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CHAPTER 11
THE REDUCTION OF THE LOTKA/VOLTERRA COMPETITION MODEL TO MODERN NICHE THEORY

11.1   Introduction

After the preparatory work of the former chapters I am now able to substantiate my claim that in ecology, too, holism-reductionism disputes notwithstanding, holistic and reductionistic research programmes co-operate and are mutually dependent. I will do so by discussing a concrete example of reduction in ecology, viz. the reduction of the Lotka/Volterra competition model (Lotka 1925; Volterra 1926) to modern niche theory (Tilman 1980, 1982; Glasser & Price 1982).

  The Lotka/Volterra model is a phenomenological (holistic) model. It describes the possible effects of competition between two species (in terms of coexistence or competitive exclusion). Modern niche theory is a mechanistic model, or rather a family of models (among others Levins 1966, 1968; MacArthur & Levins 1967; MacArthur 1968; Pianka 1969, 1974, 1983; Roughgarden 1972, 1976, 1986, May 1974; Schoener 1974, 1976, 1977, 1986, 1989; Leon & Tumpson 1975; Tilman 1980, 1982, 1985, 1988, 1990; Glasser & Price 1982, 1988; Berendse 1985; Abrams 1986, 1987a,b, 1988; Huisman 1994; Huisman & Weissing 1994; Weissing & Huisman 1994), which provides a mechanism of competition in the way of exploitation of resources by two or more species. These models also go under the name of resource-consumer models and one particularly attractive feature of them is that they can be applied to both 'predator-prey' (including plant-nutrient and herbivore-plant) interactions and competitive interactions (both between 'prey' species and between 'predator' species). Moreover, through these various types of interaction they can be used to explain the structure and dynamics of both 'prey' communities and 'predator' communities as well as the structure and dynamics of ecosystems. Thus the theory seems to have great potential for becoming the first general and unifying theory in ecology.

  I will first discuss the logistic model of population growth on which the Lotka/Volterra competition model is based, then the Lotka/Volterra model itself, and next the reduction of this model to one particular model of modern niche theory (Glasser & Price 1982). I will point to the interesting fact that, in spite of the one being reduced to the other (or rather because the one reduces the other), both models may be seen as idealizations (in the sense of the model of idealization and concretization discussed in chapter 3). After that, I will discuss some extensions and applications of modern niche theory (where auxiliary hypotheses or theories are being used) which in turn may be regarded as concretizations of the theory. In doing so, I will also provide some further clarification of conceptual issues in the field of modern niche theory, particularly those relating to the principle of coexistence through niche differentiation. And finally I will shortly discuss another model of the theory (Tilman 1980, 1982), which also reduces the Lotka/Volterra competition model but, contrary to what some believe, provides another mechanism of coexistence than niche differentiation.

11.2   Intra- and interspecific competition
11.2.1   The logistic model of population growth: intraspecific competition

The Lotka/Volterra competition model is based on the logistic model of population growth. This model, which describes a sigmoidal growth-curve for populations, was first coined by Verhulst (1838) to describe the growth of human populations and later was derived

independently by Pearl and Reed (1920) for the growth of populations in the United States. The model is based on some very simple assumptions about population growth and basically supplements a term describing geometrical growth with a term incorporating the effects of intraspecific competition. There are several ways of arriving at the model. The sources I have used in the following are Pielou (1978), Begon et al. (1996) and Krebs (1994).

The simplest model of population growth is based on the assumption that the growth of a population is determined by two processes: the birth and the death of individuals.[80] If l stands for the per caput (mean or average) birth rate (that is, the mean number of births per individual per unit of time) and m for the per caput death rate, than the change in the size of a population (the number of individuals N) in time, dN/dt, is given by

$$\frac{dN}{dt} = (l - m)N \tag{2}$$

The term between brackets, $l - m$, is also noted as r, the per caput growth rate of a population: $dN/dt.1/N = r$. (When there is no competition, r is defined as the intrinsic growth rate of a population.) Thus we may also write

$$\frac{dN}{dt} = rN \tag{3}$$

When r is greater than zero, population growth is geometric and a population may grow indefinitely. For natural populations this assumption is not very realistic, however, since the growth of natural populations is generally limited by all sorts of factors affecting either birth or death rate or both: most natural resources come in limited supplies, whence at a certain moment competition between individuals may occur; there may be other species utilizing the same resources such that population growth may also be limited by interspecific competition; individuals may become a victim of fierce climatic or weather conditions (strong winters); and individuals may fall a prey to all sorts of predators, parasites or diseases. All such factors may result in there being at some moment more deaths than births such that population growth decreases or becomes negative (that is, $r = (l - m)$ becomes negative).

The simplest additional assumption that can be made is that all sorts of external factors to a population (weather, climate, predators, parasites, interspecific competitors) play no role and that population growth is limited only by intraspecific competition. This may occur through either interference among individuals or exploitation of resources, but the logistic model itself doesn't specify any mechanism. Suppose, however, that there is only one type of resource, R, and that R is produced at a constant rate y. Suppose further that every individual of the population consumes units of X with a constant rate c. Then the total consumption rate of the population equals cN. As long as cN is smaller than y, there will be sufficient units of R to

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[80]The model described here is suited for populations with continuous reproduction. These can best be described by differential equations, in contrast to populations with discrete breeding seasons which are better described by difference equations. There are no fundamental differences between the two types of models, however, and they can be reduced to one another by integration and differentiation, respectively.

allow the population to grow. However, there will come a time when *cN* becomes equal to or exceeds *y*. Intraspecific competition will then become ever more intense as an increasing number of individuals make demands on a decreasing supply of resources. The per caput death rate *(m)* will increase with equal or decreasing birth rate *(l)*. Thus the population growth rate will decrease, may become 0 when *m* equals *l*, or even become negative. In time, because of decreased consumption, the resource supply may grow again, allowing the population to recover and this may go on in an endless cycle of growth and decay.

Over long periods of time, then, a population may oscillate around a point where *cN* equals *y* and where *l* equals *m*. At this point, *r* and hence *dN/dt* is 0, and the population is in equilibrium in the sense that at densities below this point *l* will be greater than *m* and population size will increase, while at higher densities *l* will be smaller than *m* and population size will decrease.

The populations size at equilibrium is called the carrying capacity, *K*, as it represents the maximum number of individuals than can be 'carried' (sustained) by the resources of the biotope (or of the (realized) habitat of the population).

Thus, equation (2) may provide an adequate description of a population's growth rate when *N* is close to 0, but it becomes ever more inadequate the more *N* approaches *K*. Therefore, a term must be added to the right-hand side of the equation to account for the effects of intraspecific competition. What we want is a term that goes to 1 when *N* goes to 0 (such that equation (2) is obtained again) and that goes to 0 as *N* approaches *K* (such that population growth decreases asymptotically to a certain upper value where *dN/dt* = 0). The simplest term satisfying these conditions is *(K - N)/K*, whence

$$\frac{dN}{dt} = \frac{rN(K - N)}{K} \tag{4}$$

This is the logistic model of population growth. It is easy to check that equation (2) still holds when *N* goes to 0 (because *(K - N)/K* then goes to 1) but that *dN/dt* goes to 0 as *N* approaches *K*. Thus the logistic model describes the sigmoidal growth of a population: after an initial period of geometric growth, the growth rate decreases asymptotically to 0 as *N* approaches *K*.

11.2.2 Limitations of the logistic model

The attractive feature of the logistic model is its simplicity but this is at the same time its limitation. Several objections have been raised against the model, of which I will mention the most important ones.

The main objection is that although the model may provide an adequate description of laboratory populations, which are allowed to grow under strict conditions, natural populations rarely if ever reach a constant equilibrium density (K) but rather constantly fluctuate in density. The reason for this is of course that natural populations are exposed to many other factors than are assumed in the model. The model should be seen, therefore, as a first approximation (or idealization), where it is assumed that all sorts of external factors are unimportant. One may compare this with the Hardy/Weinberg model in population genetics, which is also a first approximation (idealization) assuming that such factors as migration, mutation and selection play no role (see for example Hartl 1980).

Another objection is that the model assumes a linear relationship between the growth rate of a population and its density. This assumption is probably not very realistic and violated by most populations, but it has not been the subject of much research (see Krebs 1994). This is related to another problem, namely that the assumed density dependent 'regulation' of populations may be produced also by other, density independent (external) factors. This problem lies at the heart of the afore-mentioned (chapter 8) controversy about population regulation between among others the (density dependent) biotic school (Nicholson & Bailey 1935; Nicholson 1954; Lack 1954) and the (density independent) climate school (Andrewartha & Birch 1954, 1984).

A third objection is that the model doesn't account for time lags in the working of density on growth rate. In insects, for example, it may take several weeks or months before larvae develop into mature individuals. The logistic model may be adequate in this respect for organisms with a simple life cycle (and a stable age structure, another objection raised against the model) but has to be modified for organisms with more complex life cycles. This has led to so-called time lag models (see, among others, Wangersky & Cunningham 1956; May 1976; Pielou 1977). These models show that such lags may lead to considerable fluctuations in the density of populations instead of stable equilibrium densities.

A final objection is that the logistic model is a deterministic model which takes no account of chance processes. By contrast, stochastic models show that populations having the same initial density and per caput birth and death rates may grow at quite different rates as a result of chance fluctuations in the number of births and deaths in time. Such fluctuations may even result in populations becoming extinct, especially when they are small (MacArthur & Wilson 1967).

11.2.3   The Lotka/Volterra model: interspecific competition

The Lotka/Volterra model is an extension of the logistic model with a term incorporating the effects of interspecific competition. To represent this we need to index the relevant parameters for different species. Let N_i therefore denote the population size of species S_i, N_k the population size of species S_k, and let their respective carrying capacities and intrinsic growth rates be denoted by K_i, K_k, r_i and r_k. In order to represent the interspecific competitive effects of the one species on the other we need to convert individuals of the one species into equivalents of individuals of the other species.

Suppose, for example, that 2 individuals of species S_k have on average the same inhibitory effect on the growth of species S_i as has 1 individual of S_i itself (for instance because 2 individuals of S_k consume on average as many resource units as does 1 individual of S_i). The total (intra- and interspecific) competitive effect on the growth of S_i is then equal to the effect of $(N_i + N_k/2)$ individuals of S_i. The conversion factor (a constant; in this case ½) is called the competition coefficient and is denoted by α_{ik}. This measures the average competitive effect of S_k on the growth of S_i. When $\alpha_{ik} = 1$, 1 individual of S_k has the same competitive effect on the growth of S_i as has 1 individual of S_i itself, and when α_{ik} is larger or smaller than 1, 1 individual of S_k has, respectively, a larger or smaller competitive effect on the growth of S_i than has 1 individual of S_i itself.

Thus when N_k is multiplied by α_{ik} it is converted into a number of equivalents of S_i. The Lotka/Volterra model is obtained by substituting the term N_i in the term $(K_i - N_i)/K_i$ of the logistic model by a term representing 'N_i plus N_i-equivalents':

$$\frac{dN_i}{dt} = \frac{r_i N_i (K_i - (N_i + \alpha_{ik} N_k))}{K_i}$$

or

$$\frac{dN_i}{dt} = \frac{r_i N_i (K_i - N_i - \alpha_{ik} N_k)}{K_i} \qquad\qquad (4a)$$

In the same way α_{ki} measures the average competitive effect of S_i on the growth of S_k, and multiplying N_i by α_{ki} converts it into the number of equivalents of S_k:

$$\frac{dN_k}{dt} = \frac{r_k N_k (K_k - N_k - \alpha_{ki} N_i)}{K_k} \qquad\qquad (4b)$$

Equations (4a) en (4b) together form the Lotka/Volterra model.

11.2.4 Predictions of the Lotka/Volterra model

If all possible densities of S_i are plotted against the density of S_k (varying from 0 to N_k), a line can be drawn through the points where the population of S_i is in equilibrium (that is, where its growth rate is zero) at each density of S_k (figure 8a). The line connecting these points is called the zero isocline of S_i. Below and to the left of this line, Si increases, and above and to the right of this line, it decreases. At each point on the line, by definition, dN_i/dt = 0, and from equation (4a) we can derive that in these cases

$$r_i N_i (K_i - N_i - \alpha_{ik} N_k) = 0$$

This is true when either $r_i = 0$, or $N_i = 0$, or $K_i - N_i - \alpha_{ik}N_k = 0$. The latter can also be written as

$$N_i = K_i - \alpha_{ik} N_k$$

When $N_i = 0$, $N_k = K_i/\alpha_{ik}$, and when $N_k = 0$, $N_i = K_i$.
  Doing the same for the zero isocline of S_k (figure 8b) we obtain that when $N_k = 0$, $N_i = K_k/\alpha_{ki}$, and when $N_i = 0$, $N_k = K_k$. In this way we have obtained two sets of two points, K_i and K_i/α_{ik}, and K_k and K_k/α_{ki}, giving the zero isoclines of S_i and S_k, respectively.
There are four possible ways in which these isoclines may be positioned relative to each other and the outcome of competition is different in each case (figure 9). These cases are given by:

1) $K_i > K_k/\alpha_{ki}$ and $K_k < K_i/\alpha_{ik}$, or, equivalently, $K_i > K_k\alpha_{ik}$ and $K_k < K_i\alpha_{ki}$.
2) $K_i < K_k/\alpha_{ki}$ and $K_k > K_i/\alpha_{ik}$, or, equivalently, $K_i < K_k\alpha_{ik}$ and $K_k > K_i\alpha_{ki}$.
3) $K_i < K_k/\alpha_{ki}$ and $K_k > K_i/\alpha_{ik}$, or, equivalently, $K_i < K_k\alpha_{ik}$ and $K_k < K_i\alpha_{ki}$.
4) $K_i < K_k/\alpha_{ki}$ and $K_k < K_i/\alpha_{ik}$, or, equivalently, $K_i > K_k\alpha_{ik}$ and $K_k > K_i\alpha_{ki}$.

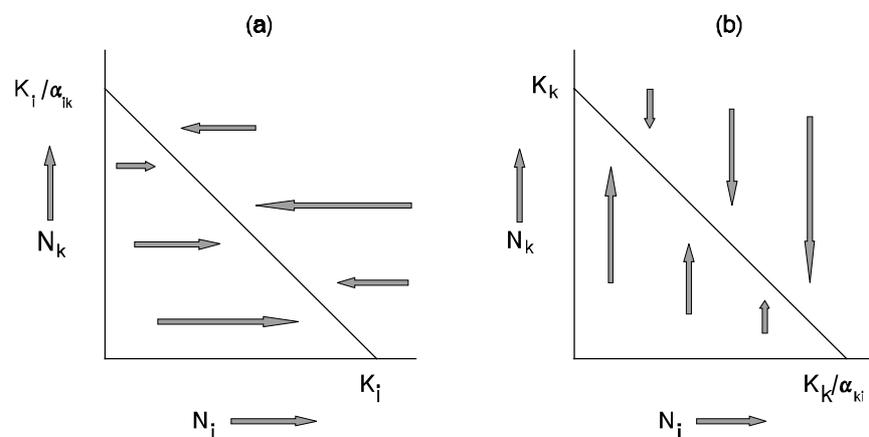In case 1 the first inequality indicates that the inhibitory *intra*specific effect which S_i has on

Figure 8: The zero isoclines generated by the Lotka-Volterra competition model for species S_i (a) and species S_k (b) (after Begon et al. 1986). See main text for explanation.

itself is larger than the *inter*specific effect exerted by S_k on S_i. However, the second inequality indicates that the *inter*specific effect of S_i on S_k is larger than the *intra*specific effect of S_k on itself. This means that S_i is a strong interspecific competitor while S_k is a weak interspecific competitor. The result is that S_i will competitively displace (exclude) S_k and that S_i will be able to reach its own carrying capacity (K_i).

In case 2 the situation is reversed: S_k is the stronger interspecific competitor; it will drive S_i to local extinction and itself reach its carrying capacity.

In case 3 both species have stronger interspecific effects on each other than they have intraspecific effects on themselves. The outcome of competition in this case is either an unstable equilibrium at intermediate densities of both species (between 0 and their *K*'s) or competitive exclusion of one of the species. Which species will be excluded depends on the initial conditions: the species with the larger initial population will drive the other to local extinction.

In case 4, finally, both species have smaller interspecific effects on each other than they have intraspecific effects on themselves. The outcome of competition in this case is a stable equilibrium combination, that is, coexistence, of both species at intermediate densities. It has been suggested that this case is possible only if each species utilizes a resource not shared with its interspecific competitor or if a shared resource is in some way heterogeneously distributed in the biotope such that it can be divided among both species. That is to say, this case would be possible only if in some way niche differentiation could occur. I will return to this later (11.3.2).

Thus the Lotka/Volterra model predicts either competitive exclusion (of the weaker interspecific competitor or the initially disadvantaged species) or stable coexistence of the two competing species.

Since the model is based on the logistic model of population growth its shares the advantage of this model (its simplicity) but also its disadvantages (see 11.2.2). Still, it has been of
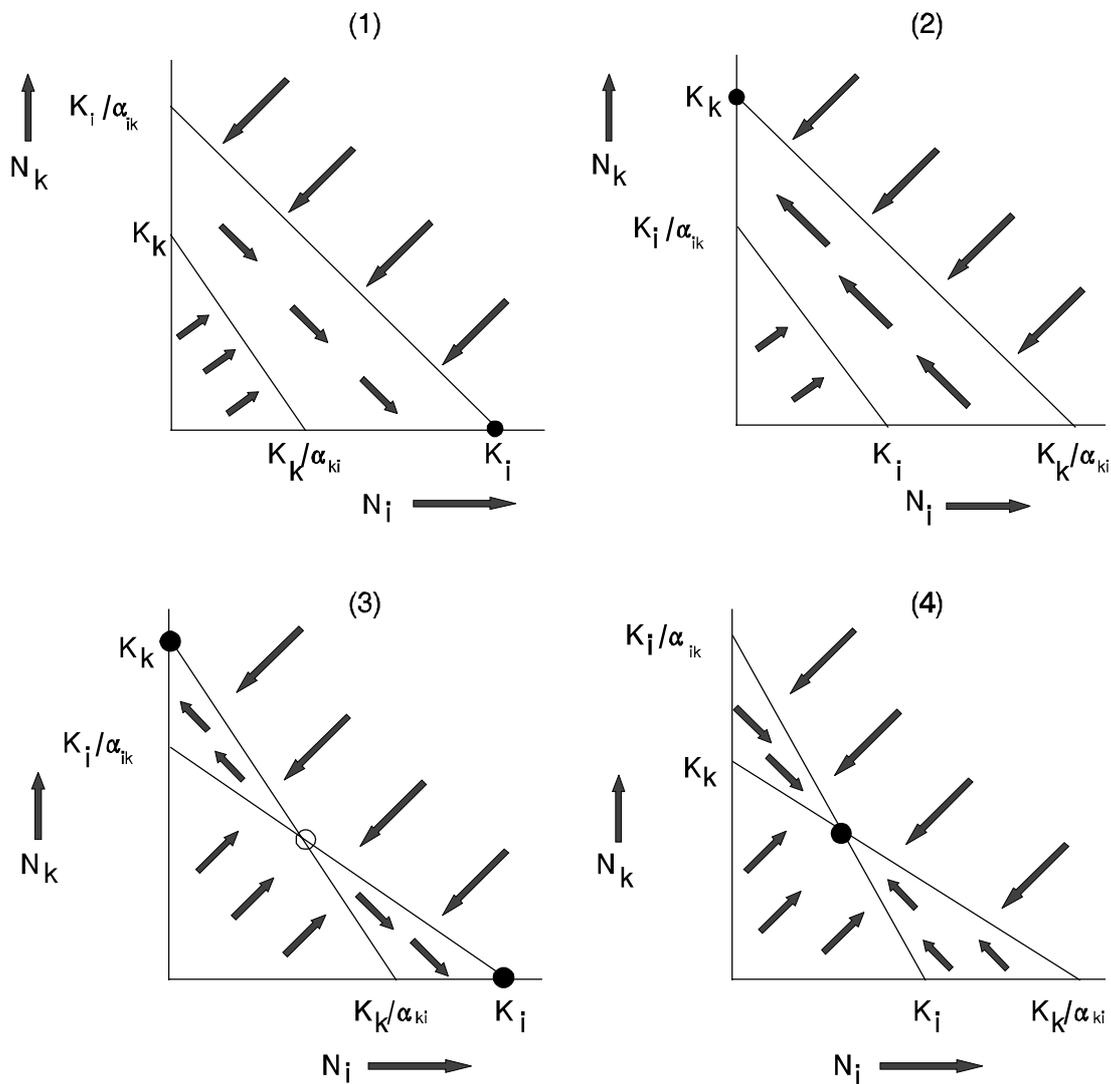
Figure 9: The four outcomes of competition generated by the Lotka-Volterra model. The solid circles indicate stable equilibrium points, the open circle an unstable equilibrium point (after Begon et al. 1986).

enormous value for the growth of ecological knowledge. It has generated an enormous amount of empirical and theoretical research and I think it won't go too far to say that it has established a whole new research tradition or research programme (eventually also leading to modern niche theory). The attention has been directed thereby at both the tenability of its theoretical principles and assumptions and the empirical testing of its predictions (through both laboratory and field experiments). The general conclusion appearing from this is that the predictions of the model seem to correspond to biologically realistic situations but that some of its assumptions are a bit too simple (see for example Begon et al. 1996; Krebs 1994). Most of the objections raised against the model are the same as those raised against the logistic

model. Both models may be seen, therefore, as first approximations or idealizations in the sense of the model of idealization and concretization mentioned in chapter 3. I will return to this in the next section.

11.3   Modern niche theory: predation and competition
11.3.1   Reduction of the Lotka/Volterra model

The main 'problem' with the Lotka/Volterra model is that it is a phenomenological model. That is to say, it indicates *that* species may influence one another but not *how*. Thus the model raises the question for a deeper explanation of its assumptions and predictions. This explanation is provided by modern niche theory, which thereby reduces the Lotka/Volterra model. Modern niche theory is a mechanistic theory, or rather a family of mechanistic models, in which both the objects of competition (resources) and a mechanism (resource exploitation by two or more species) are being specified. In the following, I will present the reduction of the Lotka/Volterra model to one particular model of modern niche theory, the model of Glasser and Price (1982).

This reduction occurs with the help of an identification hypothesis and two aggregation hypotheses. In the former (Leslie 1948; in Glasser & Price 1988, p. 58) it is assumed that the carrying capacity of a species, K_i for species S_i, can be written as the quotient of the availability, A_j, of a particular resource j, and the per caput effect, c_{ji}, of (consumption by) S_i on the availability of that resource:

$$K_i = \frac{A_j}{c_{ji}} \tag{5}$$

When there are T alternative (that is, more or less substitutable, *sensu* Tilman 1980) resources, K_i is the sum of T quotients:

$$K_i = \sum_{j=1}^{T} \left(\frac{A_j}{c_{ji}} \right) \tag{6}$$

By assuming next that

$$N_i = \sum_{j=1}^{T} n_{ji} \tag{7}$$

where n_{ji} stands for the number of individuals of S_i exploiting resource j, and by substituting equations (6) and (7) into equation (4a) and simplifying, we get for a system of S species and T resources:

$$\frac{dN_i}{dt} = r_i \sum_{j=1}^{T} \frac{n_{ji}}{A_j} \left(A_j - \sum_{i=1}^{S} c_{kj} n_{kj} \right) \tag{8}$$

Equation (8) is the model of modern niche theory presented by Glasser and Price (1982; see

also Glasser & Price 1988).

The reduction of the Lotka/Volterra competition model to this model of modern niche theory is a nice example of (deductive) heterogeneous micro-reduction (with aggregation and identification): it uses a relatively simple identification hypothesis (equation (5)) and two simple ('trivial') aggregation hypotheses (equations (6) and (7)). Because only the steps identification and 'trivial' aggregation are used, we cannot speak of emergence at the level of the Lotka/Volterra model relative to the level of modern niche theory (see chapter 5). This is somewhat counter-intuitive because the reduction pertains to interactions between species and because, as argued in former chapters, interactions between parts generally lead to emergence at the level of the whole. However, these interactions play a role in both modern niche theory and the Lotka/Volterra model. Put differently, both theories are concerned with interactions between species. In that sense they both pertain to the same level of organization (though of course modern niche theory deals also with the level of resources). It is only at the level of the effects of these interactions (competitive exclusion or coexistence, and hence the structure of communities) that emergence may occur.

It will be clear that the Lotka/Volterra model has acted as a holistic guide programme for modern niche theory and that modern niche theory has acted as a reductionistic supply programme for the Lotka/Volterra model. Thus, the reduction is also a nice example of the co-operation and mutual dependence of holistic and reductionistic research programmes in ecology (albeit so far perhaps the only example of a successful reduction resulting from such co-operation).

Incidentally, it should be noticed that, since the Lotka/Volterra model is an idealization, and since it is reduced *deductively* by modern niche theory, modern niche theory is itself also an *idealization*. In the following sections I will discuss some specific applications and extensions of the theory, whereby additional (auxiliary) hypotheses or theories are used, which may be seen as *concretizations* of the theory. In doing so, I will also discuss some further terminology in the field of modern niche theory.

11.3.2   Coexistence through niche differentiation

When n_{ji}/N_i is defined as f_{ji}, and when, in equation (8), n_{ji} is substituted by $f_{ji}N_i$, and n_{jk} by $f_{jk}N_k$, we get (Glasser & Price 1988):

$$\frac{dN_i}{dt} = r_i N_i \sum_{j=1}^{T} \frac{n_{ji}}{A_j}(A_j - \sum_{i=1}^{S} c_{jk}f_{jk}N_k) \qquad (9)$$

Next, when both sides of this equation are divided by N_i, and when it is assumed that no parameters vary with N_k (that is, all $\delta/\delta N_k$ are 0)[81], then, by differentiation, an expression

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[81]This means, among other things, that it is assumed that species do not influence each other's probability of exploiting a particular resources ($\delta f_{ji}/\delta N_k = 0$ for $i = 1,..., S$ and $j = 1,..., T$). As noted by Glasser and Price (1988, p. 66), however, in reality these probabilities may be functions of the abundances of all other resources as well as of their consumers (that is, $f_{ji} = g(N_k,A_l)$ for $k = 1,..., S$ and $l = 1,..., T$). They also note that, since it is presently

for the per caput competitive effect of S_k on S_i is obtained:

$$\frac{\delta(dN_i/N_i dt)}{\delta N_k} = -r_i \sum_{j=1}^{T} \left(\frac{c_{jk}}{A_j}\right) f_{ji} f_{jk}$$

The competition coefficient may then be written as:

$$\alpha_{ik} = \frac{\sum_{j=1}^{T} \left(\frac{c_{jk}}{A_j}\right) f_{ji} f_{jk}}{\sum_{j=1}^{T} \left(\frac{c_{ji}}{A_j}\right) f_{ji}^2} \qquad (10)$$

According to Glasser and Price (1988, p. 58), because of the assumption that no parameters vary with N_k, the frequencies in the denominator of equation 10 characterize the exploitation of resources by S_i en S_k in the absence of, respectively, interspecific and intraspecific density effects, while the frequencies in the numerator characterize the exploitation of resources by species S_i in the absence of intraspecific density effects. These terms correspond to Vandermeer's (1972) notions of (0-th) partial niches (see chapter 10).

Thus, in this model, competition coefficients, and hence conditions for coexistence, are functions of (1) the availabilities (A_j) of resources; (2) the niche breadths and niche overlap $(\Sigma f_{ji} f_{jk}/\Sigma f_{ji}^2)$[82] of the competing species; and (3) the per caput consumption rates (c_{ji} and c_{jk}) of these species. The latter depend in turn on the species' minimum resource requirements and their strategies and efficiencies of resource use (see below).

Whether competitive exclusion or coexistence occurs depends first of all on whether resources are limiting or not. In a finite world all resources are limited. However, a resource is limiting only if an increase in its availability is both necessary and sufficient for an increase in population size. Therefore, competition need not affect a population's growth rate, when it is being limited by another factor than contested resource availability (such as the weather, a toxic substance, a predator or parasite, or another resource).

In the second place it is important whether or not niche differentiation may occur. Niche differentiation is one of the mechanisms through which competing species may be able to reduce the intensity of competition (and hence the chance of competitive exclusion). Niche differentiation results in reduction of niche overlap through reductions of niche breadth. This can best be illustrated by a simple example. Suppose there are two bird species, S1 and S2,

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impossible to write such functions explicitly, modern niche theory must as yet be supplemented with the theory of exploitation strategies (Glasser 1982, 1984; see also MacArthur & Pianka 1966; MacArthur & Wilson 1967; Abrams 1987a,b, 1988). I will return to this later in the main text.

[82]As argued by Petraitis (1979), measures of niche breadth and overlap must be properly scaled to account for the frequency with which resources occur in a biotope. Glasser and Price (1982, 1988) use Petraitis' scaled maximum likelihood measures.

both exploiting the same fruits, and suppose than in each other's absence S1 consumes fruits of 4-12 mm and S2 consumes fruits of 6-14 mm. Thus, the species have strongly overlapping 1-st partial (intraspecific) niches. Niche differentiation would mean in this case that in each other's presence S1 would consume only fruits of, say, 4-9 mm, and S2 would consume only fruits of, say, 10-14 mm. That is to say, the species have 'divided up' the available food resources in such a way that their S=2-th partial (interspecific) realized niches do not overlap. Besides niche differentiation, the terms '*resource partitioning*' and '*differential resource utilization*' are also being used for this (though in my view the latter term rather indicates the results of niche differentiation than the mechanism itself). It is also possible that only one of the species changes its diet, in which case one speaks of '*niche displacement*' or '*niche shift*'.

Niche differentiation need not be complete, however. It is also possible that S1 consumes fruits of, say, 4-11 mm, and that S2 consumes fruits of, say, 9-14 mm. That is to say, coexistence may also be possible with some degree of niche overlap of the competing species. This has led to the question how different species must be in order to be able to coexist, or conversely, how similar they must be in order not to be able to coexist. This is known as the problem of '*limiting similarity*' (MacArthur & Levins 1967; May 1973, 1981; Roughgarden 1974, 1979; Schoener 1974, 1988; Abrams 1975, 1983).

In the long run (on an evolutionary scale) competition may also give rise to new sub-species or even new species, for example when changes in diet are accompanied by morphological changes (for instance in bill size or form), and thereby also become genetically fixed. In that case one speaks of '*character displacement*' (Lack 1947; Brown & Wilson 1956; Grant 1972, 1975; Fenchel 1975; Davidson 1978; Pacala & Roughgarden 1982; Schluter et al. 1985). (Another term being used for this is '*niche divergence*' but I it is not clear to me whether this concept is also meant to include the genetic changes that are, in my view, required for character displacement.) Thus, character displacement may be regarded as the evolutionary equivalent of niche differentiation. Based upon the definitions suggested in chapter 10, the chief difference between the two phenomena would be that character displacement also involves changes in the potential niches of species, whereas niche differentiation pertains only to changes in realized niches.[83]

The best known example of character displacement is formed by Darwin's finches on the Galapagos islands, which have developed into species with different body sizes, bill forms and bill sizes, and which have come to utilize different types of resources (Lack 1947). Though a plausible phenomenon (see, among others, Schoener 1974, 1984; Roughgarden 1976, 1979; Slatkin 1980; Case 1981, 1982; Taper & Case 1985; Abrams 1986), the occurrence of character displacement is still controversial and actual examples are hard to find (Strong et al. 1979; Connell 1980; Strong & Simberloff 1981; Arthur 1982).

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[83]Another difference is that character displacement can also lead to changes in the (potential and/or realized) habitats of species (Scoener 1974b, 1975). Contrary to niche differentiation, it is then no longer a mechanism of coexistence (in the same biotope or in the area of realized habitat overlap (see 10.4.3) but a mechanism to avoid competition: the ghost of competition past (Connell 1980).

11.3.3   Niche differentiation or habitat differentiation?

Because of the confusion of various niche concepts in the ecological literature, it is not surprising that there is also a lot of confusion about niche differentiation, particularly its difference from habitat differentiation. Thus, one also speaks of niche differentiation (or of differential resource utilization) when different species utilize the same resources but do so at different locations in a biotope or, for instance, at different heights in a vegetation. A famous example is MacArthur's (1958) study of different warblers which are all of roughly equal size and consume the same food (insects). MacArthur found, however, that they forage at different heights in trees and this has been regarded as a form of niche differentiation (resource partitioning). In my view, however, it is not a form of niche differentiation but a form of habitat differentiation (see 10.4.3).

   Typical of the confusion are some statements made by Begon, Harper and Townsend (1986). These authors state that "In many cases, the resources utilized by ecologically similar species are separated spatially. *Differential resource utilization* will then express itself as either a *microhabitat differentiation* between species, or even a difference in geographical distribution [that is, macrohabitat differentiation, sic]" (Begon et al. 1986, p. 283; emphasis added). In both cases they speak of niche differentiation. They also state that "The other way in which *niches can be differentiated* is on the basis of conditions. Two species may *utilize precisely the same resources* [sic]; but if their ability to do so is influenced by environmental conditions (as it is bound to be), and if they respond differently to these conditions, then each may be competitively superior in different environments. This too can express itself as either a *microhabitat differentiation*, or a [*macro-habitat differentiation*] (..) depending on whether the appropriate conditions vary on a small spatial scale [or on] a large spatial scale" (Begon et al. 1986, p. 283; emphasis added). They call this also niche differentiation. They do so, of course, because they use Hutchinson's multi-dimensional niche concept, which includes not only resources but also environmental conditions, and also because they use the community concept of habitat (H3; see the former chapter). Given the modern niche concept (theory), however, these cases are not examples of niche differentiation but of habitat differentiation (or, as indicated by the authors, but in the terms of chapter 10, microbiotope and macrobiotope differentiation).

11.3.4   Coexistence without niche differentiation

Niche differentiation is impossible when the biotope is a simple and homogeneous medium containing only one type of resource (such as in Gause's (1934) famous *Paramecium* experiments). This has led to such formulations of the competitive exclusion principle as "Two species cannot coexist on the same limiting resource" (Ricklefs 1979, p. 549).

   Armstrong and McGehee (1976, 1980) have shown, however, that this is true only when it assumed, as in most competition models, that the per caput growth rates of species are linear functions of the availability of resources, and when coexistence is considered at fixed equilibrium densities. The linearity assumption implicates, however, that the per caput growth rate of a population (r) could increase indefinitely with increasing resource availability, which is biologically absurd (see also Abrams 1980, 1987a,b). Also, there seems to be no reason why two species could not be said to coexist if their densities constantly fluctuate without either of them ever reaching equilibrium density or becoming locally extinct (see also Levin

1970). Armstrong and McGehee have shown that if coexistence is considered at fixed equilibrium densities, S species cannot coexist on $T < S$ resources, even without the linearity assumption. When the assumption of fixed densities is relaxed, but not that of linearity, S species can coexist on $T < S$ resources, except when $T = 1$. When both assumptions are relaxed simultaneously, S species can coexist on $T < S$ resources even if $T = 1$. This means that, contrary to many formulations of the competitive exclusion principle, different species may well be able to coexist in spite of having identical (S-th partial or interspecific) realized niches. (Of course, this is not to say that niche differentiation cannot be an important mechanism of coexistence in heterogeneous biotopes.)

Different species having identical realized niches (that is, in terms of Glasser and Price's model, $f_{ji} = f_{jk}$ for $j = 1$ to T resources) may be able to coexist in a biotope if they have different per caput effects, c_{ji} and c_{jk}, on any of $j = 1$ to T resources. This is defined as the quotient of R_i and e_{ij}, where R_i stands for the minimum number of resources required by each individual of species S_i, and e_{ij} for the efficiency with which individuals of species S_i exploit resource j. Thus, different species may be able to coexist in spite of having identical realized niches if they have different minimum resource requirements *(R)* or exploit resources with different efficiencies *(e)* (Glasser & Price 1982, p. 459). That such differences exist seems very likely, suggesting once more that coexistence of competitors may be much more probable than was once assumed. This is especially important with respect to plant species, since all plants require essentially the same resources (space, light, water, mineral nutrients and spore elements) and hence have strongly overlapping or identical niches. Because these are all essential (*sensu* Tilman (1980), that is, non-substitutable) resources, opportunities for niche differentiation in plants are much more limited than in animals. It is much more likely, therefore, that plants are able to coexist through differences in competitive abilities, such as measured by their consumption rates, minimum resource requirements or efficiencies of resource use (see Aarssen 1983, 1984, 1985; Tilman 1980, 1982, 1985, 1988; Huisman & Weissing 1994). I will return to this later (11.4.2 and 11.4.3).

11.3.5   Exploitation strategies

Conditions for coexistence are determined also by the resource exploitation strategies of species (which may affect both their niche breadths, consumption rates and efficiencies of resource use) and therefore by their functional responses (Holling 1965; Abrams 1980, 1987b; Glasser 1982, 1984; Glasser & Price 1982, 1988; see also note 72).

In the 'classical' theory of exploitation strategies (MacArthur & Pianka 1966; MacArthur & Wilson 1967; Pianka 1970; Schoener 1971; Maynard Smith 1972) a distinction is made between so-called *r-selected species* and *K-selected species*. The former are species with a high per caput reproductive rate (*r*). They are often species of unstable biotopes, which keep their population size far below the carrying capacity (*K*) of the biotope, are able to reproduce themselves quickly and have high dispersal abilities. This investment in reproduction and dispersal goes at the expense, however, of efficiency of resource use and hence competitive ability. *r*-Selected species are often *generalists*, therefore, with a broad biotope preference and food choice. *K*-selected species, on the other hand, are often *specialists*. They are often species of relatively stable biotopes, which keep their population size at or near the carrying capacity of the biotope and invest more in efficiency of resource use than in reproduction and dispersal.

As argued by Glasser (1982, 1984), it is likely that (obligate) generalists and specialists have evolved under conditions where N_i/K_i is large and small, respectively, but constant. Under conditions where N_i/K_i is variable, it is much more likely, however, that species have evolved with facultative strategies. He calls such species facultative strategists. When N_i/K_i is variable and large, one may expect the evolution of facultative strategists with even efficiencies of resource use ($e_{ji} = R_i/c_{ji}$), and when N_i/K_i is variable but small, one may expect the evolution of facultative strategists with uneven efficiencies of resource use. Since facultative strategists with even efficiencies of resource use are indistinguishable, qua behaviour of niche breadth, from obligate generalists, and since facultative strategists with even efficiencies strongly resemble obligate specialists (see Glasser 1982, figure 2), the obligate strategies may be seen as the two extremes of a continuum of facultative strategies (Glasser & Price 1982, p. 444). And since most biotopes are variable and facultative strategists may occur also in stable biotopes by generalizing and specializing accordingly, it may be expected that most consumers (of substitutable resources!) are facultative strategists (Glasser 1982, 1984).

11.3.6   Niche breadth, niche overlap and the intensity of competition

As shown by Glasser and Price (1982), the niche breadths of species exploiting alternative or substitutable resources (equation (9)) generally increase as the biotope is saturated (that is, as population sizes increase) and unused resources become increasingly scarce, irrespective of their exploitation strategies. However, the increase is fastest for a generalist (which exploits resources proportionate to their frequencies of occurrence in a biotope), slowest for a (sequential) specialist (which exploits a resource until it is exhausted and then moves on to the next) and intermediate for a facultative strategist (which specializes when resources are abundant but generalizes progressively as they become increasingly scarce) (Glasser 1982, 1984; Glasser & Price 1982).

Niche breadth thus generally increases with (increasing population size and) the proportion of used resources, and this holds with both intra- and interspecific competition (Glasser & Price 1982, 1988). Glasser and Price point out that this result is contrary to the conventional wisdom of population ecology that interspecific competition leads to small, non-overlapping niches. They also note, however, that the disparity may be readily resolved by distinguishing between contemporary and evolutionary effects of competition, that is, respectively, broad, overlapping niches versus small, non-overlapping niches (see below; see also Connell 1980).

Glasser and Price (1988) found that the S-th partial (interspecific) niches of model obligate specialists are indistinguishable from their 1-st partial (intraspecific) niches (because these species have fixed probabilities of exploiting alternative resources), but that the S-th partial niches of both obligate generalists and facultative strategists are smaller than their 1-st partial niches. They simulated competition between all possible pairs of generalists, specialists and facultative strategists with even and uneven efficiencies of resource use, in both biotopes with even initial resource frequencies and biotopes with uneven initial resource frequencies. They found that in sixteen of eighteen possible pairs, realized niche overlap either remained the same (when initial resource frequencies were uneven) or decreased (when initial resource frequencies were even). The two exceptions, where realized niche overlap increased, were the pair of an obligate generalist and a facultative strategist with even efficiencies of resource use (which are indistinguishable, whence competition between these species closely resembles intraspecific competition) and the pair of an obligate generalist and an obligate specialist

(which they left unexplained), both in biotopes with even initial resource frequencies. The general conclusion seems to be, therefore, that competition on an ecological time scale need not necessarily lead to small, non-overlapping (S-th partial) realized niches.

Glasser and Price (1982) simulated competition between facultative strategists with appropriate efficiencies of resource use and facultative strategists with adaptively variable (malleable) efficiencies in biotopes with different initial evenness of resource frequencies and subsequent variation. They found that the more malleable were the species' efficiencies, the faster these efficiencies changed relative to the rates with which resources were depleted or supplied, the narrower became their niches and, hence, the less their niche overlap.[84] They concluded from this that "While not necessary, this phenomenon suffices to account for character displacement" (Glasser & Price 1982, p. 445). Though I doubt whether this is correct, since character displacement requires additional genetic changes not incorporated in their model (whence perhaps their result should better be called niche divergence), it explains in any case the opposite results that may be expected from evolutionary and contemporary effects of competition (small, non-overlapping niches versus broad, overlapping ones). However, as noted by Glasser and Price, it is extremely important to realize that "Although narrow, non-overlapping niches could result from competition, because other processes may have the same result, instantaneous niche measures do not permit evaluation of the importance of competition in the evolution of species' equilibria (Wiens 1977; Connell 1980)" (Glasser & Price 1982, p. 446). This means, more generally, that hypotheses about possible effects of competition should be tested independently of these effects. As I will discuss in chapter 13, ignorance of this simple methodological rule may give rise to a lot of (inconclusive) controversy.

Finally, as pointed out by Glasser and Price, it has been thought for a long time that the intensity of competition is directly proportional to (S-th partial) realized niche overlap (for example MacArthur & Levins 1964; Abrams 1983). Their results show, however, that S-th partial niche overlap generally decreases as resources become scarce and the intensity of competition increases. This implies that the intensity of competition is not directly proportional to S-th partial niche overlap, but underestimated thereby. On the other hand, it is overestimated by the 1-st partial (intraspecific) niches of species, as these are narrowed by interspecific competition. This has serious implications for the possibilities of evaluating competition theory (see Glasser & Price 1988, pp. 63-67, for a discussion of this problem).

11.4 Other niche models
11.4.1 Multiple level models

An attractive feature of models such as equation (8) is their general applicability. That is, by summation, adding or subtracting appropriate terms they can be applied to every consumer-

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[84]Glasser (1987, in Glasser and Price 1988, p. 62) has shown that interference competition may have the same effect, that is, reduce the rate at which niche breadth increases as resources are exploited (depleted), whence the increase in niche overlap as biotopes are saturated is relatively small. This may happen through either increasing resource requirements (R_i) or reduced efficiencies of resource use (e_{ji}). In both cases, consumption rates (c_{ji}) increase.

resource (predator-prey) system, both in the absence ($j = 1$) and in the presence ($j > 1$) of competing prey species, and in both the absence ($k = i = 1$) or the presence ($k > 1$) of competing predator species. In addition, as indicated above, the model, supplemented by the theory of foraging strategies, can be applied also to both contemporary and evolutionary aspects of competition. It can be applied also to both contemporary and evolutionary aspects of predation, or, respectively, the structure of prey communities and the dynamics (succession) of biocoenoses (see Glasser & Price 1982).[85,86]

   As noted by Glasser and Price (1988, p. 68), single level models such as equation 8 are inadequate, however, for resources whose dynamics may influence the outcome of competition. More generally, therefore, we should write

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[85]The major result of Glasser and Price (1982) in this respect is that predators may increase the diversity of prey communities (a phenomenon which has been known for a longer time, and is well documented, in the form of the effects of herbivores on the diversity of plant communities). Since niche breadth generally decreases with decreasing population size (the reverse of the effect, mentioned in the main text, of competition at increasing population size and increasing scarcity of resources), a predator may reduce the niche breadths of its prey by reducing their population size. As a result, more prey species can coexist on the same set of resources, a phenomenon called species packing. More in particular, if there are several prey species and if a predator selectively consumes an otherwise competitively dominant species, formerly rare prey species may increase in abundance while others, which were previously excluded, may be able to colonize.

[86]The application to succession of biocoenoses is a simple extension of the applications to competition and predation, given that successive trophic levels are colonized successively (predators are able to colonize only when there are enough prey). Glasser and Price point out that competition is important in the first stage of colonization of any trophic level (when there are only 'prey' species), but that in the course of succession predation becomes ever more important at all levels except the highest (top predators). This leads to the expectation that in the course of succession of biocoenoses patterns of exploitation competition (only prey species) are followed each time by patterns of predation. As an example of this phenomenon, which is known as the taxon cycle, Glasser and Price mention patterns in the abundance distributions of species at a certain level, which are often initially uneven as a result of exploitation competition but later become more even as predators (facultative strategists) colonize the next level.

$$\frac{dA_j}{A_j dt} = f(A_l) - \sum_{k=1}^{S} c_{jk} n_{jk} \qquad (11a)$$

$$\frac{dN_i}{dt} = r_i \sum_{j=1}^{T} \frac{n_{ji}}{A_j} (A_j - \sum_{k=1}^{S} c_{jk} n_{jk}) \qquad (11b) \ (8)$$

where $f(A_l)$ is a function describing the growth of resource l in the absence of consumption, for $l = 1, ..., T$. When resources are non self-reproducing (for instance abiotic resources such as mineral nutrients, but also such resources as fruits and seeds), $f(A_l)$ may take the form of a chemostat model, whence

$$\frac{dA_j}{A_j dt} = I_j - E_j A_j - \sum_{k=1}^{S} c_{jk} n_{jk} \qquad (11c)$$

where I_j stands for the input rate of resource j, and E_j is a constant giving the exit rate of resource j in the absence of consumption (see also Abrams 1988, who uses another term, however, for the effect of consumption on the growth rate of resource j; see also Leon & Tumpson 1975, and Tilman 1980, 1982, for different versions of the chemostat model). Self-reproducing resources may of course be modelled in the same way as their consumers (that is, by equation (8) or (11b)).

11.4.2   Tilman's resource-ratio model

An interesting model, which specifies another mechanism of coexistence than niche differentiation, is Tilman's resource-ratio model (Tilman 1980, 1982, 1985, 1988). Tilman (1980, 1982) provides the following equations forming a multiple level model of competition and predation for S species and T resources:

$$\frac{dN_i}{N_i dt} = f_i(R_1, R_2, ..., R_t) - m_i \qquad (12a)$$

$$\frac{dR_j}{dt} = g_j(R_j) - \sum_{i=1}^{S} N_i f_i(R_1, R_2, ..., R_t) \ h_{ij}(R_1, R_2, ..., R_t) \qquad (12b)$$

where N_i is the population size of species i, R_j the availability of resource j, m_i the per caput death rate of species i, f_i the functional relation between the availabilities of all resources and

the per caput growth rate of species i,[87] g_j a function describing the supply rate of resource j, and h_{ij} a function describing the amount of resources required to produce a new individual of species i.

Like Glasser and Prices' model, Tilman's model also reduces the Lotka-Volterra competition model, but the reduction is a lot more complicated (see the appendix in Tilman 1982). It is easier seen from Tilman's graphical presentation of his model (figure 10).

Based on equations (12a) and (12b), Tilman defines (1) zero net growth isoclines for species' populations, or the set of points (in a hyperspace whose axes are being formed by the abundances of resources) where their per caput reproduction rate equals their per caput death rate (that is, $dN_i/dt = 0$); (2) supply vectors and a supply point for resources, defined as the maximum availability of resources in the absence of consumption; and (3) the consumption rates and consumption vectors for species.

The zero net growth isocline (ZNGI) of a species' population represents its minimum resource requirements. It forms the boundary between availabilities of resources that allow the species to survive and reproduce, and availabilities that don't. It can be regarded, therefore, as a representation of the species' potential niche (with respect to these resources). There is only one point on the ZNGI of a species where the levels of resources are also constant. This is the point where the species' consumption rate equals the resource supply rate. It is the point at which the species' population would equilibrate as a result of intraspecific competition and in the absence of interspecific competitors. Thus, it represents the species' 1-st partial realized niche.

Figure 10 shows that there are four possible ways in which the ZNGI's of two species, A and B, exploiting two essential resources, R1 and R2, may be situated relative to each other.[88] In case A the ZNGI of species A is always situated within (that is, closer to the resource axe than) that of species B. This means that, compared to species B, species A has lower minimum resource requirements for both resource R1 and resource R2. Neither species can survive in biotopes[89] with resource supply points lying below their ZNGI's (area 1), because such points do not meet their resource requirements (that is, do not belong to their potential niches). In biotopes with resource supply points in area 2, below the ZNGI of species B but above that of species A, species B is unable to survive and reproduce, while

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[87]Abrams (1987a, p. 63-64) points out that Tilman's formulation of $f_i(A_j)$ makes sense only when the f_i's describe the per caput reproduction of species i as a function of a single resource where others are present in surplus supplies. But except when species i has equal requirements for all resources, one would expect its per caput reproduction to increase at different rates with increasing availability of resources, depending on which resource is limiting. More properly, therefore, the functions f should be indexed for the densities of both consumers and resources.

[88]The forms of the ZNGI's of different species depend on the types of resources they exploit (whether essential, hemi-essential, or substitutable; see Tilman 1980) and on their exploitation strategies. Different forms of the ZNGI's lead to different conditions for coexistence (see Tilman 1980, 1982, 1988; Abrams 1987b, 1988).

[89]Tilman uses the term habitat instead of biotope.

A. Species A wins

B. Species B wins

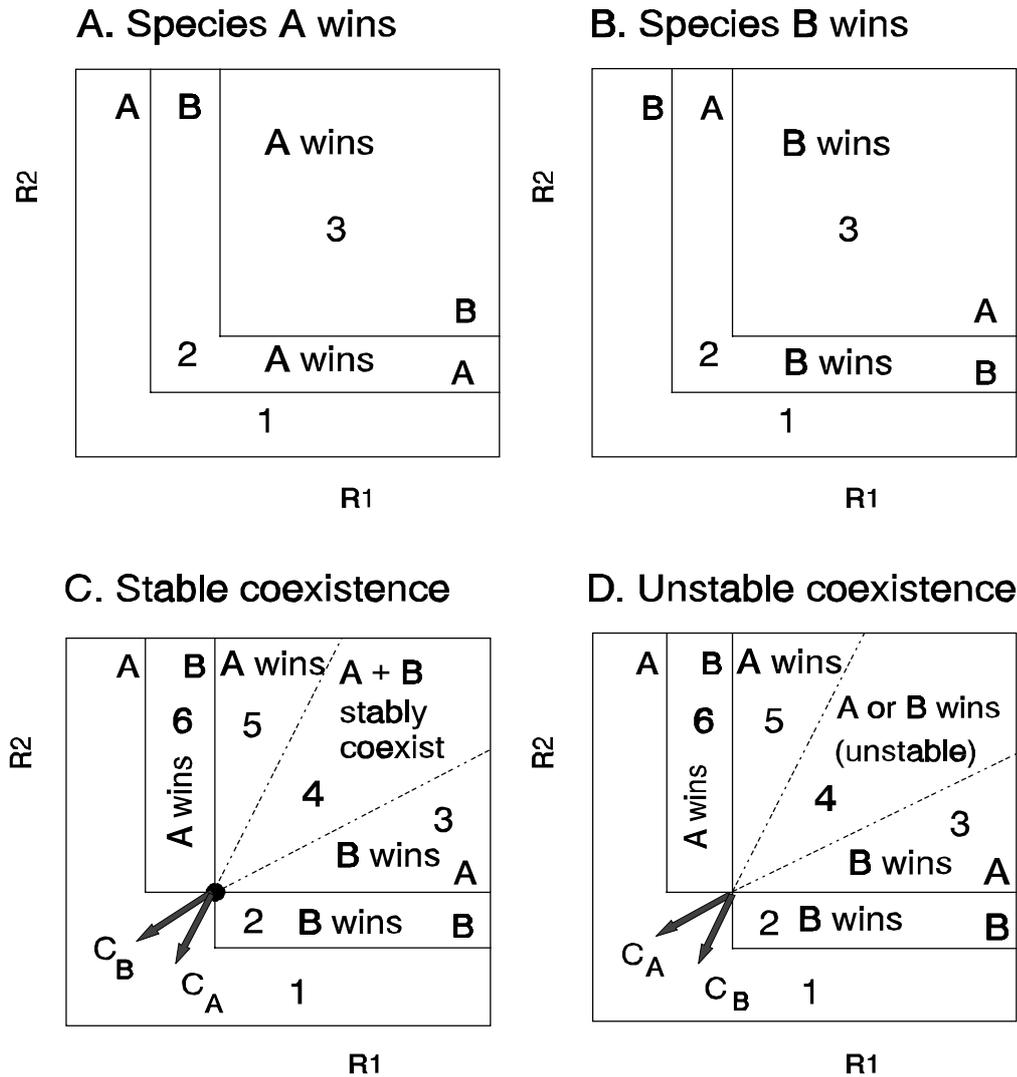## C. Stable coexistence

D. Unstable coexistence

Figure 10: The outcomes of competition generated by Tilman's model for two species, A and B, competing for resources R1 and R2 (after Tilman 1988). See main text for explanation.

species A is able to reach its equilibrium density (carrying capacity, *K*). In biotopes with supply points in area 3, species A will competitively displace species B, because it is able to reduce the resources to levels on its own ZNGI, which are to low for species B.

In case B the situation is reversed. In area 2 only species B is able to survive, and in area 3 species B will competitively displace species A.

In cases C and D the positions of the ZNGI's relative to each other imply that, compared to species B, species A is more limited by resource R1 than by resource R2, and that, compared to species A, species B is more limited by resource R2 than by resource R1. Again, neither species can survive in biotopes with resource supply points in area 1. In biotopes with supply points in area 2 species A is unable to survive, whence the system will equilibrate on

the ZNGI of species B. If resource supply points lie in area 3, both species will be limited more by R1 than by R2. Because species B has a lower minimum requirement for R1, it will competitively displace species A in all biotopes having such supply points, as it is capable of reducing R1 to a level on its own ZNGI, which is too low for species A. The reverse holds for area 5. In all biotopes with resource supply points in this area both species will be more limited by R2 than by R1. However, species A, having a lower minimum requirement for R2, will be able to reduce R2 to a level on its own ZNGI, which is too low for species B, and will thereby competitively displace species B.

It should be noted that these results will hold irrespective of the species' consumption rates of both resources (indicated by the consumption vectors C_A and C_B). It doesn't matter whether species B consumes relatively more (case C) or less (case D) of R1 than does species A. In both cases it will competitively displace species A in all biotopes with resource supply points in area 3. The same holds for species A in area 5.

The only area where the consumption rates of both species influence the outcome of competition, and where, hence, the outcome in case C is different from the one in case D, is area 4. The difference reflects the crucial assumption of Tilman's model that "For a group of species to be able to coexist along a resource gradient when competing for essential resources, they must be ranked in competitive ability for one resource in reverse order of their competitive ranking for the second resource" (Tilman 1980, p. 383). This means that "For two species to stably coexist on two resources, each species must, relative to the other species, consume proportionally more of the resource which more limits its own growth rate" (p. 375). This condition is met in case C but not in case D (see the direction of the consumption vectors C_A and C_B). In case C, species A, which is more limited by R1, consumes relatively more of R1, while species B, which is more limited by R2, consumes relatively more of R2. This means that intraspecific competition is stronger than interspecific competition (see also Tilman 1988, p. 44). The result is a stable equilibrium at the point of intersection of the species' ZNGI's. In case D, on the other hand, each species consumes more of the resource that less limits its own growth rate (and more limits the growth rate of the other: interspecific competition is stronger than intraspecific competition). When such 'non-optimal' foraging occurs, the equilibrium point is unstable and the system will eventually equilibrate at only one of the species' ZNGI's. Which species will be displaced depends on the initial conditions. Like the Lotka/Volterra model, Tilman's model also predicts that the species with the initial advantage of a larger population will competitively exclude the other. (Notice that the four possible outcomes of competition as predicted by Tilman's model correspond to the predictions of the Lotka/Volterra model. That is to say, the former reduces the latter.)

It appears from Tilman's model, then, that two species competing for two essential resources may coexist, *in spite of having identical S-th partial realized niches*, as long as two conditions are met. In the first place the biotope, or rather the resource supply point, must be such that the one species is more limited by the one resource and the other species more by the other resource. And in the second place *each species must consume relatively more of the resource that more limits its own growth rate*. Thus, as noted by Begon, Harper and Townsend (1982, p. 287-8), the key to the problem of coexistence in plants lies with the explicit attention for the dynamics of resources as well as of their consumers, and with the fact that for both species intraspecific competition may be stronger than interspecific competition.

11.4.3   Niche differentiation or balanced competitive abilities?

According to Begon, Harper and Townsend (1986, p. 287), the mechanism of coexistence in Tilman's model is niche differentiation, be it a subtle form. The reason why they think so is provided in the margin of their text: "Each species consumes more of the resource that more limits its own growth". In other words, they think the mechanism is niche differentiation because of differences in the species' consumption rates for different resources. The reasoning seems to be that the existence of differences in consumption rates would involve some form of 'differential resource utilization' (the result of niche differentiation). In the first place, however, though a species' consumption rate is of course related to its (realized) niche, it is not the same as its niche nor a part of it (see the definitions in box 6 in 10.3.5). This can be seen particularly well in equations (9) and (10), where f_{ji} and f_{jk} denote the realized niches of species S_i and S_k, and where $\Sigma f_{ji} f_{jk} / \Sigma f_{ji}^2$ denotes niche overlap. These terms are independent of the parameters c_{ji} and c_{jk}, the species' per caput consumption rates.

In the second place niche differentiation pertains to the *coming into existence* (in ecological time) of differences in resource utilization patterns by different species, not to their *existence*. Existing differences may be the result of niche differentiation, but that need not be the case (see 10.3.6). Niche differentiation may be defined as reduction of niche overlap through reductions of niche breadth, where niche breadth is defined as the range of resources a species may exploit (potential niche) or exploits (realized niche) relative to their frequency of occurrence in a biotope (see Petraitis 1979). Tilman's model mentions no such reductions. Tilman's model says nothing about shifts in, or the divergence of, the (S-th partial) realized niches of species (relative to their 1-st partial niches).

In the third place it may be noted that in Tilman's graphical model (figure 10) in all cases and in all areas except area 4 in case C, only one of the species survives and, hence, has a realized niche. In all these cases, of course, the excluded species doesn't have a realized niche (in the biotope). It is only in area 4 in case C that coexistence is possible and that both species have a realized niche. Moreover, since in this case the species equilibrate on the point of intersection of their ZNGI's, they have identical realized niches. This too indicates that the mechanism of coexistence in Tilman's model is not niche differentiation. In Tilman's model coexistence is possible only when species have *balanced competitive abilities*, as expressed by on the one hand their ZNGI's (minimum resource requirements) and on the other hand their consumption rates.

Competitive ability is often defined, also by Tilman, as a combination of (1) the ability of a species (or individual), relative to another species (individual), to tolerate reductions in the level of contested resource availability, and (2) the ability of a species (individual) to reduce contested resources for another species (individual) (see Aarssen 1983, p. 709; Tilman 1987). The first component corresponds to the minimum resource requirements of a species and hence with its ZNGI, the second with its (per caput) consumption rate. (Notice that in Glasser and Price's model the per caput consumption rate of a species S_i for resource j, c_{ji}, is defined as the quotient of the species' minimum resource requirements, R_i, and its efficiency of exploiting resource j, e_{ji}.)

The mechanism of coexistence in Tilman's model may therefore better be called *coexistence through balanced competitive abilities* (Aarssen 1983, 1984; see also Huisman & Weissing 1994). Considering his statement that "For a group of species to be able to coexist along a resource gradient when competing for essential resources, they must be ranked in **competitive**

ability for one resource in reverse order of their **competitive ranking** for the second resource" (Tilman 1980, p. 383; emphasis added) I guess that Tilman will agree with this view.

Of course this is not to say that niches, or differences between niches, are not important in Tilman's model. Because of his explicit attention for resources, and for the dynamics of resources, his model is pre-eminently a model of modern niche theory. Only, his model is not directed at coexistence through niche differentiation (probably because Tilman is primarily interested in plants and because opportunities for niche differentiation in plants are limited; see section 10.3.4).

Incidentally, Tilman's model can easily be extended to systems of more than two species and, through these extensions, can also be used, like Glasser and Price's model, to explain both the structure (species' coexistence) and dynamics (succession) of communities (see Tilman 1988, 1990).

11.5 Conclusions

It would go much too far to give an evaluation of (all models of) modern niche theory (see Schoener 1989, for such an evaluation). The general conclusion for the moment seems to be that the theory is becoming ever more adequate (be it more diverse; Schoener 1989) and that supporting evidence is accumulating (see, among others, Connell 1983; Schoener 1983, 1989; Huisman & Weissing 1994). Because of its relative simplicity on the one hand and its general applicability on the other, the theory seems to be a serious candidate for becoming the first general ecological theory.

The purpose of this chapter was not to give an evaluation of modern niche theory, however (and therefore doesn't stand or fall with this evaluation). The purpose was to show that in ecology, too, co-operation of holistic and reductionistic research programmes occurs. The reduction of the Lotka/Volterra competition model to modern niche theory provides a nice example. In this reduction, the (phenomenological) Lotka/Volterra model acted as a holistic guide programme and modern niche theory as a reductionistic supply programme. The reduction was established with the help of an identification hypothesis and two simple aggregation hypotheses and, therefore, though not dealing with emergence, provides yet another example of heterogeneous micro-reduction in biology.

Finally, since the Lotka/Volterra is an idealization, and since this model is reduced deductively by modern niche theory, it follows that modern niche theory is also an idealization. On the other hand, the various applications of (specific models of) the theory, whereby additional hypotheses or theories (such as the theory of exploitation strategies) are used, may be regarded as concretizations (approximative reductions) of the theory. Thus, we see once more that deductive and approximative reductions may go hand in hand. In the next chapter I will discuss another example.