Multispecies resource competition
Revilla Rimbach, Tomás Augusto

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2010

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
A variety of assumptions lead to a variety of mathematical models describing the dynamics of competition. Here we review the properties of three important competition models, ranging from the highly phenomenological to the highly mechanistic. We study these models for the simple case involving competition between two species, and for the more complex situation that is multispecies competition. Under a number of simplifying but reasonable assumptions, we found that all these models share the same rules regarding the existence of coexistence equilibria, local stability, and to some extend global dynamics. We also show how the small jump from two species to three, and two resources to three, involves an very big increase in the complexity of the dynamics in all models.

Keywords: *competition, resource competition, nutrient storage, coexistence, competitive exclusion, oscillations, initial conditions*
5.1 INTRODUCTION

Competition is perhaps the most studied interaction in the fields of ecology and evolution. Under competition the fitness of an individual is depressed by the presence of other individuals of the same or different species. Intraspecific competition is an important driving force of evolution; while interspecific competition is an important factor in the structuring of ecological communities (Begon et al., 2006). The causes of competition are in general very simple, organisms are forced to share limited resources like food, water, space and sexual partners. Competition manifests itself, however, in a multitude of ways. Individuals can directly fight with their enemies, preventing their access to resources (direct aggression, allelopathy); in that case we talk about interference competition. In contrast, competition can be much more indirect, not involving physical contact, when individuals make the life of their competitors more difficult by reducing the availabilities of resources, i.e. by consuming these resources. This second form is typically called exploitative competition or resource competition.

The study of competition has been greatly influenced by mathematical models. Here we review the properties of three important models (section 5.2). The first is the classical Lotka-Volterra model (Lotka, 1925; Volterra, 1926), which describes the dynamics of competition by means of interaction coefficients. This model is quite general and can be applied to both interference and exploitative competition. However, it is a phenomenological model that does not easily allow to derive the interaction coefficients from first principles. The second model, we call it the Tilman model, is more mechanistic since it does explain how competition originates from first principles of consumer-resource theory (León and Tumpson, 1975; Tilman, 1977, 1982). The third model, the Quota model, is even more mechanistic in that it allows to take resource storage into consideration. Quota models have become important in recent times, because they can predict the outcomes of competition in fluctuating environments (Ducobu et al., 1998), and because they are an important tool in the study of ecological stoichiometry (Sterner and Elser, 2002).

The purpose of this chapter is to show that besides their different formulation, all these models share very similar equilibrium and dynamical properties. We start by reviewing the interaction for the simple case of two species and two resources (section 5.3). Thereafter, our attention turns to the rules that determine the existence of equilibria (section 5.4) and local stability (section 5.5) in multispecies and multiresource systems. In the end, we discuss to which extend such local rules can be used to predict the global dynamics of competition (section 5.6).

5.2 THREE COMPETITION MODELS

5.2.1 The Lotka-Volterra model

For a long time the theoretical study of competition was dominated by the Lotka-Volterra approach (Lotka, 1925; Volterra, 1926). The Lotka-Volterra competition model describes competition among $n$ species with population densities $N_i$ using a set of differential equations
\[
\frac{dN_i}{dt} = N_i \left( r_i - \sum_{k=1}^{n} a_{ik} N_k \right)
\]  

(5.1)

In essence equation (5.1) says that the per capita growth rate \( \frac{1}{N_i} \frac{dN_i}{dt} \) of species \( i \) is linearly decreasing with the density of each population. For very low population densities, species \( i \) tends to grow exponentially with the *intrinsic* per capita rate \( r_i \). The parameters \( a_{ik} \), which quantify how strongly the per capita growth rate of species \( i \) is depressed by the presence of species \( k \), are called the *competition coefficients*. The Lotka-Volterra model is purely phenomenological; it does not refer to any explicit mechanism underlying competition, and there is no a priori reason to assume that the presence of other species should have a linear effect on a species per capita growth rate. Indeed the competition coefficients \( a_{ik} \) cannot be derived from first principles but only measured a posteriori, e.g. after having performed a competition experiment. Accordingly, the Lotka-Volterra model is mainly interesting as a conceptual tool and it has very limited predictive power in real-world scenarios.

### 5.2.2 The Tilman model

A more mechanistic class of competition models, based on the explicit consideration of resource dynamics has been more successful in this respect (León and Tumpson, 1975; Tilman, 1982; Grover, 1997). The most studied formulation of resource competition is of the form

\[
\frac{dN_i}{dt} = N_i \left\{ \mu_i(R_1, \ldots, R_m) - m_i \right\} 
\]  

(5.2a)

\[
\frac{dR_j}{dt} = \phi_j(R_j) - \sum_{i=1}^{n} c_{ji} \mu_i(R_1, \ldots, R_m) N_i
\]  

(5.2b)

The dynamics of population densities (5.2a) makes it explicit that the species are competing for \( m \) limiting resources with concentrations \( R_1, \ldots, R_m \). The model assumes that the per capita growth rate of each species \( i \) is a function \( \mu_i \) of the resource concentrations, minus the loss rates \( m_i \). The change in resource availabilities is modeled explicitly by equation (5.2b), where the resource consumption rates are proportional to the rate of growth of the populations and to the per capita content of resource \( j \) per species \( i \), i.e. growth and consumption are coupled. In the absence of the consumers the resources follow independent dynamics described the net resource supply rates \( \phi_j \). Since model (5.2) figures prominently in the works of Tilman (1977, 1980, 1982, 1988), we will call it the *Tilman model*.

### 5.2.3 The Quota model

The mechanistic formulation of the Tilman model is very basic, but not always realistic. For many systems, like algal communities, the growth rates are a direct function of the amount of stored nutrients or *quotas* (Droop, 1970, 1973; Morel, 1983; Thingstad, 1987; Grover, 1992), instead of the external concentration of resources. The new set of variables, the quotas,
must be modeled accordingly. A minimum competition model accounting for the species densities, resource concentrations and quotas is the following

\[
\frac{dN_i}{dt} = N_i \{\mu_i(Q_{1i}, \ldots, Q_{mi}) - m_i\} \tag{5.3a}
\]

\[
\frac{dQ_{ji}}{dt} = f_{ji}(R_j) - \mu_i(Q_{1i}, \ldots, Q_{mi})Q_{ji} \tag{5.3b}
\]

\[
\frac{dR_j}{dt} = \phi_j(R_j) - \sum_{i=1}^{n} f_{ji}(R_j)N_i \tag{5.3c}
\]

In this model the per capita growth rate \(\mu_i\) of species \(i\) is a non-decreasing function of the stored nutrient contents or quotas \(Q_{ji}\). The metabolization of nutrients for reproduction and maintenance \((\mu_i Q_{ji})\) happens in proportion to the per capita growth rate \(\mu_i\) of the population of species \(i\). According to \((5.3b)\), quotas increase by resource dependent consumption \(f_{ji}\), which are generally described by means of a saturating function \((Aksnes and Egge, 1991)\). Like in the Tilman model, equation \((5.3c)\) indicates that the dynamics of the resources in the absence of the consumers is governed by the net supply rate \(\phi_j\). However, resource consumption is not proportional to the growth rates, but to the consumption rates, i.e. growth and consumption are decoupled.

The quota \(Q_{ji}\) is the variable counterpart of the fixed resource contents \(c_{ji}\) in the Tilman model. Indeed, both \(Q_{ji}\) and \(c_{ji}\) have the same dimensions: resource concentrations per biomass density. Since the modelling approach behind system equations \((5.3)\) rely on the concept of quotas, we will call it the Quota model.

Resource competition models \((5.2)\) and \((5.3)\) require to specify the form in which the resources affect growth. This gives rise to a number of resource categories \((Tilman, 1982)\). The most studied categories are those of substitutable resources and essential resources. In case of substitutable resources the absence of one resource can be compensated by increasing the amounts of other resources (e.g. beans can be substituted by peas and vice versa). In case of essential resources such compensation is not possible (e.g. lack of phosphorous cannot be solved by increasing nitrogen and vice versa). For these two kinds of resources, two special cases have received special attention. Resources are called perfectly substitutable, if their effects on population growth are additive

\[
\mu_i = \sum_j \mu_{ji} \tag{5.4}
\]

where \(\mu_{ji}\) describes the dependence of the per capita growth rate of species \(i\) on the availability of resource \(j\). Resources are called perfectly essential, if they follow Liebig’s Law of the Minimum \((Von Liebig, 1840)\): at any given time the growth rate \(\mu_i\) of species \(i\) depends only on the most limiting resource. Mathematically Liebig’s law is expressed as

\[
\mu_i = \min_j[\mu_{ji}] \tag{5.5}
\]

where \(\mu_{ji}\) describes the dependence of the per capita growth rate of species \(i\) on the availability of resource \(j\), when all other resources are overabundant (non-limiting).
In the Tilman model (5.2) the $\mu_{ji}$ are typically assumed to be monotonically increasing functions of the resource concentrations $\mu_{ji}(R_j)$, frequently modeled according to Monod’s equation or Holling’s Type II functional response curve (Fig. 5.1a)

$$\mu_{ji}(R_j) = \frac{r_i R_j}{H_{ji} + R_j} \quad (5.6)$$

where $r_i$ is the maximum per capita growth rate of species $i$, which is attained for saturating concentrations of resource $j$, and $H_{ji}$ is the half-saturation constant for growth.

In the Quota model the $\mu_{ji}$ are monotonically increasing functions of the quotas $\mu_{ji}(Q_{ji})$, frequently modeled according to Droop’s (1973) formula (Fig. 5.1b)

$$\mu_{ji} = s_i \left( 1 - \frac{q_{ji}}{Q_{ji}} \right) \quad (5.7)$$

where $s_i$ is the called the apparent maximum per capita growth rate (Grover, 1997), attainable for saturating quotas of all resources and $q_{ji}$ is a threshold quota level, below which $\mu_{ji} = 0$. One must not confuse the asymptotic level $r_i$ of the Monod equation (5.6) with the asymptotic level $s_i$ of the Droop equation (5.7). In case of the Tilman model equation, the maximum growth rate can be achieved under saturating resource concentrations. In case of the Quota model, resource consumption rates $f_{ji}(R_j)$ saturate (c.f. 5.8), preventing the saturating quota levels (Grover, 1997).

The consumption rates $f_{ji}(R_j)$, tend to be modeled under as saturating functions

$$f_{ji}(R_j) = \frac{\nu_{ji} R_j}{K_{ji} + R_j} \quad (5.8)$$

where $\nu_{ji}$ is the maximum consumption rate, attainable under resource saturation, and $K_{ji}$ is the half-saturation constant for consumption. As shown in Aksnes and Egge (1991), equation (5.8) can be given a mechanistic interpretation.

Resources can be also classified according to their intrinsic dynamics as biotic (e.g. preys) or abiotic (e.g. detritus, minerals, water). Biotic resources are “self-regenerating” and their dynamics are frequently modeled using a logistic equation. Abiotic resources are typically “supplied” by some external means (fertilizer, decomposition, etc), and they are frequently modeled by a linear function

$$\phi_j = D(S_j - R_j) \quad (5.9)$$

where $D$ is the resource turnover rate and $S_j$ is the resource supply concentration. This form of supply dynamics can be realized in a chemostat or approximated through serial dilution.

### 5.3 Graphical Analysis

Most of the results described in this section are already well known, in particular for the Lotka-Volterra and the Tilman model. Nevertheless, a review is useful in order to set the stage for the more general treatment of multi-species (and multi-resource) scenarios. Competition models involving only two species can be easily studied by means of graphical methods. In phenomenological models like the Lotka-Volterra model the analysis uses the
geometry of the species nullclines in “species space”, whereas in the Tilman and Quota models this done in the “resource space”. In all these models, the system always converges to an equilibrium, and sustained oscillations are not possible.

5.3.1 Lotka-Volterra model

The Lotka-Volterra model \((5.1)\) for two competing species \(i, k = 1, 2\) is as follows

\[
\begin{align*}
\frac{dN_1}{dt} &= N_1(r_1 - a_{11}N_1 - a_{12}N_2) \\
\frac{dN_2}{dt} &= N_2(r_2 - a_{21}N_1 - a_{22}N_2)
\end{align*}
\]

The outcome of competition depends on the geometry of the nullclines of the two species (Case, 2000), i.e. the set of species densities for which \(dN_1/dt\) is equal to zero. These nullclines take the form of curves in the \(N_1N_2\)-plane, also called the species space. The nullclines of species 1 are the two straight lines \(N_1 = 0\) and \(r_1 = a_{11}N_1 + a_{12}N_2\). \(N_1\) increases in the region that is to the right of the first nullcline and to the left of the second (Fig. 5.2 solid lines), and decreases outside of this region. The nullclines of species 2 are \(N_2 = 0\) and \(r_2 = a_{21}N_1 + a_{22}N_2\). \(N_2\) increases in the region that is above the first nullcline and below the second (Fig. 5.2 dashed lines), and decreases outside of this region.

The system is at equilibrium, i.e. \(dN_1/dt = dN_2/dt = 0\), at the points where the nullclines of the two species intersect (Fig. 5.2). There are three types of equilibrium:

1. The trivial equilibrium, i.e. the origin of the \(N_1N_2\)-plane where both species have zero density (Fig. 5.2). In this point the per capita rates of change for both species are
5.3 Graphical Analysis

Figure 5.2: The outcome of the Lotka-Volterra model depends on the geometry of the nullclines of species 1 (solid lines) and 2 (dashed lines). Species 1 increases (arrows point right) in the region left to its “zero” nullcline (vertical axis) and right to its “non-zero” nullcline (solid line), and decreases otherwise (arrows point left). Species 2 increases (arrows point up) above its “zero” nullcline (horizontal axis) and below its “non-zero” nullcline (dashed line), and decreases otherwise (arrows point down). The intersection points of the nullclines (circles) correspond to equilibrium states, that can be stable (filled circle) or unstable (open circle). (a) The nullcline of species 1 is above that of species 2. Species 1 monoculture is stable and species 2 monoculture is unstable. Species 1 wins. (b) The nullcline of species 2 is above that of species 1. Species 2 monoculture is stable and species 1 monoculture is unstable. Species 2 wins. (c) The nullclines intersect at a equilibrium point \((\hat{N}_1, \hat{N}_2)\) that is above the thin dotted line connecting the two monoculture equilibria. This makes both monoculture unstable and \((\hat{N}_1, \hat{N}_2)\) globally stable. (d) The nullclines intersect below the line connecting the two monoculture equilibria. The community equilibrium \((\hat{N}_1, \hat{N}_2)\) is unstable, and both monocultures are stable. Depending on the initial conditions either species 1 or 2 wins.
positive (since \( \frac{1}{N_i} \frac{dN_i}{dt} = r_i > 0 \) if \( N_1 = N_2 = 0 \)). Hence this equilibrium is always unstable.

2. The monoculture equilibria. In the absence of species 2, species 1 exhibits logistic growth and converges to the carrying capacity \( K_1 = r_1/a_{11} \). The monoculture equilibrium \( (N_1, N_2) = (K_1, 0) \) is internally stable, i.e. stable as far as only perturbations of \( N_1 \) are involved. The monoculture equilibrium is also externally stable, i.e. stable against invasion by species 2, if the per capita growth rate of species 2 is negative at \( (K_1, 0) \), i.e. if \( r_2 - a_{21}K_1 < 0 \) or, equivalently if \( r_2/a_{21} < r_1/a_{11} \). Likewise, the monoculture of species 2 \( (N_1, N_2) = (0, K_2) \) with \( K_2 = r_2/a_{22} \) is (internally and externally) stable if \( r_1/a_{12} < r_2/a_{22} \).

3. The community equilibrium (also called coexistence or internal equilibrium). This corresponds to the intersection point of the nonzero nullclines.

In Figure 5.2 a community equilibrium exists in scenarios (c) and (d). In (c), both monocultures are externally unstable. In such a case of mutual invasion, the community equilibrium is stable. In (d), both monocultures are stable against invasion. In that case, the community equilibrium is unstable, and depending on the initial conditions species 1 or species 2 wins the competition.

Species 2 can invade the monoculture of species 1 if \( r_2/a_{21} > K_1 = r_1/a_{11} \), while species 1 can invade the monoculture of species 2 if \( r_1/a_{12} > K_2 = r_2/a_{22} \). Multiplicating these criteria for mutual invasion yields the following criterion for coexistence

\[
a_{11}a_{22} > a_{12}a_{21}
\]  

(5.10)

Condition (5.10) is often interpreted as: coexistence requires the geometric mean \( \sqrt{a_{11}a_{22}} \) of the intra-specific competition coefficients to be less than the geometric mean \( \sqrt{a_{12}a_{21}} \) of the inter-specific competition coefficients, or colloquially that intra-specific competition is more intense than inter-specific competition. Notice that the stability criterion (5.10) is a necessary but not a sufficient condition for the convergence of the system to a community equilibrium. In fact, (5.10) can be satisfied in situations where a community equilibrium does not exist like in cases (a) and (b) in Figure 5.2.

5.3.2 Tilman model

The competition of two species in model (5.2) has been extensively reviewed by Tilman (1982) and others (Hsu et al., 1977; Smith, 1995; Grover, 1997). The first conclusion that can be drawn is that two species cannot stably coexist on a single resource. This follows from a simple argument. Suppose that two species are limited by the single resource \( R_1 \). Each species \( i \) has a minimal resource requirement \( R_{1i}^* \) at which its growth rate is balanced by its loss rate \( \mu_i(R_{1i}^*) = m_i \) (Fig. 5.11). Each species will decline whenever the resource availability \( R_1 \) is below the threshold value \( R_{1i}^* \). Suppose now that species 1 happens to have the minimum requirement for resource 1: \( R_{11}^* < R_{12}^* \). In that case, it will win the competition, since the resource level \( R_1 \) will fall below the threshold level of species 2 before species 1 stops growing. This is the \( R^* \)-rule of competition for a single resource (Grover, 1997).
Figure 5.3: For two resources the nullcline of a species correspond to those resource combinations where net growth is zero. For resource concentrations above the nullcline a species increases, and for concentrations below it decreases. (a) In case of perfectly substitutable resources, the nullcline is a straight line with negative slope. (b) For perfectly essential resources the nullcline is an L-shaped line, the “corner” of which is given by the resource requirements $R_{ji}^*$. These nullcline geometries are idealizations, because in general, nullclines have more curved shapes (like in Fig. 5.4).

Put differently: two species can only coexist if they are limited by at least two different resources. Notice that these are equilibrium arguments, if resource consumption dynamics involves predator-prey cycles, two species can actually coexist on one resource (Armstrong and McGehee, 1976), but not at equilibrium.

Let us therefore focus on the more interesting case where two species compete for two resources. In principle, it is possible to study this model again in species space, like the Lotka-Volterra model. However, it is much easier to perform the analysis in the $R_1 R_2$-plane or resource space. The reason for this is that for two resources the per capita growth rates $\mu_i(R_1, R_2)$ are functions of the resource concentrations. According to (5.2a) the per capita growth rate of species $i$ is a zero if $\mu_i(R_1, R_2) = m_i$. The resource concentrations for which this is a case form a line in resource space (see Fig. 5.3). This is the nullcline of species $i$, and it is the two-dimensional extrapolation of the concept of resource requirement $R^*$. In the zone between the nullcline and the resource axes, resource concentrations are insufficient and species $i$ will decline, whereas it will increase whenever resource concentrations are above the nullcline. Depending on the type of resources, the nullclines can adopt many distinct shapes (Tilman, 1982).

In the case of perfectly substitutable resources (5.4), the nullcline is a linear decreasing function in the resource plane (Fig. 5.3a). Such scenario can be realized if the $\mu_{ji}$ are linearly dependent on the $R_j$. For perfectly essential resources the growth rates follows Liebig’s law (5.5) as in $\mu_i = \min[\mu_{1i}(R_1), \mu_{2i}(R_2)]$, thus $\mu_i = m_i$ occurs if $R_1 = R_{1i}^*$, $R_2 = R_{2i}^*$ or both, i.e. along the L-shaped line (Fig. 5.3b) with a corner defined by the resource requirements $R_{ji}^*$ the concentration of $j$ at which $\mu_i = m_i$ when all other resources are overabundant. These two examples are idealizations, in general the nullclines for substitutable and essen-
tial resources adopt shapes like in Figure 5.4, the main difference is that for substitutable resources the nullclines touch the axes, and for essential they don’t.

The outcomes of competition depend on the geometry of the nullclines of the two species, their consumption patterns given by the $c_{ji}$ and the resource supply concentrations (León and Tumpson, 1975; Tilman, 1982; Grover, 1997). First of all, if the nullclines do not intersect, the species whose nullcline lies closer to the origin is the best competitor for both resources, and it always wins the competition (e.g. species 1 in Figure 5.4a, or species 2 in Figure 5.4b), provided that the resource supply point is above its nullcline. This fact tells us that coexistence require trade-offs in resource requirements, that there cannot be superior competitors. In order to achieve coexistence, a number of conditions must be met:

1. **The nullclines must intersect.** At the community equilibrium both species show zero growth. Accordingly, the resource concentrations at equilibrium $({\hat{R}}_1, {\hat{R}}_2)$ have to belong to both nullclines and, hence, be at the intersection point of the nullclines. The configuration of the intersection also tells us that each species is limited by a different resource. For example, in Figures 5.4c and d, if $R_2$ is fixed a little bit above the intersection, $R_1$ will decrease until the nullcline of species 1 is reached and species 1 stops growing, but still allowing species 2 to grow (since its nullcline is to the left with respect to the nullcline of species 1). Thus, species 1 is limited by resource 1. Following a similar argument, we conclude that species 2 is limited by resource 2 at the intersection point. If we had changed the linetypes in the figure, we would have concluded that species 1 is limited by resource 2 and species 2 is limited by resource 1. In essence, the more steep the nullcline, the more limited is a species by the resource on the $x$-axis; conversely, the less steep the nullcline, the more limited is a species by the resource in the $y$-axis.

   - For perfectly essential resources, the nullclines are L-shaped (Fig. 5.3b), and they can intersect only once. Assuming that species 1 has the highest requirement for resource 1, $R_{11}^* > R_{12}^*$, and species has the highest requirement for resource 2, $R_{22}^* > R_{21}^*$, the intersection is the point $({\hat{R}}_1, {\hat{R}}_2) = (R_{11}^*, R_{22}^*)$, at which species 1 is limited by resource 1 and species 2 is limited by resource 2. In other words, in a community equilibrium, each species will be limited by the resource for which it has the highest requirement.
   - In the more general case, if the nullclines are curved, they may intersect more than once. In such a case, the identity of the limiting resource for each species depends on the local geometry of each intersection, in the same way as described before (e.g. put a magnifying glass around an intersection, and see if it looks like in Figs. 5.4c and d, or with the linetypes interchanged).

2. **The intersection of the nullclines must be achievable.** This requires that $dR_j/dt = 0$ for $({\hat{R}}_1, {\hat{R}}_2)$ and the corresponding equilibrium densities $(N_1, N_2)$. If resources are supplied linearly as in (5.9) we have

$$D(S_j - \hat{R}_j) - c_{j1}\mu_1(\hat{R}_1, \hat{R}_2)\hat{N}_1 - c_{j2}\mu_2(\hat{R}_1, \hat{R}_2)\hat{N}_2 = 0$$
Figure 5.4: The outcomes of competition between two species for two resources in the Tilman model. The nullclines of the two species are plotted in resource space, solid for species 1, dashed for 2. (a) The nullcline of species 1 lies below that of species 2. In this case, species 1 outcompetes species 2 (provided that species 1 is able to persist on its own). (b) In the reverse nullcline configuration species 2 outcompetes species 1. (c) The nullclines intersect in a way that makes species 1 limited by resource 1, and species 2 limited by resource 2 (this is explained in the text). At the intersection, the consumption vector of species 2, $c_2 = (c_{12}, c_{22})$, is steeper than the consumption vector of species 1, $c_1 = (c_{11}, c_{21})$. Thus, species 1 is the highest consumer of resource 1 and species is the highest consumer of resource 2. If resource supply if given by the chemostat equation (5.9), a two-species equilibrium exists if the resource supply point $S = (S_1, S_2)$ belongs to the hatched “wedge” formed by the projection of the consumption vectors at the intersection point. For this configuration of consumption vectors, the equilibrium is stable (filled dot). If $S$ does not belong to the wedge, then, depending on the resource ratios, species 1 or 2 wins. (d) When $c_1$ is steeper than $c_2$ at the intersection point, the two-species equilibrium (if it exists) is unstable (open dot) and there will be a winner that depends on the initial conditions. This is the same to say that each species prevents the invasion of the other, they mutually exclude.
Geometrically, this means that the supply point $S = (S_1, S_2)$ lies in the region bounded by two lines, the slope of which are given by the species consumption vectors $c_1 = (c_{11}, c_{21}), c_2 = (c_{12}, c_{22})$ at the intersection of the nullclines, as in Figures 5.4c, d. If the supply point happens to be outside of this region, a community equilibrium does not exist and the supply ratios determine which species will eventually outcompete the other.

3. The equilibrium must be stable. This requires that at equilibrium each species is the highest consumer of its limiting resource. This is represented in Figure 5.4c, where at the intersection, species 1 consumes a higher proportion of resource 1 compared with species 2 and vice versa, since the slope of the consumption vector of species 2 ($c_{22}/c_{12}$) is higher than the slope of the consumption vectors of species 1 ($c_{21}/c_{11}$) or

$$c_{11}c_{22} > c_{12}c_{21} \quad (5.11)$$

The same nullcline configuration, but with species 1 having the highest consumption ratio for resource 2 and species 2 the highest for resource 1 as in Figure 5.4d, results in an unstable equilibrium, and either species 1 or species 2 wins the competition depending on the initial conditions.

As we did in for the Lotka-Volterra model, we stress this time that inequality (5.11) is a necessary but not sufficient condition for stability. It may happen that inequality (5.11) holds at the nullcline intersection, but simultaneously, the resource supply point falls outside the region bounded by the projection of the consumption vectors in Figures 5.4c, d. In such a situation a community equilibrium does not exist, and one of the species always wins the competition, depending on the resource supply ratios but independently of the initial conditions. For example in Figures 5.4c, d, if $S_2/S_1$ is very high species 2 wins, and if $S_2/S_1$ is very low species 1 wins.

For perfectly essential resources the graphical analysis is more simple, since the nullclines are L-shaped (Fig. 5.3b). In this case we say that species 1 is limited by resource 1 if $R^*_{11} > R^*_{12}$ and that species 2 is limited by resource 2 if $R^*_{22} > R^*_{21}$. For perfectly essential resources coexistence is stable if each species is the highest consumer of the resource for which it has the highest requirement.

5.3.3 Quota model

In the Quota model the instantaneous growth rates depend on the quotas (5.3a). However, it is possible to demonstrate that in case of two species competing for one resource, the $R^*$-rule of the Tilman model also applies for the quota models: the species with the lower $R^*$ wins the competition [Smith and Waltman 1994, Grover 1997]. In the quota model the $R_{ji}^*$ values are computed under the assumption that the system is in equilibrium and $f_{ji}(R_{ji}^*) = m_iQ_{ji}^*$, where $Q_{ji}^*$ is the quota level of resource $j$ at which the per capita growth rate of species $i$ is balanced by its loss rate $\mu_i(Q_{ji}^*) = m_i$ (see Fig. 5.3b). In consequence, coexistence between two species requires more than one resource.
Figure 5.5: (a) In the storage based model the nullcline of species \( i \) divides the quota space of species \( i \) in zones of net positive and net negative growth. (b) The nullcline in quota space can be mapped into a “quasi-nullcline” in resource space. If resources are kept above the quasi-nullcline, species \( i \) will eventually grow, even if their quotas were initially below its nullcline in the quota space. If resources are kept below the quasi-nullcline, species \( i \) will eventually decline, even if their quotas were initially above its nullcline in the quota space.

In case of two species competing for two resources, the dynamic equations (5.3a) indicate that the line \( \mu_i(Q_{1i}, Q_{2i}) = m_i \) in the \( Q_{1i}Q_{2i} \)-plane is the nullcline of species \( i \), in quota space as seen in Figure 5.5a. Note that the quota space is species-specific, since it describes the internal nutrient state of and individual of species \( i \), but not the state of the external resources \( R_1 \) and \( R_2 \), for which both species compete. We can therefore not employ the nullclines of the two species in the same quota space and, accordingly, not consider the intersection of nullclines in quota space. There is, however, a solution for this problem.

According to the quota dynamics (5.3b), at equilibrium \( f_{ji}(R_j) = m_i Q_{ji} \). Graphically, this implies that the points along the nullcline in the quota space \( Q_{1i}Q_{2i} \) can be mapped one-to-one into a line in resource space (i.e. the \( R_1R_2 \)-plane) as seen in Figure 5.5b, which we call the “quasi-nullcline”. This is explained with more detail in Chapter 3, and essentially boils down to this: whenever all external resources are overabundant \( dQ_{ji}/dt = f_{ji}(R_j) - \mu_i Q_{ji} > 0 \) the quotas will increase above the nullcline in quota space, making species \( i \) grow. Whenever all external resources are critically low, \( dQ_{ji}/dt = f_{ji}(R_j) - \mu_i Q_{ji} < 0 \) the quotas will drop below the nullcline in quota space, making species \( i \) decline. Thus, although the instantaneous growth is independent of the external resources, there is a boundary in resource space that separates the regions of long term growth or decline: the quasi-nullcline.

For the purpose of comparing the resource requirements of the two species, the quasi-nullclines are as good as real nullclines. Thus, the outcomes of competition can be studied graphically in resource space, using the same methodology as in the Tilman model (Fig. 5.4). This is very convenient, since the analytical study of the Quota model for two species and two resources can be very complicated (Li and Smith, 2007, Chapter 2), given the fact that there are eight differential equations (two for the species, two for the resources, and...
four for the quotas). In contrast with the Tilman model, where the consumption vectors \( c_i = (c_{1i}, c_{2i}) \) are defined in terms of fixed resource contents, in the Quota model this role is taken over by the consumption rates, and we define consumption as \( f_i = (f_{1i}(R_1), f_{2i}(R_2)) \).

At the community equilibrium, when \( dQ_{1i}/dt = 0 \), these two formulations are compatible, because both fixed resource contents and quotas happen to represent equivalent concepts, just that the first is a parameter and the second is a variable. If this equivalency is expressed mathematically

\[
\begin{bmatrix}
  f_{1i}(\hat{R}_1) \\
  f_{2i}(\hat{R}_2)
\end{bmatrix}_i = m_i \begin{bmatrix}
  \hat{Q}_{1i} \\
  \hat{Q}_{2i}
\end{bmatrix} = m_i \begin{bmatrix}
  c_{1i} \\
  c_{2i}
\end{bmatrix}
\]

turns out that both \( f_i \) and \( c_i \) differ by a constant \( m_i \) but they have the same direction and orientation. Of course, out of the resource equilibrium point, both vectors do not coincide at all, since \( f_i(R_1, R_2) \) is resource dependent, whereas \( c_i \) is constant. Besides that, the outcomes of the graphical analysis will be the same as the Tilman model (Turpin, 1988, Hall et al., 2008, Chapter 3).

For example, if the quasi-nullclines of species 1 and 2 have the same arrangement as in Figure 5.4, species 1 always wins, and if they look as in Figure 5.4b, species 2 always wins. Like in the Tilman model, a two-species equilibrium requires the intersection of the quasi-nullclines, and that the resource supply point \((S_1, S_2)\) belongs to the region defined by the projection of the resource consumption vectors at the intersection \((\hat{R}_1, \hat{R}_2)\). If the quasi-nullclines are as depicted in Figure 5.4, where species 1 is limited by resource 1 and species 2 is limited by 2, coexistence will be possible when a two-species equilibrium exists and if

\[
f_{11}(\hat{R}_1)f_{22}(\hat{R}_2) > f_{12}(\hat{R}_1)f_{21}(\hat{R}_2)
\]

This inequality has the same interpretation as inequality (5.11): each species is the fastest consumer of its limiting resource. If the direction of inequality (5.12) is reversed, coexistence is unstable, and depending on the initial conditions, either species 1 or species 2 wins the competition (this would correspond to a configuration of quasi-nullclines and consumption vectors like in Fig. 5.4).

In the special case of perfectly essential resources, Liebig’s law (5.5) applies and the growth rate of species \( i \) is given by \( \mu_i = \min|\mu_{1i}(Q_{1i}), \mu_{2i}(Q_{2i})| \). In this situation the nullcline of species \( i \) in quota space is a L-shaped line defined by two quota requirements, i.e. the quotas \( Q_{1i}^* = Q_{1i}^1 \) and \( Q_{2i}^* = Q_{2i}^2 \) for which \( \mu_i = m_i \). Given equation (5.3b) at equilibrium, \( f_{ji}(R_{ji}) = m_iQ_{ji}^* \), each quota requirement is associated to a unique external resource requirement \( R_{ji}^* \). Consequently, for perfectly essential resources, the quasi-nullcline of species \( i \) in resource space is also an L-shaped curve like in Figure 5.3b.

5.3.4 Comparison of the models

In case of only two species, we find strong commonalities among the three models. In all of them, the system always ends up in an equilibrium state. In the particular case
of the Lotka-Volterra model, stronger proofs confirm that oscillations and other kinds of non-equilibrium dynamics are impossible (Smale, 1976; Hofbauer and Sigmund, 1988).

The equilibrium state can be the monoculture of one of the species, of a state of stable coexistence. In case of the Lotka-Volterra model, the geometry of the nullclines do not allow more than one coexistence equilibrium. The same is true in the Tilman and Quota models, as long as the number of resources is one or two, and the nullclines have simple shapes like in Figure 5.3. For this simple situations there are only four outcomes: (1) species 1 always wins, (2) species 2 always wins, (3) both species coexist at stable densities, and (4) either species 1 or species 2 wins the competition, the winner depending on the initial conditions. In other words, with or without coexistence, competition always leads to an equilibrium state. Another commonality is that mutual invasion always lead to stable coexistence.

In all models a requirement for coexistence is that intra-specific competition must stronger than inter-specific competition. In other words, the less the interacting species compete, the higher their chances to avoid exclusion. In the particular case of the Lotka-Volterra model this statement takes the form of inequality (5.10), where the product of the intra-specific competition coefficients is higher than the product of the inter-specific coefficients. However, competition coefficients can not tell us why competition, intra- or inter-specific, is strong or weak, since the mechanism for is absent in the model.

That is not the case for resource competition. By identifying which resource is limiting each species, we conclude that in order to survive competition, a species must try to monopolize (be the fastest consumer) its most limiting resource. When each species do that, the negative effects of resource depletion are minimized, inter-specific competition is weak and both species may coexist (given the appropriate resource supply concentrations). In contrast, when each species is least efficient in consuming its limiting resource, the effects of resource depletion are maximized, inter-specific competition is strong, and the species cannot possible coexist. This is reflected by inequalities (5.11) and (5.12). Coexistence requires specialization on different resources, meaning that two species cannot coexist on fewer than two resources, which is the “Competitive Exclusion Principle” (Gause, 1934).

The similarity between inequality (5.10) and inequalities (5.11) and (5.12) also suggests an association between the competition coefficients of the Lotka-Volterra model and the consumption rates of the resource based model, and this is often used to provide a resource-based mechanistic interpretation of competition coefficients (MacArthur, 1969, 1970). The form of the association, however, can differ greatly depending on the type of resource. To illustrate this, consider a simplified version of the Tilman model for two different scenarios: perfectly substitutable and perfectly essential resources. We make two simplifying assumptions:

1. The dependence of the per capita growth rate on the resources is linear, i.e. \( \mu_{ji} = b_{ji}R_j \) where \( b_{ji} \) is some conversion factor proportional to metabolic efficiency.

2. Competition takes place in a chemostat, where the resource renewal follows (5.9) and \( m_i = D \).

In the case of perfectly substitutable resources the per capita net rate of change of species \( i \) will becomes
\[
\frac{1}{N_i} \frac{dN_i}{dt} = \mu_i - D = b_{1i}R_1 + b_{2i}R_2 - D \tag{5.13}
\]

and the nullcline of \( i \) in the resource space will look as in Figure 5.3b. After long enough time, but before reaching the equilibrium, a mass conservation or mass balance constraint is achieved and the resource differential equations can be replaced by the algebraic relationships (Grover 1997):

\[
R_i = S_j - c_{j1}N_1 - c_{j2}N_2 \tag{5.14}
\]

If we substitute (5.14) in (5.13), we can rearrange the result in a form that is equivalent to the Lotka-Volterra model (5.1):

\[
\frac{1}{N_i} \frac{dN_i}{dt} = \frac{b_{1i}(S_1 - c_{1i}N_i - c_{1k}N_k) + b_{2i}(S_2 - c_{2i}N_i - c_{2k}N_k) - D}{r_i} = \frac{b_{1i}S_1 + b_{2i}S_2 - D - \left( b_{1i}c_{1i} + b_{2i}c_{2i} \right) N_i - \left( b_{1i}c_{1k} + b_{2i}c_{2k} \right) N_k}{a_{ii}} \tag{5.15}
\]

Accordingly, the nullclines of two species competing for two resources are linear in the space of species densities \( N_1N_2 \) as in Figure 5.2. Notice that the intrinsic growth rate \( r_i \) is defined with reference to the maximum abundance of the resources, which happens to occur when population densities are very low. As expected, the coefficients for intraspecific competition depend only on the consumption pattern of the focal species (i.e. depend on the \( b_{ji} \) and \( c_{ji} \) for species \( i \)), whereas the interspecific coefficients depend on the consumption patterns of the focal species \( i \) and its competitor \( k \) (i.e. depend on the \( b_{ji}, c_{ji} \) of species \( i \), and the \( c_{jk} \) of species \( k \)).

Now, according to the Lotka-Volterra model, the coexistence of species \( i \) and \( k \) requires that inequality (5.19) holds, i.e. \( a_{ii}a_{kk} > a_{ik}a_{ki} \). By substituting the definitions of the competition coefficients in (5.15) and rearranging we obtain the following expression

\[
\left( \frac{b_{1i}}{b_{2i}} - \frac{b_{1k}}{b_{2k}} \right) c_{1i}c_{2k} > \left( \frac{b_{1i}}{b_{2i}} - \frac{b_{1k}}{b_{2k}} \right) c_{1k}c_{2i}
\]

In this inequality, the term in parentheses is the difference between the slopes of the nullclines in resource space. According to our examination of the geometry of nullcline intersections, if species \( i \) is limited by resource 1 and species \( k \) is limited by resource 2, then the slope of the nullcline of species 1 \( b_{1i}/b_{2i} \) is higher than the slope of the nullcline of species 2 \( b_{1k}/b_{2k} \). Thus, the last inequality can be written as \( c_{1i}c_{2k} > c_{1k}c_{2i} \). On the contrary, if species \( i \) is limited by resource 2 and species \( k \) by resource 1, then the last inequality will become \( c_{1i}c_{2k} < c_{1k}c_{2i} \). In both cases, the bigger side of the inequality corresponds to the product of the consumption rates of the resources for which the species are limited at equilibrium. In other words, both alternatives are equivalent to the coexistence requirement (5.11) of the Tilman model.

In the case of perfectly essential resources, we notice some important geometrical differences. According to Liebig’s law, the per capita growth rate of species \( i \) will be expressed as


5.4 Existence of Community Equilibria

\[
\frac{1}{N_i} \frac{dN_i}{dt} = \mu_i - D = \min[b_{1i}R_1, b_{2i}R_2] - D
\]  

(5.16)

and the nullcline of \( i \) will look as in Figure 5.3b. By substituting (5.14) in (5.16) and rearranging:

\[
\frac{1}{N_i} \frac{dN_i}{dt} = \min[b_{1i}(S_1 - c_{1i}N_i - c_{1k}N_k), b_{2i}(S_2 - c_{2i}N_i - c_{2k}N_k)] - D
\]

(5.17)

Essentially, this result means that the dynamics of species \( i \) can be governed by two Lotka-Volterra equations, one that is valid when species \( i \) is limited by resource 1 and the other when species \( i \) is limited by resource 2. Like in the case of substitutable resources, the intra-specific coefficients depend only on the consumption properties of the focal species, and the inter-specific coefficients depend on the properties of both species. In consequence, the nullclines in the species space \( N_1N_2 \) are not linear, but polygonal lines as in Figure 5.6. Each segment of a nullcline corresponds to a different limiting resource (Zhang, 1991). For example, if species 1 is limited by resource 1, its nullcline will be \( r_1 = b_{1i}c_{11}N_1 + b_{1i}c_{12}N_2 \), but if its it limited by resource 2, its nullcline will be \( r_1 = b_{2i}c_{21}N_1 + b_{2i}c_{22}N_2 \). Of course, it is also possible that one of \( S_1 \) or \( S_2 \) is much bigger than the other, in which case due to Liebig’s law of minimum, the nullcline of species \( i \) will display only one segment.

As long as we only consider only two essential resources, this qualitative difference in the geometry of nullclines between perfectly substitutable and perfectly essential resources does not affect any of the general conclusions regarding coexistence. One may think that, since the nullclines for perfectly essential resources can have two segments, they may intersect more than once. This however, is impossible, since that would imply that the nullclines in resource space intersect in more than one point, which can not exist (see Fig. 5.4). However, for three and more resources the situation becomes more complex. In contrast with the two resources case, with three or more resources the nullclines in species space can cross more than once (Zhang, 1991), because the corresponding nullclines in resource space can cross at more than one point (e.g. with three resources, nullclines are surfaces, and two of them would intersect along lines, that is, a continuous set of points). In other words, with more than two resources, two species can display more than one coexistence equilibrium. Some of these equilibria are locally stable, and others are unstable. In consequence the realization of coexistence or competitive exclusion will depend on the initial conditions.

Another situation in which multiple equilibria can also occur, involves just two resources. This can happen if the nullclines (or quasi-nullclines) in resource space are curved.

5.4 Existence of Community Equilibria

Competition between two species is simple enough to be approached by graphically. However, under resource competition, even the two species case starts to become complex when considering three resources. Needless to say, adding more species also makes difficult to visualize the outcomes of competition using nullclines. In order to characterize and compare...
Figure 5.6: Nullclines of two species competing for two perfectly essential resources, performed in the species space (solid for species 1, dashed for species 2). If the resource supply concentrations are such that each species can be limited by two resources, Liebig’s law dictates that the nonzero nullclines consist of linear segments (otherwise the nullclines will look straight as in Fig. 5.2). For a given species $i$, the segment that intersects its own axis (e.g. $N_1$ for species 1) corresponds to a situation where species $i$ is limited by the resource for which it has the highest requirement. For the same species $i$, the segment that intersects the axis of its competitor (e.g. $N_2$ for species 1) corresponds to a situation where species $i$ is limited by the resource for which it has the lowest requirement. The outcomes are the same as in the Lotka-Volterra model (Fig. 5.2): (a) species 1 wins, (b) species 2 wins, (c) coexistence, (d) mutual exclusion.
the dynamics of the Lotka-Volterra and resource competition models in higher dimensions, we must rely on more “analytical” methods and less on graphical ones. We will start in this section, by studying the equilibrium states. In section 5.5, we approach the problem of the local stability of equilibria by evaluating internal stability (stability of a community of resident species) and external stability (stability of a community against invasion). Finally, in section 5.6 we will give some insights about the global dynamics of the competitive system, particularly with respect to non-equilibrium dynamics, and multiple stable states.

5.4 Existence of community equilibria

5.4.1 Lotka-Volterra model

Consider community equilibrium in the Lotka-Volterra model, i.e. an equilibrium where \( N_i > 0 \) for all species. From (5.17) with \( \frac{dN_i}{dt} = 0 \), such an equilibrium is characterized by a set of linear equations:

\[
\sum_{k=1}^{n} a_{ik} N_k = r_i \quad (5.18)
\]

Each equation represents a nullcline in a multidimensional species space. Figure 5.7 illustrates the nullcline of species 1 for the special case of three species, which corresponds to a plane in 3-dimensional resource space. \( N_1 \) grows in the region “below” the nullcline and decreases “above” the nullcline. For \( n \) species in general, a nullcline is a \( n-1 \) dimensional set (point, line, plane, volume, hypervolume, etc.). Equilibria correspond to intersections of nullclines as in Figure 5.7b. Notice that the three species equilibrium occurs in the “interior” of the species space, we call this point the internal equilibrium or community equilibrium. Equilibria between two species occur on the “borders” (coordinate planes) of species space, we call such intersections, border equilibria. Monocultures can also be considered border equilibria.

But for three and more species it is more convenient to use the language of vectors and matrices to state the conditions for the existence of equilibria. Thus, let start by defining a column vector of \( n \) species densities \( \mathbf{N} = [N_1, \ldots, N_n]^T \) and the \( n \times n \) interaction matrix \( \mathbf{A} = \{a_{ik}\} \). This allows us to write equation (5.18) in matrix form as \( \mathbf{AN} = \mathbf{r} \), where \( \mathbf{r} = (r_1, \ldots, r_n)^T \) is the column vector of intrinsic growth rates. Technically speaking, the equation \( \mathbf{AN} = \mathbf{r} \) has the solution \( \hat{\mathbf{N}} = \mathbf{A}^{-1} \mathbf{r} \), where \( \mathbf{A}^{-1} \) is the inverse of \( \mathbf{A} \) (Case, 2000).

To be a meaningful solution, the vector \( \hat{\mathbf{N}} \) thus obtained needs to have positive elements. It can be shown (Chapter 3, Appendix A) that all the elements of \( \hat{\mathbf{N}} \) are positive, and thus a community equilibrium exists, if and only if the vector \( \mathbf{r} \) lies in the cone spanned by the columns of \( \mathbf{A} \) (Fig. 5.8). If on the contrary, \( \mathbf{r} \) does not belong to the cone, the intersection of nullclines does not exist (because some nullclines are parallel), or it does exist but some components of \( \hat{\mathbf{N}} \) are negative.

The \( n \)-species community equilibrium is not the only coexistence of the system. There can be other equilibria involving \( n-1, n-2, \ldots \) down to species pairs, and monoculture equilibria. For all these border equilibria equation (5.18) and the “cone rule” apply, but the vectors and the community matrix involved include only the components (rows and columns) that correspond to the species under consideration.
Figure 5.7: Equilibrium analysis for the three species Lotka-Volterra model. (a) The nullcline of species 1: $N_1$ increases in the region below the plane and decreases above it. The round dot is the carrying capacity $K_1 = r_1/a_{11}$, or monoculture equilibrium. (b) The nullclines of three species intersecting in one of many possible ways. The 3-species equilibrium corresponds to the intersection of the three nullclines in the interior (star). An equilibrium between species $i$ and $k$ corresponds to the intersection of its nullclines and the plane $N_iN_k$ (plus signs). The intersection of the nullcline of species $i$ with its own axis (round dots) is a monoculture equilibrium. All border equilibria (monocultures, and 2-species) are internally stable but externally unstable, thus all three species coexist.

Figure 5.8: A $n$-species Lotka-Volterra system has a positive solution (all $\dot{N}_i > 0$) if the vector of intrinsic growth rates $r = (r_1, \ldots, r_n)^T$ is contained in the cone formed by the columns of the matrix of competition coefficients, $a_i = (a_{i1}, \ldots, a_{in})^T$. (a) The cone rule for a two-species system. (b) The cone rule for a three-species system.
5.4 Existence of Community Equilibria

5.4.2 Tilman model

In the graphical analysis of the two-species Tilman model, we stated that a community equilibrium has two requirements: the nullclines in resource space must intersect, and the resource supply point must fall in the region spanned by the projection of the consumption vectors at the intersection point. We will see how these conditions translate into higher dimensions.

Let us start by considering a situation where the number of species and resources is the same \( n = m \) (the more general situation \( n \neq m \) will be treated shortly after). In the \( n \) dimensional resource space \( R_1 \ldots R_n \), the nullclines are \( n - 1 \) dimensional objects: surfaces (3 resources), volumes (4 resources), and so on . . . in other words the multidimensional extrapolation of the curves in Figures 5.3 and 5.4. The intersection \( n \) nullclines can be one point \( \hat{R} = (\hat{R}_1, \ldots, \hat{R}_n) \) or multiple discrete points \( \hat{R}, \hat{R}', \hat{R}'' \ldots \) etc. In the special case of Liebig’s law (5.3) the growth rates are given by \( \mu_i = \min_j [\mu_{ij}(R_j)] \), and the multiple resource requirements \( R_i^{\star} \), give the shape of the nullcline of species \( i \). For example, if \( n = 3 \) the nullcline of species \( i \) has the appearance of three adjacent sides of a cube, with the corner given by the resource requirements \( R_i^*, R_j^*, R_k^* \). When two nullclines like these intersect, they form a line, and the intersection of this line with the third nullcline results in a point \( \hat{R} = (\hat{R}_1, \ldots, \hat{R}_n) \). Such intersection is possible if and only if each species has the highest requirement for one of the three resources. Thus, if \( n \) species are competing for \( n \) perfectly essential resources, with species \( i \) having the highest requirements for resource \( i \) (\( R_i^* > R_{ji}^*, k \neq i \)), the intersection of the nullclines occurs exactly at one point:

\[
\hat{R} = (\hat{R}_1, \hat{R}_2, \ldots, \hat{R}_n) = (R_{11}^*, R_{22}^*, \ldots, R_{nn}^*)
\]  

(5.19)

If the number of species is bigger than the number of resources \( n > m \), it is not possible (in general) for the nullclines to intersect. In consequence, there can not be an species equilibrium coexistence with less than \( n \) resources. This is the extension of the principle of competitive exclusion for the multispecies case. On the contrary, if the number of species is smaller than the number of resources \( n < m \), the intersection of nullclines are not discrete points, but continuous sets of points. For example, if \( n = 2 \) and \( m = 3 \) the nullclines of the two species intersect along a line, if \( n = 2 \) and \( m = 4 \) the nullclines intersect forming a surface.

The second requirement for equilibrium is that the intersection must be achievable, in other words that \( \hat{R} \) corresponds to a resource equilibrium. As before, let us start again with the assumption that \( n = m \). According to equation (5.2b), in an equilibrium the species densities and resource concentrations must satisfy

\[
\sum_{i=1}^{n} c_{ij} m_i N_i = \phi_j \left( R_j \right)
\]

since \( \mu_i = m_i \) at equilibrium. This equation has the same form as (5.18), i.e. a linear system in the population densities. For example if \( \phi_i \) is given by (5.9) and \( m_i = D \), equation (5.20) can be written as \( \Phi = CN \), where \( \Phi = (\phi_1, \ldots, \phi_n) \) is the resource supply vector, \( N \) is the vector of species densities, and \( C = (c_{ij}) \) is the consumption matrix, i.e. a matrix whose columns correspond to the species consumption vectors \( c_i = (c_{1i}, \ldots, c_{ni})^T \). If the
determinant of $C$ is not zero, we can compute the equilibrium densities as $\hat{N} = D^{-1}C^{-1}\hat{\phi}$, in which $\hat{\phi}$ corresponds to the supply vector evaluated at the intersection of the nullclines in resource space, i.e. $\hat{\phi} = \phi(\hat{R})$. As in the case of the Lotka-Volterra model, the cone rule also applies: $\hat{N}$ is a community equilibrium if the supply vector $\phi$ falls in the cone formed by the columns of the consumption matrix, the $c_i$. In case of linear resource renewal as in (5.9), the cone rule can be stated more explicitly as follows: the supply point $S = (S_1, \ldots, S_n)$ falls in the cone spanned by lines originating at the nullcline crossing $\hat{R}$, with the orientation (slope) of these lines given by the species consumption vectors $c_i$. In the $R_1R_2$ space this cone is the hatched “wedge” in Figures 5.4,c,d.

As stated before, the nullclines could intersect at more than one point. This could happen in two ways. First, under the assumption that $n = m$, the nullclines could intersect in several discrete points ($\hat{R}, \hat{R}', \hat{R}'', \ldots$) if they are curved like in Figure (5.4). If the cone rule holds at a given intersection point, that point corresponds to a community equilibrium. As a second alternative, consider that the number of resources is higher than the number of species considered. The intersection of nullclines will be a continuous set of points $\Re$. This situation does in fact happens for $n = m$, because in addition to the $n$-species community, we must consider all equilibria with $n-1, n-2, \ldots$ species, which also compete for the same $m$ resources. As an example, consider three species and three resources: the nullclines of the three species intersect at one or more discrete points, but the nullclines of any species pair intersect in along a lines. In this case the cone rule also holds because: (1) we can define the supply vector and the cone of consumption vectors at any point in resource space, and (2) the supply vector could be contained in the consumption cone at one point along the intersection line. In principle, nothing prevents that this situation occurs more than once, resulting in species-pair multiple equilibria.

5.4.3 Quota model

The requirements for equilibrium in the quota model are almost the same as in the Tilman model. First, the quasi-nullclines in the external resource space must intersect. Second, the resource supply vector must be part of the cone formed by the species consumption vectors.

In the multidimensional Quota model, the quasi-nullclines are defined in the same way as in the two-dimensional resource space (Fig. 5.5): by mapping each point of the nullcline of species $i$ in its quota space $Q_{1i} \cdots Q_{mi}$ into the resource space $R_1 \cdots R_m$. If the number of resources is equal or higher than the number of species ($m \geq n$), the quasi-nullclines can intersect at more than one point, either because they are curved, or because the number of resources is larger than the number of species considered. On contrary, if the number of resources is less than the number of species ($m < n$) the quasi-nullclines will not (in general) have a common intersection, and equilibrium coexistence is not possible at all.

In an equilibrium, the resource concentrations and species densities must satisfy the equilibrium condition of the resources in (5.3c):

$$\sum_{i=1}^{n} f_{ji}(R_j)N_i = \phi_j(R_j)$$  \hspace{1cm} (5.21)
These equations can be written in matrix form as $\mathbf{\phi} = \mathbf{F}\mathbf{N}$, where $\mathbf{F} = \{f_{ij}(R_j)\}$ is the consumption matrix, and the columns of this matrix represent the species consumption vectors $\mathbf{f}_i = \{f_{1i}(R_1), \ldots, f_{ni}(R_n)\}^T$. If the number of resources is equal to the number of species, species densities in a community equilibrium are given by $\hat{\mathbf{N}} = \mathbf{F}^{-1}\mathbf{\phi}$ (provided that the determinant of $\hat{\mathbf{F}}$ is not zero). The main difference between this solution at that of the Tilman model, is that both the consumption matrix and resource the supply vector must be evaluated at the intersection of the quasi-nullclines. As in the Lotka-Volterra and the Tilman models, the cone rule applies: a positive solution for $\hat{\mathbf{N}}$ requires that the supply vector belongs to the cone formed by the consumption vectors at the nullcline intersection(s). In the case where resource supply is described by the chemostat equation (5.9), the coexistence equilibrium exists if the resource supply point $\mathbf{S} = (S_1, \ldots, S_m)$ falls in the cone formed by lines oriented according to the consumption vectors, at the quasi-nullcline intersection(s).

The main difference with the Tilman model, is that in the Quota model, the cone formed by the consumption vectors has different sizes (e.g. is more “open” or “closed”) and orientations at the different intersection points, because the $f_i(R)$ are functions in resource space.

### 5.4.4 Comparison

In the three models it is possible to relate the species densities in equilibrium, $\hat{\mathbf{N}}_i$, using a system of linear equations (5.18, 5.20, and 5.21). Such system can be written in matrix form as (c.f. Table 5.1 for details):

$$
\mathbf{M}\hat{\mathbf{N}} = \mathbf{\rho}
$$

with $\hat{\mathbf{N}} = (\hat{N}_1, \ldots, \hat{N}_n)^T$. In the Lotka-Volterra model $\mathbf{M}$ is the matrix of competition coefficients $\mathbf{A} = [a_{ik}]$ measuring the effect of species $k$ upon $i$. The $\mathbf{A}$ matrix is usually called the community matrix. In the Tilman model $\mathbf{M}$ is the matrix of resource contents $\mathbf{C} = [c_{ij}]$, and in the Quota model it is the matrix of consumption rates at equilibrium $\tilde{\mathbf{F}} = \{f_{ij}(\hat{R}_j)\}$. The vector $\mathbf{\rho}$ contains positive terms, and its magnitude can be taken as an indication of how “good” is the environment. For example, in case of the Lotka-Volterra model $\mathbf{M}$ is the vector of the maximum per capita growth rates, which occur when population densities are low, when (intra- and inter-specific) competition is negligible. In case of resource competition models, $\mathbf{\rho}$ indicates how fast the resources recover from consumption.

Whether a solution $\hat{\mathbf{N}}$ for (5.22) is feasible or not, depends on several factors. In the particular case of the Lotka-Volterra model the matrix $\mathbf{M} = \mathbf{A}$ has the same number of rows and columns, and $\hat{\mathbf{N}}$ can be computed as $\hat{\mathbf{N}} = \mathbf{M}^{-1}\mathbf{\rho}$, as long as $\mathbf{M}$ can be inverted. If $\mathbf{M}$ cannot be inverted, this means that some of the rows or columns of $\mathbf{M}$ are linearly dependent, in other words that some nullclines are parallel. If $\mathbf{M}$ can be inverted, it could happen that the solution has one or more negative densities. In both cases, a feasible solution does not exist, either because the nullclines do not intersect, or because they intersect outside of the positive orthant.

For the resource competition models, the feasibility of $\hat{\mathbf{N}}$ requires the intersection of the nullclines (Tilman model) or quasi-nullclines (Quota model) in the space of resources. In
In general, if the number of resources is less than the number of species, such intersection does not occur, and the community equilibrium does not exist. If the number of resources and species are equal, we can compute the $\hat{N}$ by the method of matrix inversion like in the Lotka-Volterra model, provided that $M = C$ (Tilman model) or $M = \hat{F}$ (Quota model) is invertible. Likewise, the community equilibrium may not exist because some rows or columns of $M$ are linearly dependent, or simply because the solution contains negative densities. In the more general case when the number of resources is higher than the number of species (e.g. at the border equilibria), the solution(s) $\hat{N}$ may be feasible, but we cannot use the method of matrix inversion to find them (the number of rows and columns of $M$ do not match).

Besides all these details, there is a common pattern in all models: the “cone rule” implies the existence of community equilibria. The logic behind this rule has to do with the idea that an equilibrium is a state in which all forces (in the most general sense) are exactly balanced, such that the net effects are zero. In the case of the Lotka-Volterra model, the community equilibrium is a state in which the tendency of population growth is counter-balanced by intra- and inter-specific competition. In resource competition models a coexistence equilibrium corresponds to a state where resource renewal is counterbalanced by resource consumption. Indeed, the equilibrium equation (5.22) can be rewritten as an exercise in which mechanical forces must be balanced (e.g. like in Halliday and Resnick (1974) textbook):

$$\rho - \sum v_i \hat{N}_i = 0 \quad (5.23)$$

where $\mathbf{0}$ is a vector of zeros, and the vector $v_i$ is the $i$-th column of $M$. In equation (5.23) $\rho$ can be interpreted as the force exercised by a stretched spring, $v_i$ as gravity and $\hat{N}_i$ as the mass of an object. In Figure 5.9b we can see that the different forces will cancel each other only if the spring is contained in the cone defined by the force vectors associated with the masses, and solving $\hat{N}_i$ is analogous with finding the right masses $w_i$. If the spring were outside of the cone like in Figure 5.9c, force balancing requires that we change in the direction of gravity or the sign of one of the masses, which are both absurd (we could reposition the objects or vary their masses, but that would represent a different system or equilibrium, e.g. different consumption vectors or densities). Back to the original problem of equilibrium feasibility: since $M$ is positive (e.g. gravity points downwards, never upwards) and $\rho$ is positive (e.g. springs pull when stretched, they do not push), $\hat{N}$ will be positive (masses are positive) if and only if the vector $\rho$ belongs to the cone formed by the columns of $M$.

A multispecies system will have, in general, many equilibrium points, and in all of them the cone rule applies. This can be justified again by means of the mechanical analogy. Consider three objects: the cone associated with the equilibrium looks like the apex of a pyramid with three faces (like in Fig. 5.8a). If we take away one of the objects, the cone associated with the equilibrium of two objects looks as in Figures 5.9b or 5.8b, i.e. the corner of a triangle. If we take away two objects, the cone associated to the equilibrium for one object is just a line. The cone rule holds for all these “border equilibria”. The cone rule also holds for all “internal equilibria”: just assume that the floor in Figure 5.9b is irregular. Under this circumstance, we can place the two objects in many ways (one on top of a bump and the other in a depression, both on top of bumps, or both in depressions), but in all cases a state of equilibrium demands that the spring ends up in the cone defined by the
Figure 5.9: Interpretation of the “cone rule”, using Tilman’s model in (a) and a mechanical example in (b). In Tilman’s model, the magnitude of the supply vector $\phi$ is proportional to the distance between the supply point and the resource concentrations (i.e. $\phi_j = D(S_j - R_j)$ according to (5.9)). In the mechanical example the force exercised by the spring is proportional the elongation caused by fixing to the roof (i.e. $ky = k|\Delta y|$ according to Hooke’s law). In Tilman’s model the consumption vector of a species is given by its resource contents as $c_i = (c_{i1}, \ldots, c_{im})^T$, but the total consumption is proportional to the size of the population $N_i$ (a scalar). In the mechanical example, each object “pulls” the spring along wires, where $g_i$ is the component gravity’s acceleration $(g)$ along the wire of object $i$. The force of the pull is proportional to the object’s mass $(g_iw_i)$. In both examples, the vector pointing upwards $(\phi$ or $ky$) belongs to the cone defined by dashed lines, the slope of which are given by the vectors pointing downwards $(c_i$ or $g_i$). In (c) the spring is attached to the roof, but outside of the cone. As a consequence, an equilibrium of forces does not exist. To restore the equilibrium, the vector associated to object 2 should point upwards and left, but this would require that gravity $(g)$ points left, or that $w_2$ becomes negative!
wires that joins the objects to the spring, otherwise there will be a net acceleration (**ergo** no equilibrium).

### 5.5 Stability of equilibria

The analogy with force balance implied by the cone rule does not mean that community equilibria are stable, just only that they exist. In Figure [5.9](http://example.com), the competitive system is at equilibrium, but it may happen that a tiny variation in densities \(N_i\) or resources \(R_j\) results in further increase of decrease in the vectors. As a consequence the right-hand-side of equation (5.23) may not return to 0 and the equilibrium is unstable (imagine a chair balanced in one leg). In this next section we treat the issue of local stability properties of the models in more detail.

#### 5.5.1 Internal vs external stability

Graphical analysis (section 5.3) is very useful for assessing the stability of systems of two species. High-dimensional scenarios however, require more powerful methods, which rely on the analysis of the jacobian matrix of the system. But even for a small number of species like \(n = 3\), it can be very difficult to perform such analysis.

A partial solution to this problem starts by considering that given \(n\) species, there can be many equilibria associated with communities made of \(n-1\), \(n-2\), \ldots, 1 species, i.e. border equilibria. In a border equilibria, we have two sets of species: the set \(K\) of residents for which \(N_k > 0\), and the set \(L\) of potential invaders for which \(N_1 = 0\). It can be shown ([Hofbauer and Sigmund, 1988](#) [Case, 2000](#), Chapter 3) that an equilibrium is locally stable, if and only if, it is both **internally** and **externally** stable. Internal stability refers to stability against perturbations in the community of resident species \(K\). External stability refers to stability against invasion by small numbers of invaders from \(L\).

By decomposing the difficult problem of stability into the smaller problems of internal and external stability, it is often possible to obtain a qualitative picture of the global dynamics of the competitive system (section 5.6). Of the two problems, external stability is much easier to address than internal stability. Thus, we start with external stability and continue later with internal stability.

#### 5.5.2 External stability

In principle, external stability is more easy to study than internal stability. It boils down to ask whether invaders can grow when rare in a system where the residents are in equilibrium. Formally, a border equilibrium is externally stable if the growth rate of all the invaders, considered independently, is negative. Notice that it is only necessary to consider each invader separately ([Case, 2000](#) [Huisman and Weissing, 2001](#), Chapter 3), i.e. we do not have to consider the simultaneous invasion of several invaders. The sign of an invader’s growth rate is given its net per capita growth rate:
5.5 Stability of equilibria

\[
\frac{dN_l}{N_l} = r_l - \sum_{k \in K} a_{lk} \tilde{N}_k \quad (5.24a)
\]

\[
\frac{dN_l}{N_l} = \mu_l (\tilde{R}_1, \ldots, \tilde{R}_m) - m_l \quad (5.24b)
\]

\[
\frac{dN_l}{N_l} = \mu_l (\tilde{Q}_1, \ldots, \tilde{Q}_m) - m_l \quad (5.24c)
\]

where (5.24a) corresponds to the Lotka-Volterra model, (5.24b) corresponds to the Tilman model, and (5.24c) to the Quota model.

In case of Lotka-Volterra model the net per capita growth rate is a function of the equilibrium densities of the residents, which is determined by equation (5.18), with \( N_l = 0 \) for all the invader species. In case of three species, the sign of the net growth can be determined by nullcline analysis. For example in Figure (5.7), consider species \( k = 1, 2 \) as the residents and \( l = 3 \) the invader. We can see that the equilibrium point the residents \( (\tilde{N}_1, \tilde{N}_2, 0) \) lies below the nullcline of species 3, the invader. In consequence, species can grow when rare, \( N_3^{-1} \frac{dN_3}{dt} < 0 \). We conclude that the border equilibrium \( (\tilde{N}_1, \tilde{N}_2, 0) \) is externally unstable. If the point were above species 3 nullcline, the resident community would be externally stable.

In case of the Tilman model, the net per capita growth rate of an invader is a function of the resource concentrations left by residents \( \tilde{R}_j \). In case of competition for three resources, it would be possible represent graphically the conditions under which the invader’s net growth rate is positive or negative: the resource equilibrium point \( (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3) \) is at the intersection of the nullclines of the residents, if this point lies “above” the nullcline of the invader, it will grow and the resident equilibrium is externally unstable. If \( (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3) \) lies “below” the invader’s nullcline, the resident equilibrium is externally stable against this invader. If \( (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3) \) lies below the nullcline of any possible invader, the resident equilibrium is externally stable in general.

In the Quota model, the growth of an invader is a function of its quotas. Since an invader is assumed to be rare, it has an insignificant influence on the external environment. However, the external environment has an enormous effect on the invaders, meaning that the quotas of the invader attain a quasi-steady-state (Di Toro, 1980) with the external resource levels \( \tilde{R}_j \), set by the residents. In consequence, the sign of the invader’s net growth depends, indirectly, on the external resource concentrations. Thus the determination of the external stability follows the same rules as in the Tilman model (Chapter 3). In using a graphical representation, we conclude that a border equilibrium is externally stable if the resource levels set by the residents are below the quasi-nullclines of all possible invaders.

5.5.3 Internal stability

In order to assess the internal stability of the equilibrium of the resident species \( (k \in K) \), we just have to ignore the part of the system associated with the invaders \( (l \in L) \). That part include the invaders population densities in case of the Lotka-Volterra and Tilman model, as well as the quotas in case of the Quota model.
The local stability the resident sub-system is determined by the properties of its jacobian matrix. The jacobian matrix consists of the derivatives of the differential equations with respect to the time dependent variables. An equilibrium point will be locally stable if the all the eigenvalues of the jacobian matrix evaluated in that equilibrium have negative real parts. An important special case corresponds to the equilibrium in which all \( n \) species are present, i.e. the community equilibrium. The conditions for the stability of the community equilibrium also apply to the internal stability of all border equilibria, since they are smaller versions of the community equilibrium (they just happen to have less than \( n \) species). Thus, we will focus on the stability of the community equilibrium.

5.5.3.1 Lotka-Volterra model

The jacobian matrix of the \( n \)-species equilibrium in the Lotka-Volterra model is given by (Strobeck, 1973; May, 1974; Hofbauer and Sigmund, 1988; Case, 2000):

\[
J = -DA
\]  

(5.25)

In this equation \( D \) is the diagonal matrix formed by the products \( r_i \hat{N}_i \). In case of two species the equilibrium is globally stable if the determinant of the community matrix \( A \) is positive, which is the same as inequality (5.10). This means that in a two-species Lotka-Volterra system, internal stability is determined only by properties of the community matrix.

5.5.3.2 Tilman model

In the Tilman model of \( n \) species and \( m \) resources, the jacobian matrix has \( n + m \) rows and columns. Given two reasonable assumptions (Huisman and Weissing, 2001), the stability of the equilibrium can be determined with a smaller jacobian having \( n \) rows and columns. First, consider that the competition takes place in a chemostat. In this situation the resource renewal is described by equation (5.9) and the species loss rates are equal to the resource turnover rate \( m_i = D \). After enough time, a mass balance constraint allow us to replace the differential equations of the resources with simple algebraic relationships (Appendix A). Second, assume that resources are perfectly essential. Thus, at the equilibrium each species growth rate becomes a function of a single resource, the resource for which it has the highest requirement (this is a prerequisite for equilibrium). Let us assume that species \( i \) is limited by resource \( i \), i.e. \( \mu_i = \mu_i(R_i) \). Under these assumptions, the jacobian matrix of the differential equations for the species densities (5.21) adopts the form:

\[
J = -DC
\]  

(5.26)

where \( D \) is a diagonal matrix whose elements are \( (\partial \mu_i/\partial R_i)\hat{N}_i \) evaluated at the equilibrium, and \( C = \{c_{ji}\} \) is the matrix of resource contents.

For two species in equilibrium, it is easy to show (León and Tumpson, 1975; Tilman, 1980, 1982) that the eigenvalues of the jacobian have negative real parts if the determinant of \( C \) is positive, i.e. when inequality (5.11) holds. In the two-species scenario, stability is determined by the properties of the consumption matrix alone.
5.5 Stability of Equilibria

5.5.3 Quota model

In contrast with the Lotka-Volterra and the Tilman models, the jacobian matrix in the Quota model is much bigger. For example, a system of $n$ species and $m$ resources has a jacobian matrix with $n + m + n \times m$ rows and columns, because in addition to the resources we must consider all the quotas. Thus, a system of 2 species and 2 resources requires a $8 \times 8$ matrix jacobian, and for 3 species and 3 resources we must deal with a $15 \times 15$ jacobian.

This problem can be greatly simplified if we use the same assumptions as in the Tilman model, i.e. competition takes place in a chemostat and $m_i = D$, and resources are perfectly essential (Appendix A). In addition, consider that the time scale of the quota dynamics is much faster that that of resource consumption and population growth (Di Toro, 1980), such that the quota is at quasi-steady-state ($\frac{dQ_{ji}}{dt} \approx 0$). This allows us obtain the jacobian matrix of a much simpler system, that involves only the equations of the species densities (Appendix B):

$$J = -D\hat{F}$$

(5.27)

where $D$ is a diagonal matrix with elements $\hat{N}_i \frac{\partial \mu_i}{\partial R_i}$ and $\hat{F} = \{ f_{ji}(\hat{R}_j) \}$ is the consumption matrix evaluated at the equilibrium. In Chapter 3, we do not employ the chemostat assumption and quasi-steady-state for quotas, but the result is similar in some aspects. Notice, that the derivative $\frac{\partial \mu_i}{\partial R_i}$ makes sense only because of the quasi-steady-state assumption for the quotas, such that $\frac{\partial \mu_i}{\partial Q_{ji}} \approx \frac{\partial \mu_i}{\partial Q_{ii}} \frac{\partial Q_{ii}}{\partial R_i}$. In a quasi-steady-state, the quotas must respond rapidly to keep up with changes in the external resources, so $Q_{ii} \approx Q_{ii}(R_i)$.

For two species and two essential resources the community equilibrium is stable if the determinant of $\hat{F}$ is positive, which coincides with the result of the graphical analysis (5.12). There is strong support for the conjecture that this is a sufficient condition for the stability of the community equilibrium (Li and Smith, 2007; Hall et al., 2008, Chapter 3) under less restrictive assumptions than the ones used here.

5.5.4 Comparison

In the three models, external stability is decided when all the invasion rates of the invaders considered alone are negative. Invasion rates are functions of different sets of variables: resident densities (Lotka-Volterra model), resource concentrations (Tilman model), or invader quotas (Quota model). However, in the resource competition models invasion rates also depend on the residents densities in an indirect way. In the Tilman model for example, the equilibrium condition of the resources \( \hat{R}_j = \phi_j^{-1} \left( \sum_{k \in \mathcal{K}} c_{jk} \hat{N}_k \right) \) in the net per capita growth rate of invader \( l \) (5.24b). Unfortunately in case of the Quota model, there is not such a simple way to relate the net per capita growth rate of an invader with the densities of the residents via the resources, even under the chemostat and quota quasi-steady-state assumptions.

Internal stability is determined by the properties of the jacobian matrix at the equilibrium. Since the three models differ in the number and nature of the dynamical equations, their jacobian matrices are different. However, given some simplifying assumptions, we can reduce the number of equations in a $n$-species resource competition model (Tilman
and Quota) to the same number of equations of a \( n \)-species Lotka-Volterra model. The corresponding jacobian matrix becomes:

\[
J = -DM
\]  

(5.28)

where \( D \) is a diagonal matrix that contains the species densities at equilibrium multiplied by rate terms, and \( M \) is the same matrix that determines the feasibility of the equilibrium (see section 5.4): the community matrix \( A \) (Lotka-Volterra), the matrix of resource contents \( C \) (Tilman model) or the consumption matrix \( \hat{F} \) at the equilibrium (Quota model). We will call \( M \) simply the interaction matrix because it contains the direct effects of one the interaction of species with another, or the indirect effects of the indirect interaction of one species on another via shared resources. Table 5.1 put all this results together for comparison.

The similarity of the jacobian matrices tells us that in the proximity of the equilibrium, both resource competition models behave similarly as the Lotka-Volterra model. Interestingly, some important features of the local dynamics can be outlined by looking at the structure of the interaction matrix \( M \) instead of the full jacobian. For example consider the \( 3 \times 3 \) matrix \( M \) in Figure 5.10. The following pattern is found (Strobeck, 1973; May and Leonard, 1975; Gilpin, 1975; Hofbauer and Sigmund, 1988; Weissing, 1991; Huisman and Weissing, 2001, 2002; Revilla and Weissing, 2008):

1. If the diagonal elements are bigger than the off-diagonal elements \( (a > b, c; e > d, f; i > g, h) \), the equilibrium is likely to be stable.

2. If the diagonal elements are smaller than the off-diagonal elements \( (a < b, c; e < d, f; i < g, h) \), the equilibrium is unstable.

3. If the elements of the band above the diagonal are the biggest ones \( (b > a, c; f > d, e; g > h, i) \), the system tend to display oscillations around the equilibrium. The equilibrium may be stable or unstable.

From the first prediction follows a necessary but not sufficient condition for local stability: stability requires that the determinant and the principal minors of \( M \) are positive. In terms of the Lotka-Volterra model, this stability requirement is met when the intra-specific competition coefficients tend to be much higher than the inter-specific coefficients. In terms of
both resource competition models, this requirement is met when each species tend to consume more of those resources for which they experience the strongest limitation. For this configuration, inter-specific competition is weak in comparison to intra-specific competition. If the matrix $M$ is diagonally dominant ($a > b + c; e > d + f; i > g + h$), we can make an even stronger prediction: the equilibrium will be stable (this follows from Gershgorin’s circle theorem, Strobeck, 1973).

The second prediction describe the opposite situation. For the Lotka-Volterra it means that intra-specific coefficients tend to be small in comparison with inter-specific coefficients. In terms of the resource competition models, each species tends to consume less of the resources for which they experience limitation and comparatively more of the resources that are limiting for other species. This creates an unstable situation in which any imbalance in favor of one species gets amplified in time. Unstable equilibria are characterized by matrices with negative determinants and principal minors.

The third prediction involves a matrix configuration lying between the two extremes discussed above. In the Lotka-Volterra model, it is difficult to say which one, intra- or inter-specific competition, is higher on average. In resource competition models, this configuration corresponds to a scenario in which each species tend to consume those resources for which they have intermediate requirements. If the determinant of the $M$ is positive, the equilibrium may be stable or unstable, but if negative, it will be unstable.
5.6.1 Competitive oscillations

The pioneer works of May and Leonard (1975) and Gilpin (1975) with the Lotka-Volterra model revealed that oscillations are possible for the 3-, 4- and 5-species scenario. Smale (1976) showed that given a high enough number of species \((n \geq 5)\) the Lotka-Volterra equations are compatible with any kind of global dynamics (e.g. equilibrium, cycles, chaos). In contrast, the classic two-species case only leads to equilibrium solutions (Smale 1976; Hofbauer and Sigmund, 1988).

For three species, competitive oscillations can be predicted using nullcline analysis. In the example of Figure 5.11 we can see that 2-species equilibria do not exist. We can also see that each species can be invaded only by one of the other species, but not by two. This indicates that the monocultures are unstable, but in closer examination monocultures are externally stable against one species and externally unstable against the other, i.e. monocultures are saddle points. This results in a sequence of species replacements: species 1 excludes species 2, species 3 excludes species 1 and species 2 excludes species 3. The situation resembles the game of Rock-Paper-Scissors: rock crushes scissors, paper wraps rock and scissors cuts paper. For more species (Gilpin, 1975), such competitive oscillations will be caused by the same mechanism, non-transitivity in competitive dominance.

The configuration of nullclines in Figure 5.11 corresponds to a community matrix where the competition coefficients of the band above the diagonal are bigger than the other entries of the matrix, i.e. \(a_{12} > a_{11}, a_{13}; a_{23} > a_{21}, a_{22}; a_{31} > a_{32}, a_{33}\). It turns out that such a structure corresponds with the prediction of oscillations around the internal equilibrium (section 5.5.3). Were the diagonal elements the biggest ones, we would have a configuration of nullclines where each species can invade (Fig. 5.7) and a locally stable community equilibrium (section 5.5.3). Thus the community matrix determines the stability of all equilibria (internal, borders, monocultures) and the global dynamics of the system.

Non-transitivity can also explain the competitive oscillations in resource competition models (Huisman and Weissing, 1999, 2001, 2002; Revilla and Weissing, 2008, Chaper 2, 3, 4). Consider three species, and three essential resources, in which species \(i\) tends to be more limited by \(i\). Using graphical analysis for each of the resource planes as in Figure 5.4, it is possible to show that when each species tends to consume more of the resource for which it has intermediate requirements, the monocultures will be externally stable against one invader and unstable against the other, and that there would not be any 2-species equilibrium. In consequence the system oscillates. A consumption matrix \(C\) (Tilman model) or \(\hat{F}\) (Quota model) describing this consumption pattern will be a consumption matrix associated with oscillations around the internal equilibrium (section 5.5.3). Like in the Lotka-Volterra model, this is an example where the local stability of the internal equilibrium is related to the global dynamics of the system.

Thus, in all the three models, the structure of the interaction matrix \(M\) (\(A, C\) or \(\hat{F}\)), not only determines the existence of internal equilibria and its local dynamics, it also plays a role the determination of the global dynamics. The extent of this role, however, has its limitations. With three species there are simply too many equilibrium configurations, and thus many possible global dynamics. For example in the Lotka-Volterra model Zeeman (1990) compiled a list of 33 phase plane configurations, some of them shown in Figure 5.12.

122
Figure 5.11: Competitive oscillations in the Lotka-Volterra model. In this arrangement of nullclines, 2-species equilibria do not exist. If we consider species pairs: species 1 excludes species 2, species 3 excludes species 1 and species 2 excludes species 3. This results in a sequence of species replacement $1 \rightarrow 3 \rightarrow 2 \rightarrow 1$ that drives the oscillations. There is an internal equilibrium, the intersection point of the three nullclines. If the internal equilibrium is stable, the system achieves a stable 3-species equilibrium coexistence, but if the equilibrium is unstable the oscillations will develop into limit cycles or heteroclinic cycles. Figure taken from Gilpin (1975).
Figure 5.12: The dynamics of the three-species Lotka-Volterra model can be represented in a triangular phase plane or “simplex”. The vertex of the triangles represent monoculture equilibria, the intersection of a trajectory and an edge represents a border equilibrium, and the community equilibrium lies in the interior. Closed circles denote stable equilibria, open circles denote unstable equilibria, and the absence of a circle denote saddle points. This figure shows some of the 33 possible equilibrium configurations. Taken from Zeeman (1990).
Case 27 for example, describe the dynamics associated with the nullplane configuration in Figure 5.11 because there is a rock-paper-scissors oscillation involving the monocultures, and an oscillatory dynamics around the community equilibrium. If the internal equilibrium is stable the oscillations dampen out, but if it is unstable the oscillations persist in the form of limit cycles or heteroclinic cycles. However, cases number 32 and 33 do not display a rock-paper-scissors oscillation involving the monocultures, even though there are oscillations around the community equilibrium. In these two cases the oscillations are transient.

The same complications occur in resource competition models (Baer et al., 2006, Chapter 4), plus more. In the Tilman model, the limiting resource of a species at the community equilibrium may not be the same in a border equilibrium, but the consumption matrix $C$ is fixed for all equilibria. In case of the Quota model, we have that in addition the consumption matrix $F$ can have different configurations at the different equilibria. In addition, the three models can display multiple limit cycles (Hofbauer and So, 1994; Baer et al., 2006, Chapter 4). All these details tell us that the prediction of global dynamics in terms of the community matrix $(A)$ or the consumption matrix $(C, \hat{F})$ must be regarded as statistical rules or “rules of thumb”.

5.6.2 Multiple stable states

In the 2-species Lotka-Volterra model the only instance of alternative stable states corresponds to the case where both monocultures are externally stable (Fig. 5.24). In the 2-species resource competition model, and as long as the nullclines (or quasi-nullclines) in resource space have simple shapes (i.e. they intersect only once), we have the same situation (Fig. 5.23). In these simple cases, the single community equilibrium sits in the boundary of the attraction basins of both monocultures.

It takes very little to change from this simple picture to a complex one. In the case of the Lotka-Volterra model, the inclusion of a third species increases the number of border equilibria. These border equilibria vary in their external and internal stability characteristics, and the combined effect of their attractions and repulsions results in a complex global dynamics in which the realization of coexistence itself becomes dependent on the initial conditions. An example is case 26 in the classification of Zeeman (1990), shown in Figure 5.12, depending on the initial conditions the system may converge to the community equilibrium state of high diversity, or to the monoculture of one of the species and low diversity.

Given a set of $n$ species, the number of border equilibria having $k = 2$ to $n-1$ species in the Lotka-Volterra model can be as high as

$$\sum_{k=2}^{n-1} \frac{n!}{k!(n-k)!}$$

which increases rapidly with $n$. For example $n = 3$ can have 3 border equilibria, $n = 4$ can have 10, and $n = 5$ can have 27. As the number of species considered increases, the diversity of a community becomes increasingly dependent on the initial conditions.

The situation for resource competition models is even more complex. Only in the simplest case of substitutable resources and linear resource dependence, we can have nullclines in
Figure 5.13: A possible configuration of nullclines in species space (the $\dot{N}_i = 0$), for two species competing for four perfectly essential resources. (a) The system has three alternative stable states, the monocultures and the community equilibrium. Coexistence depends on the initial conditions. (b) The system has two alternative stable states of coexistence. Depending on the initial conditions, the species coexist as community in which species 1 is numerically dominant, or as a community in which species 2 is numerically dominant. Figures taken from Zhang (1991).

species space that resemble those of the Lotka-Volterra model (5.15), and we can expect a similar amount of border equilibria. In more general cases however, the nullclines in species space are nonlinear like in (5.17). According to Zhang (1991), when two species compete for more than two essential resources, there can be than one 2-species equilibrium, as shown in Figure 5.13. At each of these equilibria a species may be limited by the same resource or by a different one. If we extrapolate these results to $n$ species and $m$ resources, we conclude that the number of border equilibria is much higher than in the $n$-species Lotka-Volterra model. Thus the influence of the initial conditions on the possibilities of coexistence are much more important.

5.7 Conclusions and Implications

The Lotka-Volterra (5.1), Tilman (5.2) and Quota (5.3) models, can be formulated in terms of any number of species and resources, but most of time they are studied for the special case of only two species and one or two resources. However, the insights from the graphical analysis of these low-dimensional cases can be extrapolated, to the most interesting cases of many species and many resources. As a result of such extrapolation, we found that the same rules regarding the existence of equilibria and local stability apply to all of these models. The ubiquitous “cone rule” for example, applies simply because the effect of any species upon other species or resources is independent of the presence of the other species (this however, would not be the case if higher order interactions take place (Abrams, 1983; Morin et al., 1988)).
In all the three models it is possible to define an interaction matrix $M$. In the Lotka-Volterra model such matrix, the community matrix, is the collection of the direct effects one species on all the others. In both resource competition models this is the consumption matrix, and it contains the indirect effects of one species on all the others via the shared resources. The interaction matrix determines the feasibility of the equilibrium and important aspects of its stability. In cases where the number of species and resources is “low”, like three species, we can rely on the structural properties of this interaction matrix to make some predictions about the dynamics in the proximity of the equilibrium and the global dynamics of competition. Thus for example, if each species tends to be the highest (comparatively) consumer of its most limiting resource, intra-specific competition (self-regulation) is more intense that inter-specific competition, a situation that facilitates the assembly of a community via invasion, and promotes the global stability of the community. On the contrary, if each species tends to be the lowest consumer of its most limiting resource, intra-specific competition is weak compared with inter-specific competition, the community will be globally unstable and coexistence via invasion unlikely.

Between the extremes of strong intra-specific competition and strong inter-specific competition lies an extensive region for which it is difficult to say that intra- and inter-specific competition are comparable, on average. It may be in fact that the intra- and inter-specific effects are comparable in magnitude, but it is also likely that each species tends to interact more intensely with a some species and weakly with with rest. This last alternative can lead to non-transitive relationships of competitive dominance, like in the game of Rock-Paper-Scissors. Non-transitivity can generate oscillations and chaos (May and Leonard, 1975; Gilpin, 1976; Huisman and Weissing, 1999, 2002; Revilla and Weissing, 2008), and these oscillations even if transitory, may allow the coexistence of many species on few resources or delay the realization of competitive exclusion. The feasibility of such competitive oscillations rest upon the existence of trade-offs in competitive abilities (Huisman et al., 2001).

But as the number of species and resources increases, our ability to predict the global dynamics in terms of the structure of the interaction matrix becomes very limited. As the number of species and resources increases, the number of equilibrium configurations increases rapidly, the identity of the limiting resources becomes more variable among the different equilibria (Zhang, 1991), and the consumption patterns also vary among equilibria (Chapter 4). We hypothesize that unless inter-specific competition is very weak or very strong (or intra-specific competition very strong or very weak), multispecies competition has a highly unpredictable global dynamic, with strong dependence on the initial conditions (even when chaotic dynamics does not occur).

Another important conclusion of the present work is that given some reasonable assumptions, it is possible to transform the Tilman model (5.12) into a model that is more (5.15) or less (5.17) similar to the classic Lotka-Volterra model. This transformation can also be done for other simple resource competition models (e.g. MacArthur, 1969, 1970) using different assumptions. In these transformations the general goal is to obtain a set of equations with the form:

$$\frac{dN_i}{dt} = N_i G_i(N_1, \ldots, N_n)$$

(5.29)
Appendix A: The chemostat assumption

where the per capita rate function $G_i$ can adopt any shape, simple or complicated, as long as it is a decreasing function of the population densities ($\frac{\partial G_i}{\partial N_k} < 0$). Equation (5.29) is the Generalized Lotka-Volterra model (GLV), of which the classical Lotka-Volterra model is just a special case. Other examples include the $\theta$-logistic competition model of Ayala et al. (1973) and the energy and interference based models introduced by Schoener (1976). The interesting thing about GLV’s is that almost any kind of complex dynamics can be expected if the number of species is five or more (Smale, 1976). An important implication is that if two different resource competition models can be transformed into a GLV, they can in principle display similar complex dynamics, even if their mechanistic underpinnings are different.

Appendix A: The Chemostat Assumption

Let us assume that in both resource competition models (Tilman and Quota), the dynamics takes place in a chemostat. In such scenario the per capita loss rates of the populations are equal to the flow rate of the chemostat, $m_i = D$. Given enough time the total amount of resource $j$, attains a steady-state value, irrespective if an equilibrium has been attained or not. This allows us to substitute the differential equations of the resources by algebraic relationships, reducing the dimensionality of the system.

In the Tilman model the total amount of resource $j$ at time $t$, $T_j(t)$, is the sum of the external resource concentrations and the resources sequestered by the populations:

$$T_j(t) = R_j(t) + \sum_{i} c_{ji} N_i(t) \quad (5.30)$$

Taking time derivatives on both sides we get

$$\frac{dT_j}{dt} = \frac{dR_j}{dt} + \sum_{i} c_{ji} \frac{dN_i}{dt}$$

and replacing the expressions for $dR_j/dt$ and $dN_i/dt$ given in the model (5.2), the equation above is:

$$\frac{dT_j}{dt} = D(S_j - R_j) - \sum_{i} c_{ji} \mu_i N_i + \sum_{i} c_{ji} (\mu_i - D) N_i$$

The last equation can be integrated from $t = 0$ to $t = \tau$, which results in $T_j(\tau) = S_j + [T_j(0) - S_j]e^{-D\tau}$. As $\tau \to \infty$ the left-hand side of (5.30) converges to $S_j$, and the concentration of the external resources can be expressed as:

$$R_j = S_j - \sum_{i} c_{ji} N_i \quad (5.31)$$
Appendix B: The Jacobian matrix of the quota model

Equation (5.31) is a mass balance constraint. In the Quota model we can also derive a mass balance constraint. In the Quota model, the concentration of resource \( j \) stored by a species is equal to its quota for that resource times its population density. Thus the total concentration of resource \( j \) is:

\[
T_k(t) = R_k(t) + \sum_i Q_{ki}(t)N_i(t)
\]  

(5.32)

Taking time derivatives on both sides we get:

\[
\frac{dT_j}{dt} = \frac{dR_j}{dt} + \sum_i Q_{ji} \frac{dN_i}{dt} + \sum_i N_i \frac{dQ_{ji}}{dt}
\]

and replacing the definitions of \( \frac{dR_j}{dt}, \frac{dQ_{ji}}{dt} \) and \( \frac{dN_i}{dt} \) from (5.3) we obtain:

\[
\frac{dT_i}{dt} = D[S_j - R_j] - \sum_j f_{ji}N_i + \sum_i Q_{ji} (\mu_i - D)N_i + \sum_i N_i (f_{ji} - \mu_i Q_{ji})
\]

\[
\frac{dT_i}{dt} = D[S_j - (R_j + \sum_i Q_{ji}N_i)]
\]

\[
\frac{dT_i}{dt} = D[S_j - T_j]
\]

And like in the Tilman model, the total concentration of resource \( T_j \) in (5.32) converges to \( S_j \) given enough time, and the concentration of external resources is given by:

\[
R_j = S_j - \sum_i Q_{ji}N_i
\]  

(5.33)

APPENDIX B: THE JACOBIAN MATRIX OF THE QUOTA MODEL

In order to obtain a simplified expression for the jacobian of the Quota model, we make the following assumptions:

1. The number of species equals the number of resources.
2. Resources are perfectly essential according to equation (5.5).
3. Competition takes place in a chemostat, thus the mass balance constraint (Appendix A) applies. Thus, the differential equations of the external resources \( R_j \) can ignored, and \( R_j \) be substituted by (5.33).
4. The dynamics of the quotas are much faster than the dynamics of external resource concentrations and population densities (Di Toro, 1980). As a consequence, the quotas will be in a quasi-steady-state, i.e. they satisfy \( \frac{dQ_{ji}}{dt} \approx 0 \), even if the system is far from the equilibrium. In consequence, the differential equations of the quotas can be substituted by:

\[
f_{ji}(R_j) \approx \mu_i \dot{Q}_{ji}
\]  

(5.34)
Appendix B: The Jacobian matrix of the quota model

where $\tilde{Q}_{ji}$ is the steady state (not equilibrium!) quota.

These assumptions result in a reduced system formed by the $n$ differential equations (5.33). The jacobian matrix of this subsystem has elements

$$\frac{\partial \dot{N}_i}{\partial N_k} = N_i \frac{\partial \mu_i}{\partial N_k} + (\mu_i - D) \frac{\partial \dot{N}_i}{\partial N_k}$$

Since resources are perfectly essential $\mu_i$ is a univariate function in the vicinity of the equilibrium. If species $i$ is limited by resource $i$, then $\mu_i = \mu_i(Q_{ii})$ and by the chain rule

$$\frac{\partial \dot{N}_i}{\partial N_k} = N_i \frac{\partial \mu_i}{\partial Q_{ii}} \frac{\partial Q_{ii}}{\partial \dot{R}_i} \frac{\partial \dot{R}_i}{\partial N_k} + \delta_{ik}(\mu_i - D)$$

where $\delta_{ik}$ is 1 if $i = k$ and 0 if $i \neq k$. Using (5.33) with $Q_{ik} = \tilde{Q}_{ik}$ we have $\partial \dot{R}_i/\partial N_k = -\tilde{Q}_{ik}$ and replacing $\tilde{Q}_{ik}$ with (5.34)

$$\frac{\partial \dot{N}_i}{\partial N_k} = -N_i \frac{\partial \mu_i}{\partial Q_{ii}} \frac{\partial Q_{ii}}{\partial \dot{R}_i} \frac{\dot{R}_i}{\mu_k} + \delta_{ik}(\mu_i - D)$$

In the equilibrium $\mu_i = \mu_k = D$, and the last equation becomes

$$\frac{\partial \dot{N}_i}{\partial N_k} = -\frac{\dot{N}_i}{D} \frac{\partial \mu_i}{\partial Q_{ii}} \frac{\partial Q_{ii}}{\partial \dot{R}_i} \frac{\dot{R}_i}{\mu_k}$$

(5.35)

where the * indicates evaluation of variables and derivatives at the equilibrium. Equation (5.35) can be written in matrix form as

$$J = -D\hat{\Phi}$$

$J = \{\frac{\partial N_i}{\partial N_k}\}$ is the jacobian matrix of the reduced system. $D = \text{diag} \left\{ \frac{N_i}{D} \frac{\partial \mu_i}{\partial Q_{ii}} \frac{\partial Q_{ii}}{\partial \dot{R}_i} \right\}$ is a diagonal matrix with positive elements in the diagonal. And $\hat{\Phi} = \{f_{ik}(\hat{R}_i)\} = \{f_{ij}(\hat{R}_j)\}$ is the consumption matrix.