiner (1982) suggested a suitable neighbourhood model for performance would be

$$P = \frac{P_{\max}}{1 + W}$$

where P is performance, $P_{\max}$ is performance without competition and W is the total competitive effect of all neighbours. As a general measure of W, he suggests dividing the space around an individual into concentric zones and calculating

$$W = \sum_{i=1}^{i=n} \frac{1}{d_i^2} \sum_{j=1}^{j=m} C_j N_{ij}$$

where d_i is the mean distance to the ith zone, C_j is the mean effect of an individual of the jth species, and N_{ij} is the number of individuals of species j in neighbourhood i. If we are dealing with only one species (or if the species are similar in competitive effects), then, the j terms disappear, leaving

$$W = \sum_{i=1}^{i=n} \frac{1}{d_i^2} C N_i$$

where C is simply a constant expressing the competitive effects of one individual.

This can be expanded to

$$W = C\left(\frac{N_1}{d_1^2} + \frac{N_2}{d_2^2} + \frac{N_3}{d_3^2} + \cdots + \frac{N_n}{d_n^2}\right)$$

Notice that the impact of each neighbour is divided by the square of the distance, a recognition that effects fall off rapidly with distance.

Using this simple model, Weiner was able to predict reproductive performance of two species of *Polygonum* with greater than 80% success. Using another annual plant, *Arabidopsis thalliana*, Silander and Pacala (1985) were able to account for 64% of the variation in its reproductive output. By analysing residuals, they were further able to show that a radius of only 5 cm was satisfactory for predicting neighbour effects.

Silander and Pacala (1990) have worked further with this approach. They begin by noting that models of plant competition must deal with certain unique features of plants: sedentariness, neighbourhood (local) interactions, plasticity and shared resource requirements. They then incorporate the neighbourhood model into a mechanistic demographic model. This began with the neighbourhood model described above, but incorporated a survivorship and fecundity submodel, each of which allowed neighbour effects to decrease performance according to a series of interference coefficients giving the impact of each neighbour on a focal plant. They then calibrated the model, estimating parameters from field plots of two annual plants, velvet leaf (*Abutilon theophrasti*) and pigweed (*Amaranthus retroflexus*). Surprisingly, perhaps, they concluded that information on spatial distributions had relatively little effect on the dynamics of their system. This appeared to occur because the mean effects of neighbours were so large that the neighbourhood interactions added little information. That is, the complex neighbourhood model reduced itself to a non-spatial model. Spatial models may only be necessary, they conclude, when populations are clumped, or when there are low or variable numbers of neighbours.

The strength of this kind of analysis is that it focuses attention upon individual responses to effects of neighbours. "Individuals respond primarily to local conditions and proximal neighbours" (Silander and Pacala, 1985). The general approach may be equally applicable to benthic and terrritorial animals where spacing is both important and measurable. The weakness is that it requires a great deal of information about the location of each individual in relation to its neighbours. While it therefore serves as an important reminder of small scale interactions, in most cases we find it necessary to ignore those local and individual responses in order to find more general patterns.

Models that explicitly incorporate the spatial patterns of competitors are a logical extension of neighbourhood models. Silvertown et al. (1992) observe that spatial arrangements of neighbours may be important in determining competitive interactions and species patterns in vegetation. Cellular automatons can be used to explore such patterns. "A cellular automaton uses a regular lattice of cells, the states of which are completely defined by local rules. Each cell may have one of a range of states, for example representing vacant space or occupancy by a particular species or group of species." Using previously published data on rates of invasion of five grass species into neighbouring species (Thórhallsdóttir, 1990), a set of species in which there is a fairly strong competitive hierarchy, Silvertown et al. examined the possible interactions of these species in a lattice of 40 × 40 cells. If the initial arrangement of species was random, three of the five species went extinct quickly owing to the rapid invasion of their cells by the two dominant species, *Agrostis stolonifera* and *Holcus lanatus*. If species were arranged in bands across the lattice, however, the patterns of replacement were more complicated. If the competitive dominants were arranged side by side, with the weaker competitors below them in the lattice, *Holcus* was able to rapidly invade the neighbouring *Poa*, thereby creating a broad barrier that *Agrostis* was unable to break through. Silvertown et al. conclude that assuming a random arrangement of neighbours in spatially explicit models may hide interesting dynamics that would result from other spatial patterns. Further, the patterns observed in plant communities may be the result of spatially explicit competition rather than environmental heterogeneity. At the same time, such models assume a homogeneous environment; in the absence of environmental heterogeneity, it is not unreasonable to expect something else, in this case spatial arrangements and competition, will affect pattern.

9.10.1 Adding in asymmetry

Thomas and Weiner (1989) note that the neighbourhood models presented above do not include the inherent asymmetry of plant competition, "with larger plants having a disproportionate effect on smaller plants."

In a simple neighbourhood competition model, W, the total effect of all neighbours can be represented as

$$W = \sum_{i=1}^{n} kS_iD_i^2$$

where k is a constant estimating the effect of a neighbour, S_i is the size of the ith neighbour, D_i is the distance to the ith neighbour and n is the number of neighbours within a prescribed distance of the focal plant.

Asymmetry can be added by discounting the effect of neighbours smaller than the target individual by a factor $1 - A$, where A is the measure of competitive asymmetry varying from 0 (completely symmetric competition) to 1 (completely asymmetric competition). One then has two equations and an if–then statement. If neighbours are $\geq$ the focal plant, the above equation is used. But if the neighbours are smaller, then the equation is replaced by

$$W = \sum_{i=1}^{n} kS_id_i^{-2}(1 - A)$$

Thomas and Weiner then tested for the presence of asymmetry, and the size of A, by fitting the equation to two natural monospecific populations (*Impatiens pallida* and *Pinus rigida*) and an experimental monoculture (*Ambrosia artemisifolia*). The best fit equations were obtained with large asymmetry values (1.0, 0.7 and 0.8, respectively), and these were significant improvements over the null hypothesis of symmetric competition ($A = 0$).

The incorporation of asymmetry into neighbourhood models seems useful, but the above if–then structure is only a partial improvement. If asymmetry really is a consequence of the difference in size between the neighbour and the focal plant, such an if–then structure may be unwarranted. The equation assumes that all neighbours bigger than the focal plant are equivalent. Only smaller plants are different. A neighbour that is twice as big as a focal plant is equally unlikely to be the competitive equivalent of a neighbour the same size as the focal plant. Therefore, rather than having a conditional value of asymmetry which is used only when the neighbours are smaller than the focal plant, it would seem more realistic to weigh every $kS_id_i^{-2}$ term by an asymmetry value which is a function of the difference in size between the focal plant and every neighbour.

Thomas and Weiner (1989) also warn against using neighbourhood analysis to detect competition or to determine its 'importance', since both of these depend upon the quality of the measure of interference that is used. Concluding that competition is unimportant on the basis of low r^2 values may reflect, instead, a failure to incorporate asymmetry or other measures of neighbourhood conditions.

The final question, perhaps, is whether in the field, these sorts of spatially explicit interactions are relevant, given the degree of heterogeneity found in most resources (Chapter 2). Even in areas of tropical lowland rain forest, there is growing evidence that much of the diversity comes from extremely heterogeneous and regularly disturbed substrates (Salo et al., 1986; Kalliola et al., 1991). Pielou (1975) has taken Silvertown's scenario to the other extreme, assuming that species occur along strong environmental gradients, and exploring how zones of species will interact along these gradients. Again zones develop, but in Pielou's models, they are the result of competition coefficients being dependent upon the environment, whereas in Silvertown et al., they are the result of interactions among pairs of species in a homogenous environment. As Pielou observes, all such models are of interest because they show us what might happen in nature. Whether they actually do occur is of secondary importance since the models provide reference points for thinking about the dynamics of natural communities. In this way, both Silvertown's and Pielou's models fall into the realm of simulations (that is, outside the boundaries in Fig. 4.15); they allow us to explore possibilities beyond what we normally find in real systems, what might happen rather than what probably does.

9.11 COMPETITION IN FORESTS: THE JABOWA AND FORET MODELS

Several similar models have been developed to predict changes in forest composition under a variety of management scenarios (Botkin, 1977, 1993; Shugart et al., 1981; Urban and Shugart, 1992). These two models are designed to be predictive, and so are rather more complicated than exploratory models such as those of Pielou and Skellam. The JABOWA model, for example, was developed co-operatively as part of the Hubbard Brook Ecosystem study in New Hampshire, USA. I did not include this class of model in the first edition, which only goes to show the degree to which ecology has become fragmented, with disciplines like forestry tending to develop in isolation. Part of the reason for writing this book was to pull together apparently disparate studies, and so JABOWA and FORET, along with Pielou and Skellam, are here in the second edition.

The JABOWA model simulates the behaviour of a forest by simulating the growth of individual trees in small forest plots. It does so by exploring competitive interactions among trees in small patches of land. Owing to the size of this model, we shall explore only its basic conceptual structure, but in many ways this is quite sufficient. Sklar et al. (1990) introduce ecosystem models with the following observation: "Development of the conceptual model is probably the most important step in the modelling process. It focuses attention on the

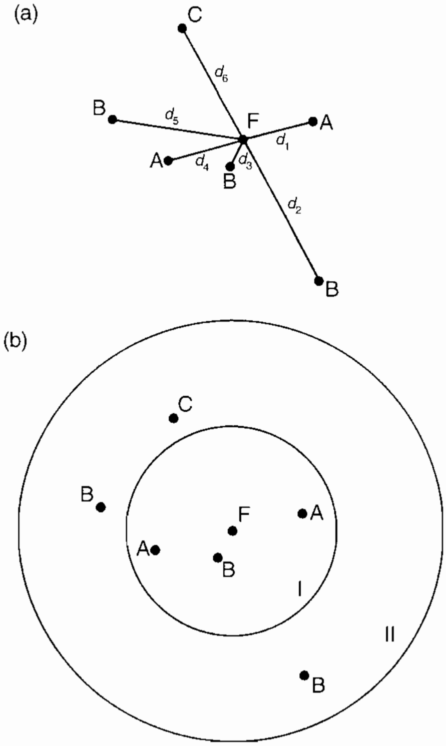


Fig. 9.18 A neighbourhood description of six plants of species A, B or C around a focal individual F. Two zones, I and II, provide different possible neighbourhoods.

definition and bounding of the problem, and on identification of the hierarchy of goals and objectives. Finding the level of organisation required by the model to adequately address objectives of the investigator(s) is the key to developing appropriate conceptual designs" (p. 625).

We have already encountered the use of patches, or cells, in other competition models. Large areas of landscape can be modelled, but the standard size cell in JABOWA is 10 m on a side. Trees grow by gathering resources within this patch, and light is assumed to be a key resource. A tree growing in the open collects radiant energy in proportion to leaf area, and its growth will be proportional to leaf area. The growth equation is

$$\delta(D^2H) = R\,\mathrm{LA}\left(1 - \frac{DH}{D_{\max}H_{\max}}\right)$$

where D is the diameter of the tree, H is its height, $D_{\max}$ and $H_{\max}$ are the maxima known for each species, LA is leaf area, and R is a constant. The growth of the tree, then is in proportion to the amount of sunlight the tree receives, reduced by the $(1 - DH/D_{\max}H_{\max})$ which is proportional to the surface area of the tree stem; these are the non-photosynthetic trunk tissues of the tree, which respire and consume photosynthate.

Generally speaking there are two types of trees, shade tolerant and intolerant. The former grow well under low light, but are saturated at moderate light levels. Shade intolerant trees grow poorly in the shade, but better than the shade tolerant ones in bright light. Photosynthesis is therefore represented by

$$r = a_1(1 - \mathrm{e}^{-a_2(\mathrm{AL}-a_3)})$$

where r is the relative rate of photosynthesis, AL is the light available to the tree, and a_1, a_2, and a_3, are constants that give reasonable fits to measured photosynthesis curves for shade tolerant and intolerant trees.

AL is the term that incorporates competition. The amount of light available to each tree is determined (and diminished) by comparing the height of each tree to that of all the other trees in the plot, and decreasing the light intensity available by the amount of shading that occurs from the leaves of taller neighbouring trees. Competition therefore is asymmetric, and assumed to be above ground (or at least, more realistically, proportional to the above ground attributes of the stand).

For regeneration to occur, patches must arise. It seems reasonable to assume that a tree remains healthy throughout its life with a small but definite probability of dying in any year. If a tree dies, there is more light available for seedlings. New saplings are added each year, based upon the amount of light available and relative tolerances to shade (and with temperature and soil moisture considered as well). If, for example, light levels are high, shade intolerant species such as cherry are added. If light is very low, only shade tolerant species such as beech are added.

Both the probability of any tree dying, and the regeneration, allow for some random variation. This is thus a stochastic model. Natural ecosystems, are, says Botkin, inherently variable, and the model must incorporate some of this variability in order to be useful. If, for example, one wants to simulate possible changes in fertility due to atmospheric deposition of nitrogen, or increases in growing season due to global warming, it is important to know whether the change in the selected factor is important enough to obscure cause changes given the inherent stochasticity of real forest stands.

A model such as this can be subjected to steady modification and improvement as the knowledge of tree species ecology accumulates (Botkin, 1993; Sklar et al., 1990; Urban and Shugart, 1992). Since the objective is to closely simulate the behaviour of real forests, the progressive refinement of coefficients and sub-models is worthwhile, bearing in mind Pielou's admonition about not toying around with every possible scenario for exploratory models. Rigler (1982) and Peters (1992) have both strongly expressed doubt about the validity of large scale computer models with large numbers of coefficients, pointing out that as the number of species increases, the number of pairwise interactions increases rapidly to the point where the model becomes unwieldy (see also Wimsatt, 1982; McIntosh, 1985; Rigler and Peters, 1996), a topic to which we shall return in the final chapter. In contrast, Starfield and Bleloch (1986) have argued that the real challenge is to simplify nature intelligently, but many workers continue to use large simulation models (e.g. Sklar et al., 1990; Ondok, 1990; Mitsch and Jørgensen, 1990).

Perhaps the apparent utility of the JABOWA and FORET models arises out of two fortunate circumstances. First, the number of trees in deciduous forest is relative small, unlike the large numbers of species in lakes; therefore, a species by species approach is not overwhelming. Second, strong asymmetric competition structures the forest around a single factor: competition for light. Many other complex interactions can be safely ignored, or added on as secondary factors for independent evaluation. Again, this may contrast with lakes where there are complex food webs and unpredictable multispecies interactions for a variety of resources. Perhaps some systems are inherently easier than others to simplify. Certainly, forestry can be viewed as one of the most important sub-disciplines of ecology, and the fact that competition plays the central role in forest simulation models nicely ties together the theory of this chapter with the practical management of real landscapes for conservation purposes.

Another advantage of this kind of model is that properties of vegetation including species composition and population structure are predicted from simple mechanistic assumptions about individual plants in local environments (e.g. Doyle, 1981; Clark, 1990). Prentice and Leemans (1990) have introduced a related model, FORSKA, which in addition, simulates vertical structure, and they illustrate its application to conifer forests (*Pinus sylvestris*, *Picea abies*) in central Sweden. Clark (1990) similarly begins with the growth of individual plants and explores how limited resources and density dependence produce the 3/2 power law of plant thinning (Harper, 1977; Westoby, 1984). In Clark's approach, the resource limited growth rate r is determined by levels of both a below-ground nutrient, $R(t)$ and light, I_p,

$$r = r_{\max}\left[\frac{R(t)}{K_R + R(t)}\right]\left[\frac{I_p}{K_I + I_p}\right]$$

where $r_{\max}$ is maximum growth rate and K_R and K_I are half-saturation constants for the nutrient and light. The changes within the nutrient pool, and light availability, are then independently simulated to measure the effects of neighbours. While these added mechanistic elements increase realism, particularly with the possibility of independent effects by above and below ground resources, the model is focused upon a narrow set of conditions: thinning in same aged stands of a single species. The added detail in the model is partly possible because only one species needs to be considered.

9.12 THE LATERAL PRESSURE MODEL FOR GLOBAL CONFLICT

The realm of war studies introduces an entire new vocabulary, where states 'collide', where dominant states are 'hegemons', where 'the elusive aspects of peace can be explained in part as corollaries of the security dilemma', and where threats are 'mortal' and opportunities 'unprecedented' (e.g. Choucri and North, 1993). Once one cuts through the jargon, one enters a familiar realm where neighbours compete with one another, where they exert 'lateral pressure' to extend their powers beyond their boundaries, and where the three 'master variables' are population, technology and access to resources.

"To a large extent all countries compete for resources and for power and influence within the national system" begin Choucri and North (1993) in their discussion of competition for global dominance. Dominants (or, in their terms, hegemons) are "high-capability, high lateral pressure states (or empires) characterised by large and growing populations, high and advancing technology and substantial access to resources . . .". Choucri and North (1993) divide nation states into six categories based upon their ability to crowd their neighbours (that is, in war studies jargon, 'exert lateral pressure'. These range from alpha profile countries with large and advancing population, technologies and resource access (e.g. the United States) to zeta profile countries with low population density, primitive technology and limited resource access (e.g. Chad, Mauritania).

In their book *Nations in Conflict*, Choucri and North (1975) introduce a dynamic model to explore competition among nation states. Colonial area, intensity of interactions, military expenditures, alliances and violent behaviour were the five principal components of their model (Fig. 9.19). This model

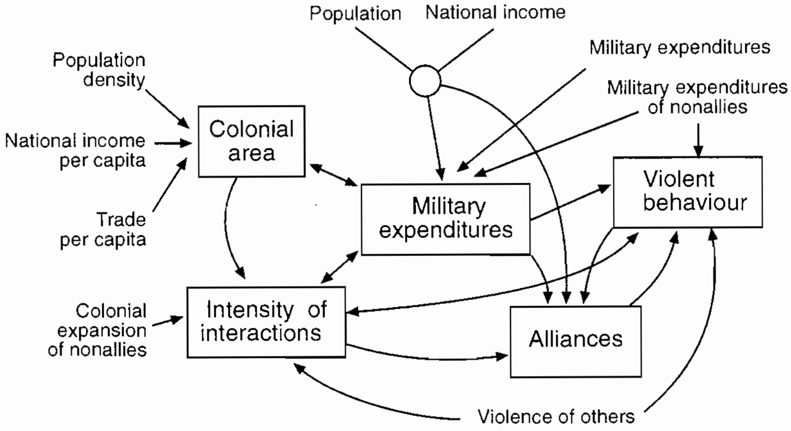


Fig. 9.19 The dynamics of international violence. (From Choucri and North, 1993.)

has been used to explore the origins of World War I and the Japanese rise to power between 1914 and 1941. However, the value of this modelling approach is still in question. One is reminded of the Lokta–Volterra and Tilman models, which, while useful for exploring the results of a series of assumptions, may not be easily applied to the real world. The conclusions of Choucri and North nearly 20 years after their book will sound all too familiar to ecologists "... we have enriched our theoretical understanding of shifts in modes of lateral pressure and explored what would (or could) happen if Japan had adopted different policies or had been confronted by different adversaries" (p. 319). They conclude (p. 324) "... the extended lateral pressure framework still remains too inclusive, extensive, and loosely joined to be fully tested as a general theory".

9.13 THE RICHARDSON ARMS RACE MODEL

"The Richardson arms race model constitutes one of the most important models of arms race phenomena and, at the same time, one of the most influential formal models in all of the international relations literature" (Intriligator and Brito, 1989, p. 218). An arms race is "the dynamic process of interaction between two countries in their acquisition of weapons" (p. 220). Arms provide the means to damage a neighbour, a process that Chapter 1 defined as interference competition. Perhaps more importantly, however, arms also provide a means to reduce exploitation competition by enforcing control of space to ensure monopolistic exploitation of resources. Even if a war never occurs, then, the threat provided by weapons can ensure that resource competition is minimized. The benefit, then is the resources obtained, and the period during which one's population is not subjected to losses from warfare. The cost of this competition can be measured as the economic and administrative burden of conducting an arms race. Such costs are included in the Richardson Model, first proposed in 1939 to describe the rate of change over time of arms stocks in two countries (Fig. 9.20). Richardson later covered the topic as a book, *Arms and Insecurity*, in 1960 (see also Richardson, 1951).

If $M_A(t)$ is the stock of missiles at time t in country A, then

$$\mathrm{d}M_A/\mathrm{d}t = a_1 M_B - a_2 M_A + a_3$$
$$\mathrm{d}M_B/\mathrm{d}t = b_1 M_A - b_2 M_B + b_3$$

In this model, $\mathrm{d}M_A/\mathrm{d}t$ is the sum of three separate influences, M_B being the defence term, determined by the stock of weapons possessed by the opponent, and M_A being the fatigue term, measured by the size of one's own arsenal. The constants represent the weighting of the defence term, the weighting of the fatigue term and a constant 'grievance term' representing all other factors. Further a_1 and b_1 are positive because each country is threatened by its neighbours weapons, and a_2 and b_2 are positive because the burden of maintaining the

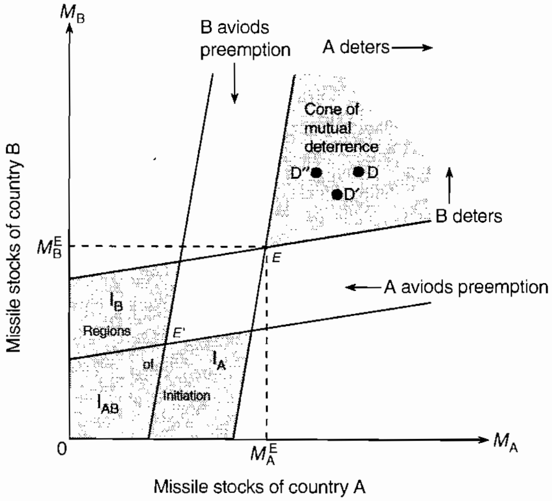


Fig. 9.20 The Richardson model explores possible changes in missible stocks of two competing countries.

existing stockpiles reduces the resources for additional weapons. As with other competition models, one can seek an equilibrium point where there is no change in missile stocks; an equilibrium occurs if the terms a_3 and b_3 are positive. This equilibrium is stable if

$$(a_1/a_2)(b_1/b_2) < 1.$$

At stable equilibrium, if missile stocks increase, the force of the fatigue terms reduces them, and if missile stocks decrease, the defence term creates increased production. A variety of other war models also exist, including the stock adjustment model, the Brito model and the differential game model; Intriligator and Brito (1989) provide a brief introduction to each and compare them with the Richardson model.

An extension simulates the possible consequences of warfare. The number of missiles possessed by a country is reduced by the number it fires, and by defending missiles launched against them from the other side. Of particular interest is the missile force that must be maintained in order to deter the enemy from attacking first, that is, the number that must survive a surprise attack and remain for a retaliatory second strike. This requires determining the minimum unacceptable damage the opponent is willing to incur and solving for the number of surviving missiles necessary to inflict that number of casualties. "It is then possible to solve for the minimum level of missiles required for country A to deter country B by inflicting this level of casualties" (p. 228).

If each country is acting to deter the other, then, given certain assumptions, it is possible to determine the minimum number of missiles required for each side. These conditions can be represented geometrically in the $M_A - M_B$ phase space (Fig. 9.20). E is the equilibrium number of missiles, and the shaded cone on the upper right is the zone of mutual deterrence where each country has an arsenal sufficient to deter the other. "Arms control through arms limitation or reduction is feasible as long as the situation remains in the cone of mutual deterrence" (p. 229).

To avoid a pre-emptive strike by one's opponent, it may be advantageous to never have "so many missiles relative to those on the other side that it may appear to the other side that an attack could be successfully carried out. If the other side believes that such an attack could be carried out, it might be forced to make its own preemeptive strike in order to take advantage of the element of surprise . . .". The regions marked A or B avoids pre-emption indicate regions where the difference between arsenals is such that neither can pre-empt the other by striking first. In this case, the larger cone with vertex at E' is the one within which both sides avoid pre-emption.

The regions near the origin are danger zones because they describe circumstances under which one side or the other may decide that the benefits of initiating war outweigh the costs. "Region I_{AB} is most dangerous of all: because each side can successfully attack the other, neither can avoid preemption and neither can deter the other. Each is forced to initiate the war in order to take advantage of striking first" (p. 230).

Intriligator and Brito (1989) criticize such models for treating the arms race as a mechanistic interaction between two entities, rather than as a product of the decision of defence planners. Perhaps they have more confidence in the abilities of defence planners that many readers will have. These models are also of interest because they take competitive interactions to the largest possible ecological scale, and because they require the user to consider how a neighbour's actions will be perceived by its opponent. The latter complexity is not normally required in competition models because it is assumed that the organisms involved are not consciously pursing a particular strategy, but responding more or less instantaneously to resource levels and the abundance of neighbours.

9.14 TWO GRAPHICAL MODELS FOR RESOURCE PARTITIONING

It is frequently assumed that all models require equations, but some useful models are graphical. Of course, these models can often be formulated mathematically, but the form in which they are generally used is pictorial. Often such models are used to summarize existing understanding of ecological processes, and to make qualitative predictions about patterns in nature. The best example

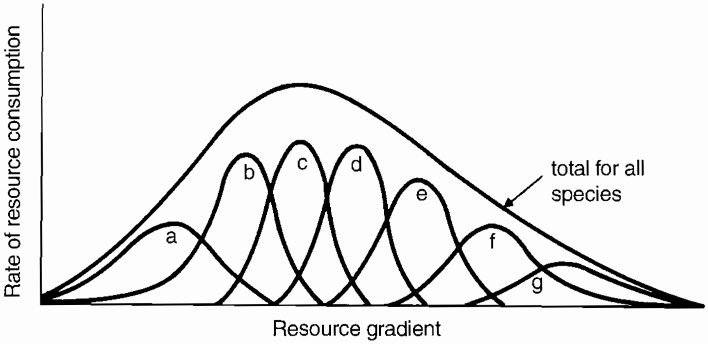


Fig. 9.21 Resource partitioning in a hypothetical community comprised of seven populations (after Pianka, 1981). Each curve represents the resource utilization by a different species. The wider the curve is, the less specialized the *realized* niche of the species. Adding together the demands of all species produces the upper curve.

of this is the picture of resource partitioning presented in Fig. 9.21, some of the mathematics of which are described in MacArthur (1972) and May (1974). The following section explores some of the impacts this picture has had upon the sorts of questions that ecologists ask and the kinds of data that they collect. The patterns of the model are first described, and then two competing models proposing to account for these patterns are presented.

9.14.1 Patterns

The pictorial representation of resource partitioning illustrates how seven species of organisms can co-exist by using different sections of a resource continuum (Fig. 9.21). As we saw in section 9.3, each species is assumed to have a bell-shaped resource utilization curve, and the zones of overlap are assumed to show areas where there is interspecific competition for resources (for example, MacArthur, 1972; Vandermeer, 1972; Cody, 1974; Whittaker and Levin, 1975; May, 1981; Pianka, 1973, 1981; Giller, 1984; Arthur, 1987). The model is so widely used in studies of competition that it deserves closer attention. In considering this model it is essential to distinguish between realized and fundamental niches. Fundamental niches are resource-use patterns which occur in the absence of competitive effects produced by neighbours of different species. They can be measured only by experimental removals of neighbours, or possibly by finding natural situations where neighbours are absent. Realized niches are resource-use patterns which occur in the presence of other species, and if competition affects realized niche width, then realized niches will be narrower than fundamental niches. Field studies which describe species distributions and resource consumption provide information only on realized niches. Some of the confusion in the current literature arises from using words like niche without specifying whether it is realized or fundamental (for example, Cody, 1974; Pianka, 1981).

At the same time as zoologists such as Hutchinson and MacArthur were formulating their ideas of niche theory and resource utilisation curves (e.g. section 9.3), similar ideas were languishing in two German scientific papers published by Ellenberg. American zoologists often seem little aware of basic concepts of plant ecology, particularly when they are published in Europe, but being published in German was an additional unfortunate obstacle. Fortunately, these ideas have now been expanded and clarified in two English treatments (Mueller-Dombois and Ellenberg, 1974; Austin, 1990), and the summary here is based upon these latter treatments.

Austin (1990) begins his description of this 'much neglected pioneering work which addressed multispecies competition along a gradient' by summarizing Ellenberg's experimental investigations on the distribution of grass species along a moisture gradient: "In experiments on species response to a watertable gradient from water at the soil surface to a watertable at a depth of 140 cm, he observed that the species biomass optima in monoculture tended to coincide. When the species were grown in multispecies mixtures under the same conditions, their optima were displaced. The ecological optima and shape of response curve differed from the physiological optima and response under monoculture conditions. Ellenberg interpreted this as being due to competition. The shifts in optima corresponded to phytosociological observations on the species relative performance in the field. Examination of the field behaviour of a wide variety of species in relation to gradients of light, water, nitrogen, etc. led to the conclusion that competitive ability was distinct from physiological performance . . .".

Ellenberg used the term 'physiological response curve' for a species distribution in the absence of competition; this is the equivalent of the fundamental niche. The term 'ecological response curve' was, then, a species distribution which resulted from competition, what zoologists call the realized niche. Further, by comparing ecological and physiological response curves, it was possible to imagine a number of ways in which competition might influence the distributions of species along gradients (Fig. 9.22). Competition might, as in the MacArthur model, produce narrower resource utilization curves (line 1), but it might equally be one-sided, causing the displacement of a species' apparent optimum either up or down the gradient (line 2). In some cases, the competitive dominant occupied a favoured zone, excluding the weaker competitor to the extremes of a gradient, and generating a bimodal ecological response curve.

Ellenberg supplemented these theoretical patterns with a wealth of empirical data from the distribution of species along gradients of nitrogen, water and pH. The grass *Briza media*, for example, illustrates the three patterns shown in Figure 9.22, having a distribution narrowed by competitors along the nitrogen gradient, having an optimum displaced by competitors along a water gradient, and being forced into a bimodal distribution along pH gradients.

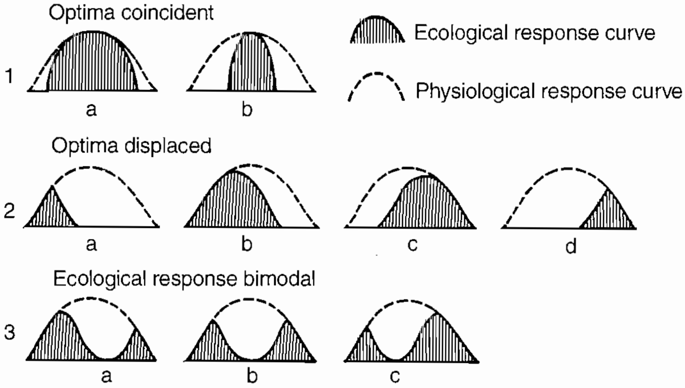


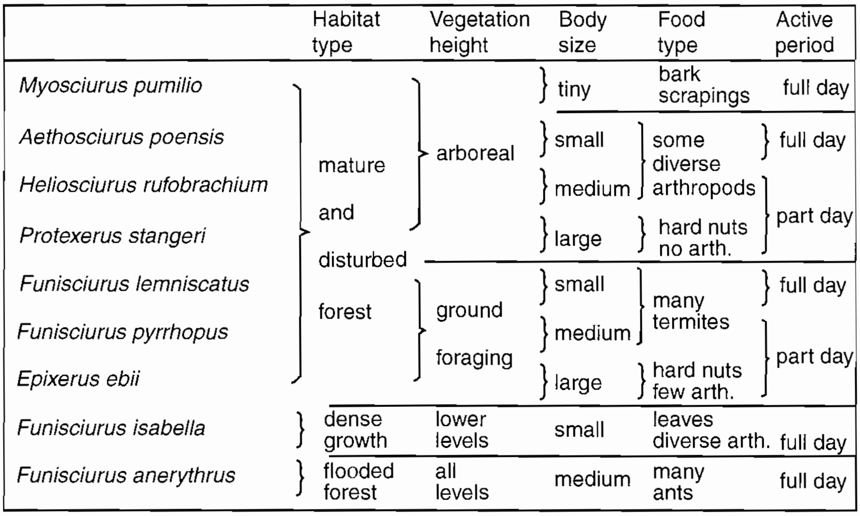
Fig. 9.22 Types of species distribution patterns along an environmental gradient with and without competition following Mueller-Dombois and Ellenberg (1974). (From Austin, 1990.)

Austin (1976, 1990) extensively studied the shapes of species distributions along gradients. The bell-shaped normal curves used both by MacArthur (1972) and his co-workers, and by plant ecologists studying vegetation gradients (e.g. Gauch, 1982; Orloci, 1978) are, he says, rarely found in nature. Realised niches/ecological response curves are usually skewed, and so are fundamental niches/physiological response curves. Austin concludes: " . . . the shape of the physiological response curve will play a critical role in determining the outcome of competition . . . ".

9.14.2 Competition, co-existence and resource partitioning

That species in nature use different resources and occupy different habitats is a basic truth of natural history. Figure 9.23, for example, shows the main dimensions of resource partitioning for African rain forest squirrels. The recent example and the many cited in Schoener (1974) illustrate the view of Hutchinson (1959) that "the process of natural selection . . . leads to the evolution of sympatric species which at equilibrium occupy distinct niches . . . . The empirical reasons for adopting this view and the correlative view that the boundaries of realised niches are set by competition are mainly indirect."

If species co-exist by using different niches, then knowledge of the number and kind of niches in a community clearly permits predictions about the number of species likely to be found there. Unfortunately, niches are usually recognizable only when species are filling them. This would not prevent important advances in predictive ecology, however, for if one can describe niches occupied in one example of an ecosystem, then one can reasonably predict that similar niches occur in other examples of that system. Thus, a periodic table of niches (see Pianka, 1983) may be possible for each community type in



	Habitat type	Vegetation height	Body size	Food type	Active period
Myosciurus pumilio	mature and disturbed forest	arboreal	tiny	bark scrapings	full day
Aethosciurus poensis			small	some diverse arthropods	full day
Heliosciurus rufobrachium			medium		part day
Protexerus stangeri			large	hard nuts no arth.	
Funisciurus lemniscatus		ground foraging	small	many termites	full day
Funisciurus pyrrhopus			medium		part day
Epixerus ebii			large	hard nuts few arth.	
Funisciurus isabella	dense growth	lower levels	small	leaves diverse arth.	full day
Funisciurus anerythrus	flooded forest	all levels	medium	many ants	full day

Fig. 9.23 Resource partitioning by rain forest squirrels in Gabon. Horizontal lines indicate nearly complete separation between the characteristics. Food types include only those which differentiate species. Squirrels may either forage for most of the day (full day) or return to their nests several hours before sunset (part day). (After Emmons, 1980; consult Schoener, 1974, and Giller, 1984, for other examples.)

the biosphere. Moreover, if only a few axes are necessary to account for the niche differentiation, then general predictions may be possible. Figure 9.23 suggests, for example, that vegetation height and food type would be two main axes we would need in order to understand and predict species composition of squirrels in tropical rain forest. Similarly, Diamond (1975) proposes that branch size and fruit size will enable us to understand the composition of tropical fruit pigeon communities. Schoener (1974) and Giller (1984) provide other examples. Thus, studies of niche differentiation provide both a description of community organization and the possibility of predicting composition in other related community types.

There is the problem that there is no obvious upper limit to the number of species which can fit into a community, since one can always postulate additional niches. Consider regeneration niches in plant communities. Grubb's (1977) review certainly suggests that there are more than enough regeneration niches to account for the diversity of plants and plant communities. Another example of this is the remarkable number if niches which insects can find to exploit on a single plant species, bracken (*Pteridium aquilinum*) (Lawton, 1984). Still another is the array of species, tissue types and locations available to parasites (Holmes and Price, 1986; Stock and Holmes, 1987, 1988). There are so many possibilities for niche differentiation that one wonders whether general theories are possible, or whether ecologists will become no more than natural historians painstakingly documenting the niches of each species in each community.

This raises the question of whether such niches can even be recognized unless they are already occupied, and whether some communities can be predicted to have vacant niches (Price, 1984b; Herbold and Moyle, 1986).

Arthur (1987) proposes testing whether resource partitioning actually permits co-existence. First, it is important to realize that resource partitioning is proposed to account only for stable co-existence; it is not essential for non-equilibrium co-existence (recall section 6.6). Secondly, there are five potential causes of stable co-existence, only one of which is resource partitioning (Arthur, 1987). Given this context, Arthur proposes three steps to demonstrate conclusively that resource partitioning is the cause of stable co-existence: (1) demonstration of stable co-existence in a system with a given level of resource heterogeneity; (2) demonstration of competitive exclusion in a less heterogeneous system; and (3) quantification of resource utilization functions for the two species showing that significant separation is possible in (1) but not in (2).

Resource partitioning describes an obvious pattern in nature, but how is it related to competition? Realized niches are often assumed to be different among species and similar to fundamental niches. The validity of assumption is the key issue for interpreting resource partitioning. There are grave difficulties in describing patterns and inferring processes without considering alternative processes which could generate the same patterns (for example, Connor and Simberloff, 1979; Shipley and Keddy, 1987; Chapter 4). Alternative models and competing hypotheses can be produced by considering the possible differences between realized and fundamental niches. Figure 9.24 shows two possible responses to a removal experiment contrasting realized with fundamental niches. They assign fundamentally different roles to competition.

Without careful experimental manipulations, the interpretation of resource partitioning often has Panglossian overtones. That is, it assumes a near perfect world of neatly partitioned resources and competition only serving to sharpen the boundaries of species distributions. There is a place for everything, and everything is in its place (section 6.6). Similarly, the fictional Professor Pangloss asserted that whatever happens in this world, it is the best of all possible worlds. In the case of the Lisbon earthquake, which killed more than 30 000 people in 1755, he comments "... all that is for the best; for if there is a volcano in Lisbon, it could not be elsewhere; for it is impossible that things are not where they are; for all is well" (Voltaire, 1759). Let us therefore turn our attention to experimental analyses of patterns of resource partitioning.

9.14.3 Model 1: differentiation of fundamental niches

One model of process assumes that resource partitioning results from different fundamental niches. The differentiation of fundamental niches is assumed to be the result of past competition selection for specialization. Each organism is specialized to harvest a particular region of the resource continuum for the obvious reason that 'a jack of all trades is a master of none'

(MacArthur, 1972; Rosenzweig, 1979; Pianka, 1983). MacArthur observed that '... since competition often puts a premium on efficiency, this assumption implies a division of labor among specialists. It is the ultimate reason we have so many species'.

One of the most well-developed areas of enquiry using this model addresses the amount of permissable overlap in resource utilization by adjacent species. MacArthur (1972) showed that there were good theoretical reasons for expecting the maxima of adjacent resource utilization curves to be separated by $\sqrt{\sigma}$, where σ is the standard deviation of the curves (see also Schoener, 1974). Some of the arguments for such co-evolution of competitiors are summarized by Roughgarden (1983). The observation (section 9.3) that pairs of similar species tend to differ by ratios of from 1.2 to 1.4 (Hutchinson, 1959) actually predates such models by more than a decade, so the models do not so much predict ratios of limiting similarity as explain why they might be found. Simberloff (1983b) provides a critical review of the problems involved in exploring real data to test for unusually large differences in size ratios of co-existing species.

Such models assume that competition is relatively unimportant at present, serving only to produce minor differences between realized and fundamental niches (Fig. 9.24, left). That is, we cannot detect competition today because

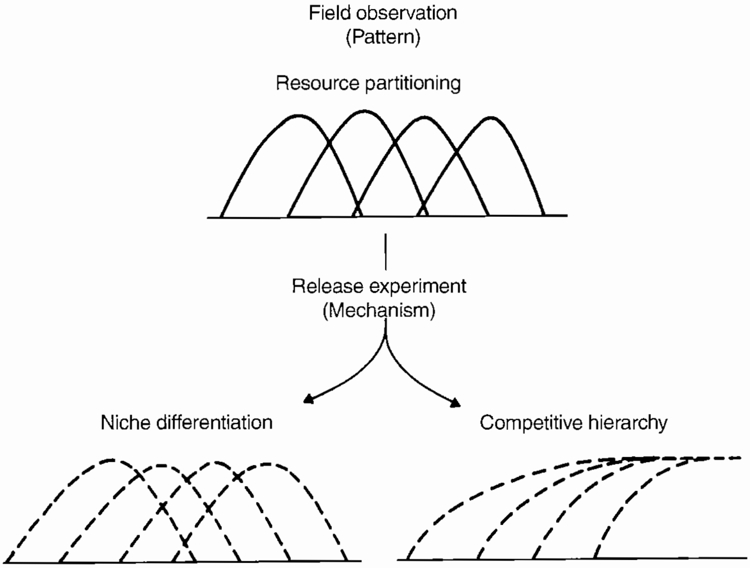


Fig. 9.24 Two competiting models to account for resource partitioning. The top presents field observations (realized niches and physiological response curves) and the bottom presents the possibilities of differentiated fundamental niches (left) and competitive hierarchies operating on inclusive fundamental niches (right). Only experiments can distinguish between the two lower models.

evolution has produced patterns of resource use which minimize interspecific competition. This view has been called the 'ghost of competition past' (Connell, 1980). Although it provides us with a convenient explanation for niche differentiation, and one that fits nicely with the theme of this book, its existence is rather more difficult to demonstrate. Connell (1980) proposed a rigorous series of experiments (section 4.3.2) which need to be done to demonstrate that the ghost was there, but community ecology and competition research are still haunted by mere assertions of its presence. The first published example of such an experiment appears to be Turkington and Mehrhoff (1989).

A second common assumption is that the zones of overlap in resource use are a measure of competition, such that the greater the zone of overlap between two species is, the greater the intensity of interspecific competition (MacArthur, 1972; Schoener, 1974; May, 1974, 1981). This would be very convenient if it were true, and this view is probably very popular because 'competition' could be measured from descriptive data. It has been widely used to estimate competition coefficients in the community matrix, and has been defended recently by Schoener (1983). It is also wrong. Overlap in resource utilization curves tells us nothing about the intensity of interspecific competition, and it would be a serious error to construct a community matrix estimating competition co-efficients from niche overlap. There is a simple *reductio ad absurdum* for this approach. Imagine two species sharing the resource continuum in the complete absence of competition: perhaps a predator is keeping population density very low, perhaps they are limited by a second resource. Since there is no competition their distributions merely reflect their fundamental niches, and overlap in the resource utilization curves, even if it is extensive, is occurring in the absence of competition. Now assume that two species are competing intensely. Since one of the tenets of the model is that competition reduces the width of resource utilization curves, the competition is so intense that there is complete competitive exclusion and no overlap whatsoever. Compare these two situations. In the situation with no competition there is extensive overlap, and in the situation with intense competition there is no overlap. Both of these situations are entirely consistent with the mechanisms normally postulated for the model, yet they demonstrate that niche overlap is smallest where competition is most intense. A similar point was made in the model describing habitat selection discussed above. Only controlled experiments can determine whether fundamental niches are differentiated in the manner assumed. The importance of such distinctions becomes clear when one of many possible competing hypotheses is considered.

Another important criticism is provided by Siefert and Siefert (1976). They note that if competition co-efficients are estimated from descriptive data, they can take situations of overlap owing to mutualism or symbiosis and measure them as competition! This reinforces the point that studies of niche overlap may 'find' competition only because it was already assumed to be there. The tendency to ignore possible mutualisms in favour of competition is explored further in Chapter 8.

9.14.4 Model 2: competitive hierarchy

The competitive hierarchy model proposes an alternative series of mechanisms to account for the observed pattern of resource partitioning and the differential distribution of species along environmental gradients. This model has been implicit in varying degrees in studies from a wide range of systems (for example, Connell, 1961, 1972; Miller, 1967; Sharitz and McCormick, 1973; Mueller-Dombois and Ellenberg, 1974; Colwell and Fuentes, 1975; Rabinowitz, 1978; Wilson and Keddy, 1986b) but has not been formalized to the degree that is desirable. There are three assumptions made by the model. First, it is assumed that the species in the community have inclusive niches; i.e. the gradient is a gradient of resource quantity, with all species having best performance (size, growth rate and reproductive output) at the same end of the gradient. Miller (1967) and Colwell and Fuentes (1975) provided many examples of this, and it may be the commonest situation for plants, which all share a requirement for a few basic resources: light, water and mineral nutrients. A second assumption is that the species vary in competitive ability in a predictable manner and that competitive ability is an inherent characteristic of a species, perhaps having something to do with rates of resource acquisition and capacity to interfere with neighbours. Lastly, it assumes that competitive abilities are negatively correlated with fundamental niche width, perhaps because of an inherent trade-off between ability for interference competition and ability to tolerate low resource levels. This is illustrated in Fig. 9.25 (top), where six species are ranked in competitive ability in order from A (dominant) to F (subordinant). The outcome is species differentially distributed along a gradient (resource partitioning), as shown in Fig. 9.25 (middle). However, the mechanism is a dominance hierarchy with the competitive dominant occupying the preferred end of the gradient, and the subordinants displaced down the gradient a distance directly determined by their position in the competitive hierarchy (see also Fig. 9.24).

Unlike the resource partitioning model, the competitive hierarchy model is predictive. Given a knowledge of fundamental niches or competitive abilities in the preferred region, one can predict the order in which species will be distributed along the gradient. This assumes, of course, that competitive ability is an inherent trait of a species rather than a trait which is strongly dependent upon the environment. If this is the case, then measuring competitive ability should allow us to predict the distribution of organisms in such communities.

There is another interesting parallel here. At the beginning of this chapter we compared the Lotka–Volterra model with the resource competition model, and found that although they both yielded similar predictions, the latter model was preferable because it specified the mechanism of interaction. With respect to resource partitioning, we have a similar set of circumstances: two models which generate the same outcome, but one placing more emphasis on the mechanism.

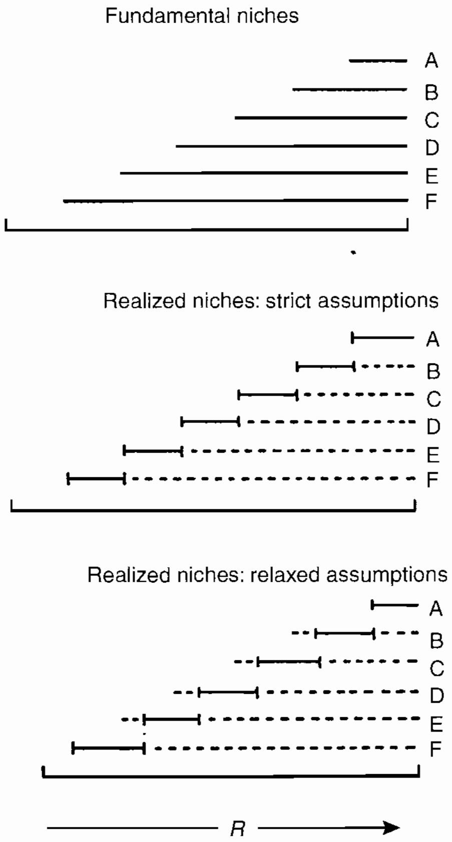


Fig. 9.25 Aspects of the competitive hierarchy model. (top) The fundmental niches of six species with competitive abilities arranged in a hierarchy from the dominant A to the subordinant F. (middle) The observed field distributions of the species in the top panel assuming that in each interaction the dominant excludes the subordinant right to the very limits of its physiological tolerance limits. The broken lines illustrate the species distributions which would be detected by a competitive release experiment. (bottom) Relaxing an assumption. Near its tolerance limits each dominant is competitively excluded by its adjacent subordinant. The distribution patterns remain the same except that each species is displaced slightly up the gradient. The broken lines showing the results of a release experiment emphasize that competition has very different effects on distributional limits of species depending upon whether the limit is adjacent to a dominant or a subordinant.

9.14.5 A variant on the competitive hierarchy

In its simplest form it is assumed that the transition from dominant to subordinant occurs at the exact point where the dominant reaches its physiological tolerance limits (Fig. 9.25, middle). This would be true in the cases of absolute asymmetry; that is, where the dominant affects the subordinant, but the subordinant has no effect upon the dominant. Suppose that this assumption is relaxed slightly. The consequence is that the transition from the dominant to the subordinant occurs only near the lower distributional limits of the dominant, since there is presumably some point at which the dominant is so weakened by environmental effects that it can be excluded by the subordinant (Fig. 9.25, bottom). Another way of expressing this is to say that we have relaxed the assumption that for each dominant–subordinant interaction the realized and fundamental niches of the dominant must be identical. Depending upon how far one relaxed this assumption, one could produce a series of cases intermediate between resource partitioning and strict competitive hierarchies. The order of species distributions would remain identical, but the distributions of species would shift slightly up the gradient towards the preferred end.

In this case competition is again affecting both ends of a species' distribution, but it plays a major role at one end and a minor role at the other. Field experiments may have to take this possibility into account. The essential issue in distinguishing between these two possibilities becomes the behaviour of the dominant–subordinant interaction near the distributional limits of the dominant.

9.14.6 Centrifugal organization of communities

This competitive hierarchy model and the foregoing model of behaviour and habitat use (Pimm and Rosenzweig, 1981; Rosenzweig, 1981) are closely related, and suggest a general model of community organization. Rosenzweig and Abramsky (1986) have recently extended their model of habitat use by proposing a type of community structure termed centrifugal organization. In such situations, a group of *n* species has shared preference for a central habitat type, but each has another peripheral habitat in which it is the best competitor; the number of different peripheral habitats then determines the number of species which can co-exist. This is a variant on the more usual form of inclusive niche structure (Miller, 1967; Colwell and Fuentes, 1975) where species have overlapping fundamental niches along only one axis. The centrifugal model has been extended to more complex communities by postulating that not just single habitats, but entire environmental gradients (or niche axes) may radiate outward from the central preferred habitat, accommodating many more species than in the Rosenzweig and Abramsky version (Fig. 9.26) (Keddy, 1990; Wisheu and Keddy, 1992). Near the centre species may have entirely inclusive fundamental niches, but nearer the periphery, species' fundamental niches may include only a few adjacent neighbouring species in the direction of the central habitat. In the latter case competition would be simply 'one sided' and removal experiments would then be predicted to show that in the absence of neighbours, species could grow nearer the

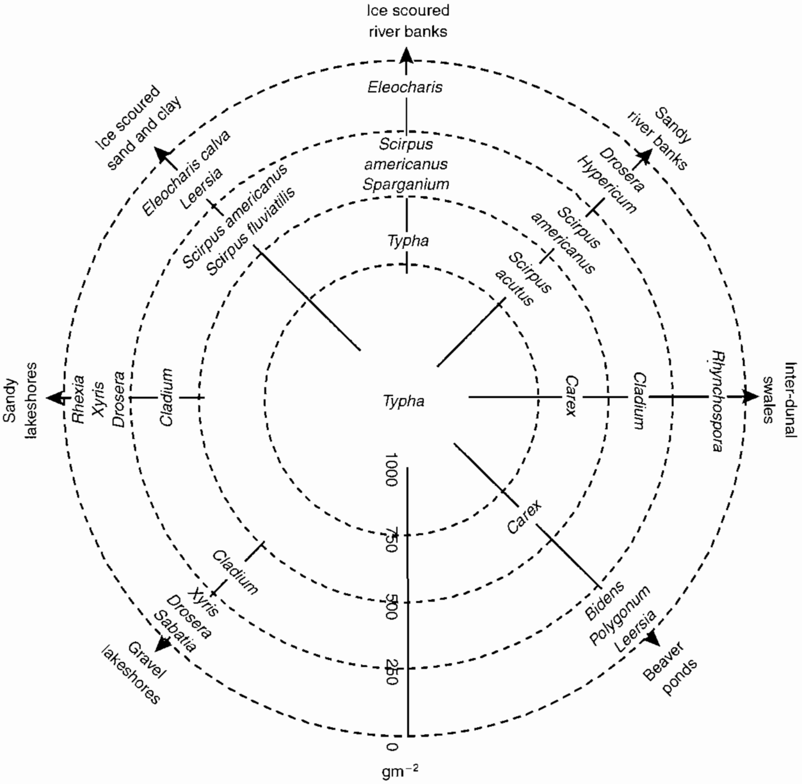


Fig. 9.26 Competitive hierarchies along different biomass gradients produce centrifugal organization of wetland plant communities. Species have inclusive niches along each axis with shared preference for the fertile, undisturbed central region. This region is dominated by a few canopy-forming, clonal perennials, primarily *Typha* sp. (After Keddy, 1990.)

central habitat but not nearer the periphery. There is evidence that wetland plant communities are organized in this fashion (Keddy, 1990). In wetland plants the central habitat has low disturbance and high fertility, and is dominated by large leafy species capable of forming dense canopies. Different constraints, such as kinds and combinations of infertility and disturbance, create radiating axes along which different groups of species and vegetation types are arrayed. Rare species occur only in peripheral habitats with low biomass (Moore et al., 1989). The model has also been explored for desert rodents (Rosenzweig and Abramsky, 1986), a wide array of forest types (Keddy and MacLellan, 1990) and a selection of other vegetation types (Wisheu and Keddy, 1992).

9.14.7 Using simulation to compare and contrast models for resource partitioning

Does resource partitioning arise from niche differentiation or competitive hierarchies and shared preferences – recall Figure 9.24. Malanson (1997) used a simulation model to compare these two possible mechanisms for resource partitioning. This model was an extreme simplification of the Jabowa – FORET model, which simulates the competition and population dynamics of forests (section 9.10). The key ideas are that each tree has a maximum growth rate, the larger trees shade smaller trees, and that poor quality sites also reduce growth. Malanson modified the model to explore site quality gradients of 50 × 80 and 50 × 120 cells, representing a continuous strip of forest. The output from the model was the distribution (and therefore zonation patterns) of three tree species along a hypothetical gradient.

The co-evolution model (distinct niches) generally resulted in sharper species boundaries than the hierarchy model (inclusive niches), producing a stronger zonation pattern, but the differences were subtle. The hierarchy model also had more outliers because when gaps were created by the simulation, species had broader tolerance limits and thereby could occur further along the gradient.

Simulated removal experiments were also conducted by removing the middle species at year 500, and observing changes in the marginal two for a further 100 years of simulated time. Both species expanded their distributions in both the co-evolution and hierarchy models, but in the hierarchy model the invasion was asymmetric, leading to initially skewed distributions. If a simulated natural disturbance regime was superimposed, the marginal species invaded more rapidly because there were already isolated individuals established in the middle. After 100 years, the boundary between two species remained blurred.

The shape of species distributions along environmental gradients has been a contentious issue in ecology, with Austin (1976, 1990) insisting that gaussian or bell-shaped distributions such as those used by MacArthur (section 9.3) simply are not to be expected in nature; in most cases distributions are skewed. Malanson observes that the hierarchy model tended to produce similarly skewed distributions in his simulations. He concludes that these "simulations indicate that only subtle differences in species distributions, even with removal or addition experiments, may differentiate between the ghost of competition past and the hierarchical model of plant competition."

If removal experiments cannot distinguish between the two models even when all the factors in favour of the co-evolution model are present then other field tests will need to be devised.

9.14.8 More on response curves

Malanson (1997) observed that the hierarchy model tended to produce similarly skewed distributions in his simulations. Austin et al. (1994) therefore suggest using a far more flexible model for species responses to gradients, the beta function

$$\mu = k(x - a)^{\alpha}(b - x)^{\gamma}$$

or, equivalently, $\log(\mu) = \log(k)\alpha \log(x - a) = \gamma \log(b - x)$ where a and b are the endpoints of a species range, k is a scaling parameter that largely adjusts the curve height, and α and γ are further shape parameters. The location of the maximum is given by

$$\frac{\alpha b - \gamma a}{\alpha + \gamma}$$

When $\alpha = \gamma$ the maximum is at the midpoint of the range. The skewness of the response curve is defined by the ratio of α to γ, and the kurtosis (flatness) is determined by their absolute values. The advantage to this function is its flexibility in fitting complex response curves. Austin et al. (1994) suggest that it can be used to test for skewness in response curves, which is of some interest since a majority of species in nature seem to have skewed responses. However, Oksanen (1997) counters that the location of the optimum and the skewness are correlated so that these parameters cannot be estimated independently, and further, the decision as to whether a and b are the endpoints of the species or endpoints of the gradient alters the shape that is fitted.

There thus remains a problem with the fitting of response curves to real data. A related problem is the choice of response curves for multivariate models of species distributions along gradients in ordination studies. On one hand, one can appreciate that the Gaussian curve is an artificial construct, but one that may be very useful for exploratory models (e.g. section 9.1), and is simple and well-understood. On the other hand, the more one tries to find curves that simulate real data, the more complex the models must become. How much effort is warranted? Perhaps before too much more time and journal space are spent trying to come up with equations to model response curves, or to explore sets of models using different shaped response curves, we need to re-evaluate the point of the exercise. Are we trying to make some approximate guess as to how nature might work, or are we trying to precisely represent the patterns in nature? If the latter is the case, what is the purpose of the exercise?

9.14.9 Comparison of models for resource partitioning

That different populations use different resources and habitats is basic natural history. What is less clear are the mechanisms which underlie these patterns. The resource partitioning model places emphasis upon the mechanisms of differentiated fundamental niches, whereas the competitive hierarchy model places emphasis upon proximal competitive interactions. The resource partitioning model assumes that evolution, to avoid interspecific competition, has produced different fundamental niches, whereas the competitive hierarchy model assumes that there are inherent trade-offs between fundamental niche width and competitive ability. The evidence for evaluating the biological reality of these models comes from two very different sources. Those who use descriptive data tend to assume that resource partitioning comes from different fundamental niches, whereas those who conduct field experiments often find evidence of competitive hierarchies. It would be tempting to assume that the former group does not find inclusive niches because it never looks for them.

This illustrates an important point about the value of models, and the potential for both use and abuse. If the model is treated as a demonstrated truth, then there is always the temptation to collect yet another set of data demonstrating the existence of this truth. There is no doubt that communities have populations with different realized niches (Schoener, 1974; Giller, 1984) as the model illustrates. However, this is no reason to assume that the mechanisms presumed to underlie the model, particularly the similarity of realized and fundamental niches, are correct. Competing hypotheses need to be advanced and tested. The same model can therefore act either as a hindrance or as a stimulator to the advancement of science, depending upon how it is used as a research tool.

A problem in evaluating models occurs when different models with different assumptions make identical predictions (B. Shipley, pers. commun.). For example, the observation that the number of species in a community reaches a maximum at some intermediate level of disturbance is well recognized, but there are different mechanisms proposed to account for it (for example, Grime, 1973, 1979; Connell, 1978; Huston, 1979; Tilman, 1982). The foregoing models therefore cannot be evaluated by comparing their predictions, because their predictions are the same. In such cases the best research strategy appears to be comparing and contrasting the assumptions of the models and designing experiments to compare the validity of these assumptions.

As an alternative, what we may need is not critical tests so much as a resolution. Some communities may have populations with different fundamental niches, whereas others may have inclusive fundamental niches. For example, Yodzis (1978, 1986) postulated that competition for 'resources' is fundamentally different from competition for space, the former having symmetric and the latter asymmetric interactions. Another possibility is that communities with strong resource gradients (such as mountain sides or shorelines) evolve very different structuring from communities occupying relatively homogeneous habitats (old fields or prairie parkland); of course, homogeneity is in the eye of the beholder, so it may similarly be that sessile organisms generally experience strong localized gradients, whereas birds and mammals tend to experience relatively more-homogeneous conditions. Lastly, it may be important to consider the kind of gradient itself. If there are gradients of resource quantity (food abundance, moisture and soil nutrients), they may be fundamentally different from gradients of resource quality (kind of food and ratios of nutrients). The resolution is therefore likely to require explicit consideration of the kinds of resources and their distributions in nature. Meanwhile, ecologists cannot automatically assume that all communities fall conveniently into one model.

Inclusive niches and competitive hierarchies in freshwater fish

Cetrachid sunfishes are a group of spiny-rayed fresh water fishes that dominate the fish faunas of small lakes over much of central North America. In Michigan, for example, there are 7–10 species, five of which are in the genus *Lepomis*. Within a lake, the species show typical resource partitioning. The principal habitat types are emergent vegetation, open water and substrate. The pumpkinseed (*L. gibbosus*) feeds near the substrate whereas the bluegill (*L. macrochirus*) is found higher in the water column, with further separation among species based upon food size. The green sunfish (*L. cyanellus*) is restricted to the shallowest inshore habitats (Wootton, 1990). In summarizing many of his studies (e.g. Werner and Hall, 1976, 1979), Werner (1984) says "The above patterns in resource partitioning suggest strong competitive interactions among species . . ." (p. 364). In order to study this competition, fish were introduced into small experimental ponds, where habitat and diet could be measured in different mixtures of species. "Each species, when stocked in ponds alone, preferred the vegetation habitat where larger prey are found and evidently higher foraging rates are possible. In the presence of congeners, however, the bluegill and pumpkinseed underwent dramatic niche shifts to the plankton and sediment habitats respectively." The green sunfish remained in the preferred vegetation habitat. Thus, to put it in other words (section 9.14), there is shared preference for the habitat with the highest resource supplies, the habitat with the greatest rate of foraging per unit time. The apparent resource partitioning is actually the result of competitive displacement of subordinates by dominants, that is asymmetric competition and inclusive niches. Measures of niche overlap based upon diet or habitat (e.g., Wootton, 1990) would therefore be quite misleading descriptors of the kind of competition occurring among these fish. There is a further complication: as fish increase in size, their diet changes, a phenomenon Werner labels ontogenetic niche shifts. Large pumpkinseeds, for example, can crush snails, whereas fish less than 45 mm in length cannot eat snails, and even those fish between 45 and 80 mm feed only on small easily crushed snails (Wootton, 1990). Werner concludes "That we need to be more critical of the sort of evidence we accept in community ecology is clear; major advances will not be made, however, through arguments as to whether descriptive patterns in community structure fit our expectations based upon current competition theory" (p. 381).

A test for competitive hierarchies with marine algae

One of the most thorough tests of the competitive hierarchy model to date has been carried out in the intertidal zone with three species of algae: *Fucus spiralis*, *F. vesiculosus* and *F. serratus*. Where there is closed vegetation these species form three contiguous zones. Physical factors varying with elevation include drought, freezing, and limitations upon phosphorus uptake, since the latter occurs only during immersion. The physiological data on these species suggest that the landward limits of distribution are set by their physical competence, with the uppermost species, *F. spiralis*, being the most stress tolerant. Karez and Chapman (1998) postulated two explicit hypotheses: (1) The competitive ranking would be *F. serratus* > *F. vesiculosus* > *F. spiralis* and (2) the fundamental niche breadth would be the reverse, *F. serratus* < *F. vesiculosus* < *F. spiralis*. Competition experiments were started with algal germlings grown in culture upon ceramic tile; after a period of hardening in the field, the plants were returned to the laboratory and cut with a diamond saw into 1 cm^2 segments. These squares of ceramic plate with attached juveniles could then be assembled at high or low density, and as monocultures or mixtures.

All analyses showed unequivocally that *F. vesiculosus* was dominant over *F. spiralis*, as predicted, but *F. vesiculosus* also appeared to be dominant over *F. spiralis*. That is, the species in the middle zone was competitively superior to the species higher and lower upon the shore. Transplant experiments showed different results for germlings and adults. With germlings, all three species survived in all three zones, although each performed best when transplanted to their own zones of natural occurrence. None grew better when transplanted to deeper, supposedly more benign sections of the gradient; in fact, *F. spiralis* and *F. vesiculosus* clearly performed worst in the lowermost zone. In sharp contrast, adults all showed greatest survival and highest dry mass in the lowest elevation.

These results are not in accord with the competitive hierarchy model. The relaxed version was viewed more favourably. "This variant seems more realistic compared with the originally strict assumptions of sharp borders of occurrence inevitably linked with invariable competitive ability and permits dominant/subordinate pairs to change rank under different environmental conditions . . ." (p. 490). There is a suggestion here that as with vascular plants (Shipley et al., 1989), juveniles and adults may have very different ecological attributes. Niche differentiation may occur at the seedling stage, whereas inclusive niches may be a property of adult interactions.

There is, of course, no need for a particular model to be correct. A model may simply provide a useful reference point against which we can gauge the rather more complex circumstances in real ecological communities. In such cases, it may even be better to have a model which is deliberately biased in one direction so that we know that reality lies only in the opposite direction from the reference point. Of course, there is always the temptation to try and rescue a model. Karez and Chapman (1998), to their credit, do not try to do so, although they charitably observe that "It can be argued that the mid-intertidal zone is the central benign habitat, where desiccation is still not severe and light extinction by the water column is insufficient to limit growth rates" (p. 492). They discount this possibility, probably with good reasons.

I am rather more sympathetic, for while I know rather little about marine algae, I am struck by the possible similarity to elevation gradients in forests, where the upper elevations are limited by exposure and drought, and the lower by cold and water accumulation, in which case intermediate positions are indeed the preferred habitat. Figure 2.9 shows such an example from a forestry text book. However, unless one has faith that nature is guided by a few underlying principles, one should exercise caution in assuming that rocky ocean shores are similar to forest on mountainsides, and this is particularly the case when such an assumption conveniently accords with a model to which one might feel a certain parental attachment. In general, we may be too willing to continue to care for a teenage model that has clearly outgrown our home and become abusive, even seeking out friends who are willing to adopt the model as their own. Both of these are to be discouraged; ape parenting instincts should be regarded with scepticism. There is, of course, a period when suckling and defence may be necessary to ensure that a model is fairly evaluated, but eventually it must be weaned and thrust from the nest to fend for itself.

9.15 OBSTACLES TO TESTING MODELS

Debates over the validity of models illustrates the problems encountered in constructing and evaluating models. Here I will briefly introduce some models and then summarize some arguments that occurred. I do so at some length because such criticisms illustrate not only debates over particular models, but over the entire issue of whether and how one can invalidate a model once it has been proposed. Without some means of invalidating models, the length of this chapter will simply increase with each new edition. How are we to decide which models to keep and which to discard? The challenge an author faces in writing such a chapter is little different from that faced by a scientist in deciding which models to adopt for continued use in their discipline.

9.15.1 How many data are needed to falsify a model?

In a second large computer modelling exercise (recall section 9.5), Tilman (1988) explored the consequences of a simple model of biomass partitioning in plants:

$$\mathrm{RGR}_{\max} = P_{\mathrm{m}}[1 - (S + R)/B] - r$$

where $\mathrm{RGR}_{\max}$ is the maximal relative growth rate, P_{m} is the maximal rate of photosynthesis per unit leaf biomass, r is the respiration rate per unit biomass, *B* is the total biomass of the individual plant, *R* is its root biomass, *S* is its stem biomass and leaf biomass is $L = B - S - R$. In this case, $\mathrm{RGR}_{\mathrm{max}}$ is assumed to be an increasing function of leaf allocation. I have not included this model in more detail, an author's prerogative as described above, in part because its predictions (e.g. that tall plants with high above ground allocation replace small plants with greater below ground allocation through succession) are neither unexpected nor different from other models.

Shipley and Peters collected comparative data on 68 species of herbaceous wetland plants. All were grown under standardized conditions, and both $\mathrm{RGR}_{\mathrm{max}}$ and shoot allocation were measured. Based upon these data, Shipley and Peters (1990) concluded that Tilman's model was invalid, because RGR was not correlated with shoot allocation in wetland plants.

In his first rebuttal Tilman (1991a) argues that the relationship between RGR and leaf biomass "was not an assumption at all, but a prediction of the model for a case in which all individual plants were assumed to have similar physiologies" (p. 1269). Therefore falsifying the RGR–leaf biomass relationship does not falsify the model. He then turns to their data and argues (1) that leaf allocation in his model is not the same as the shoot allocation that they measured, (2) that other published data show that the postulated relationships are widespread, and (3) (most remarkably), that because the wetland plants occur in different habitats, they do not provide a valid set to test the data. (This conclusion is reached by dividing wetlands into: uplands, meadows, shores, marshes, fens, standing water and bogs, and subjectively assigning the species used by Shipley and Peters into these different 'habitats'.)

Shipley and Peters (1991) respond that with respect to the philosophy of testing models: "Tilman (1991) cannot save the simplified version of Allocate [his model] by invoking physiological differences because the proposed explanations were derived by ignoring such differences. Although Tilman (1991) holds that the negative correlation, described above, is a prediction rather than an assumption, the difference is trivial. Simulation models are only devices to reveal the logical consequences of proposed assumptions in a deductive argument; if any step in the logical argument is shown to be false, then all further steps, being logically dependent upon it, can be rejected" (p. 1277).

They then continue that, with respect to data, the comparative data set on wetland plants is one of the largest available, and in a group of species that has already been subjected to extensive ecological study (e.g. Gaudet and Keddy, 1988, 1995; Shipley et al., 1990; Boutin and Keddy, 1993); if such a well known data set cannot be used as a tool to evaluate a model, what hope is there of ever doing so? Will every model, once published, have an indefinite life-span, however poor its fit to reality? With regard to Tilman's point (1), the morphology of these species is such that the distinction between shoots and leaves is relatively unimportant, particularly for seedlings and members of the monocotyledonae. Moreover, this is the period of life at which the greatest differences in RGR occur. With regard to point (2), both the Shipley and Peters data set, and a larger one by Hunt and Lloyd (1987) using 132 species, are the only large ones available, and both show the same patterns that falsify the Tilman model. Shipley and Peters show that in the extensive list of counter examples provided by Tilman (1991a), nearly all contained fewer than five species, making any inferences about general patterns of shot biomass and growth rates invalid.

The editors of *The American Naturalist* then allowed Tilman a second opportunity to rebut Shipley and Peters. He continues (Tilman, 1991b) "I have argued repeatedly that one of the major strengths of mechanistic models is that they are often simpler than the traditional phenomenological models" (p. 1284). He concludes that in his studies of five or six (depending upon the particular paper) prairie plants, R* "can be measured on numerous species and used to predict patterns in natural, species communities" (p. 1285).

I have spent some time on this, and the arguments are worth the effort of following in detail, because this exchange focuses attention upon an important issue. Here is a Princeton Monograph which has been frequently cited in the ecological literature, usually in a context implying that it is both well founded and widely accepted. There has been only one convincing attempt at validation, and it shows a major assumption to be false. Yet the author of the model tries to rescue it by arguing that in principle, the falsification of models using data should not indicate that a model is 'wrong' and therefore not useful in explaining other patterns (p. 1282). And in any case, the author continues, if there is any doubt remaining, the data used to invalidate the model (Hunt and Lloyd, 1987; Shipley and Peters, 1990) are not reliable any way.

What are we to conclude? My own opinion is that the wide acceptance of any model requires some belief that it reflects reality; if it does not, it is useful only in showing us how nature does not work. In this case, the two largest data sets available falsify a model, and yet the author attempts to explain away the data rather than admit the model is wrong. Moreover, with respect to point (3), the habitat affinities given by Tilman are entirely subjective, and, having worked upon such species myself for some twenty years, I do not agree with the tabulation provided (and note that this table was apparently constructed without reference to the many published studies on this flora!).

Since Shipley and Peters (1991) did not reply to Tilman's second rebuttal; let us give them the last word with a quotation from their first reply: "The full model ... involves 21 independent variables for each cohort of each species plus three variables describing the physical environment at each point in space. In a single $1/4\,m^2$ quadrat of herbaceous vegetation, one can find up to 25 species of angiosperms .... Thus, assuming that the 25 species observed are the only ones in the species pool, assuming no differences among cohorts, and assuming a homogenous environment, one would have to measure 528 (i.e., $21 \times 25 + 3$) parameters. Such requirements are beyond the capacities of even large ecological laboratories, yet a larger model is almost certainly needed because most systems contain many more species, because cohorts are different, and because environments are rarely temporally or spatially homogeneous" (p. 1281).

What are we to conclude from this exchange? Certainly, Tilman's second rebuttal attempts to shift attention away from large data sets, with 68 and 132 species respectively, to a small one (his own) that uses only 5 or (in some cases) 6 species. Further, he states that R* predicts the outcomes of his Minnesota experiments, when as we will see in the next section, this is incorrect. This exchange of papers forces us to fully confront and question the value of large multi-parameter models in the study of competition and how, if at all, we can separate useful ones from those which are invalid.

9.15.2 Interpretation of a field experiment on plant competition

Are experiments being used properly to test models? Let us examine one paper (Wedin and Tilman, 1993) from the lengthy series (e.g. Wedin and Tilman, 1990; Tilman and Wedin, 1991a,b; Johnson et al., 1992) that has been published from a single plant competition experiment run on old field vegetation in Minnesota : a brief introduction to this work can also be found in Keddy (1991b). The experiment tests for hierarchies across habitats by using 4 prairie grasses (five species were used in earlier work (Keddy, 1991b) but one does not appear in this latest set of analyses) grown at ten fertility levels.

Two outcomes might be distinguished: (1) The same hierarchy emerges in all habitats; this is consistent with the data reviewed in Chapter 5, or (2) a different hierarchy emerges in each habitat; this is consistent with predictions made by the model in section 9.6. If light to soil nutrient ratios affect competitive outcomes (Tilman, 1986), where better to find them than along an experimentally created soil fertility gradient?

The introduction to Wedin and Tilman (1993) does not, however, address the power of this experiment to explicitly test the resource–ratio hypothesis in question, and does not erect competing hypotheses for outcomes. This is so important that it bears repeating. If a different species dominated in each of the 10 different soil fertility levels, the resource–ratio hypothesis is supported. If the same species dominated each soil fertility level, competitive hierarchies are widespread and resource ratios need not be invoked to account for field distributions.

Part of the very power of this test to falsify rests in its inherent bias in favour of conclusions that support the model. That is to say, it is not a completely fair test for distinguishing between hierarchies and resource ratios. Here is the logic. Recall from Chapter 5 that the more similar the species that are interacting, the lower the probability of finding consistent hierarchies across different habitats. Similar species are, by definition, less likely to exhibit strong differences in relative competitive ability (Chapters 5 and 6). All species in this experiment are perennial grasses, and therefore they are relatively similar. In contrast, if the experiment included species ranging from grasses to rosette forbs to annuals, we might more reasonably expect a hierarchy to emerge. Therefore, if consistent hierarchies still emerge, it is even more dramatic evidence of their generality and significance.

The published results stretch a full 17 pages. Yet an important table is omitted: a table of competitive performance for each of the four species in the 10 habitats. The authors do tell us, however, that irrespective of the environment, the same species (*Schizachyrium scoparium*) won: "By year 5, *Schizachyrium* displaced or greatly reduced the biomass of both *Poa* and *Agropyron* on the soil mixture gradient ... independent of the wide range of starting conditions". That is, the same species dominated irrespective of soil nutrient levels. More remarkably, "large differences in experimental starting conditions had almost no effect on the 5 year outcome of competition."

This appears to be a crisp and definitive result. Clear competitive hierarchies emerged, just as with all other plant communities. The empirical patterns in Chapter 5 are again confirmed; the resource ratio model made incorrect predictions.

The paper, however, concludes ambiguously that "... resource pre-emption and asymmetric competition models predict that initial conditions remain important and are magnified during competition .... Our conclusions that initial conditions had no long term impact on interspecific competition in 3 out of 4 species pairs over most of the experimental productivity gradient contradicts existing generalizations about plant competition."

In short, there is a long list of publications from this single experiment, yet one could read them all without noticing that the experiment falsifies the model that inspired it. If models cannot be falsified when a fishery collapses (section 9.2.2), nor when two large data sets conflict with its central assumption (section 9.15.1), nor when the outcome of a key experiment produces an opposite outcome (section 9.15.2), then there is apparently no mechanism available to remove false models from the realm of scientific popularity.

9.16 CONCLUSION

The foregoing models illustrate exploratory, descriptive and, to a lesser extent, predictive models used in the study of competition. It is not yet clear whether any of them will provide a foundation for a solid body of competition theory. One route forward may lie in carefully designed mechanistic models based on realistic assumptions. Experimentalists could then interact with modellers by testing the assumptions used to construct the models, and testing whether these assumptions generate the expected predictions (for example, Austin, 1986). It will probably be less useful to succumb to the temptation to refine existing models endlessly in the hope that increased complexity of mathematics will generate a closer approximation to reality. Going by this route there is a genuine risk that models will simply be enlarged and elaborated to make them explain everything, rather than having them serve as clear signposts and reference points.

Mechanistic models may be unable to attain the accuracy of prediction provided by simple correlation models; the quantitative description of general ecological patterns may therefore be the goal for which we ought to strive (for example, Peters, 1980a; Rigler, 1982). The advantage of this approach is that it provides an easy measure of the validity of a model – r^2. The higher the percentage of variation in nature accounted for by the model (as measured by r^2), the more useful the model. Models such as this were not examined in this chapter because they do not deal with mechanisms such as competition, only with the resulting patterns such as the relationship between algal biomass and dissolved phosphorus in lakes.

However, such correlational approaches to the study of competition can be expanded in a mechanistic direction. One of the best examples comes from the studies of 'self-thinning' in plant monocultures referred to in Chapter 2 (Fig. 2.4). There is a general and well-established relationship between the mean mass of individuals and the density at which they are grown (Harper, 1977; Westoby, 1984) with a slope of –3/2. This empirical relationship (which is often known as the '–3/2 law') has broad generality, in that it can be applied to many kinds of plants grown both in the field and under laboratory conditions (Harper, 1977; Gorham, 1979) and can be clearly related to principles of geometry (Whittington, 1984). Thus, simple models already exist to predict plant performance from density, and there is little doubt that the principal mechanism is intraspecific competition for limiting resources. Such empirical approaches could be expanded and applied to other areas of ecology, such as competitive hierarchies (Chapter 5) and competition gradients (Chapter 7).

At present the greatest impact of models upon the study of competition has not been the accuracy of their predictions or the realism of their assumptions. Rather, they have provided the context or setting which defines the sort of questions that are thought to be interesting.

QUESTIONS FOR DISCUSSION

1. What are the benefits of constructing ecological models?
2. Are there any ways to overcome the inherent trade-off between precision and generality? What do we mean when we say that combining the two depends upon the skill of the modeller?
3. Why has resource partitioning had such an impact upon the ecological literature?
4. What should be the objectives for the next generation of ecological models? Can we specify criteria which these models should satisfy?

5. Compare and contrast the benefits of mechanistic models as opposed to simple predictive models.
6. Is Panglossianism a philosophical attitude or a falsifiable hypothesis for the nature of the world?
7. What kinds of models would be of most use in maintaining the biological diversity of our biosphere? Are they likely to have anything to do with competition?