Multispecies Resource Competition

Tomás Revilla

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CONTENTS

SAMENVATTING

Deze dissertatie spitst zich toe op de theoretische studie van competitie over grondstoffen tussen een groot aantal soorten. Om dit proces te bestuderen maken wij gebruik van het zogeheten 'nutriëntenopslagmodel', dat gebaseerd is op competitie tussen algensoorten. Dit model is zowel relevant voor de ecologie van plankton als het gebied van de ecologische stoichiometrie. Eerder onderzoek beschouwde steeds maar een klein aantal soorten, wat in sterk contrast is met de honderden soorten die normaal aanwezig zijn in ecologische gemeenschappen.

Dankzij analytische en numerieke methoden kunnen we concluderen dat competitiemodellen met grote aantallen soorten en nutriëntenopslag kunnen leiden tot rijke en gecompliceerde dynamica, zoals oscillaties, chaos en de coëxistentie van veel soorten op slechts een aantal grondstoffen. Voor een groot deel is dit het gevolg van de specifieke 'trade-offs' in de consumptiepatronen van soorten, wat ook opgaat voor de wat minder realistische modellen van competitie over grondstoffen. Daarbij laat de vergelijking met andere modellen zien dat er algemene regels zijn die de competitiedynamica tussen vele soorten bepalen en dat dergelijke regels onafhankelijk zijn van de onderliggende mechanismen. Een dergelijke robuustheid is goed niews voor een niche-gebaseerd perspectief op de gemeenschapsecologie, waarin soortsdiversiteit het gevolg is van soortseigenschappen. Echter, de toevoeging van meer mechanistische details, zoals nutriëntenopslag, laat zien dat de uitkomst van competitie zeer lastig te voorspellen wordt, omdat een zeer kleine verandering in de biologische parameters of begincondities al kan leiden tot een andere uitkomst, variërend van coëxistentie in een ecologisch evenwicht, coëxistentie buiten een ecologisch evenwicht, chaotische dynamiek of competitieve uitsluiting. De implicatie van deze contrasterende resultaten is dat competitieve gemeenschappen zich consistent kunnen gedragen vanuit een statistisch oogpunt, maar juist niet wanneer ieder geval afzonderlijk wordt bekeken.

SUMMARY

The main focus of this thesis is the study of competition for resources among many species, from a theoretical position. This is accomplished using the "nutrient storage model" of algal competition. This model is of considerable relevance in plankton ecology and in the field of ecological stoichiometry. Unfortunately, previous research considered just a few species in contrast with the hundreds that are present in real communities.

Thanks to analytical and numerical approaches, we can conclude that multispecies competition models with nutrient storage display a rich and complicated dynamics including oscillations, chaos and the coexistence of many species on few resources. To a great extent, the different dynamics are the consequence of specific trade-offs in the species consumption policies, which is also the case for less realistic models of resource competition. In addition, the comparison with other models reveal that there are general rules governing the multispecies dynamics, and such rules are independent of the underlying mechanisms. This robustness is good news for a niche based perspective of community ecology, in which diversity is the consequence of the species properties. However, the addition of more mechanistic detail, like the introduction of nutrient storage, reveals that predictability becomes rather difficult, not to say pointless, because very small variation in biological parameters or initial conditions can lead to equilibrium coexistence, nonequilibrium coexistence, chaotic dynamics, or competitive exclusion. The implication of these contrasting results is that competitive communities may behave in a consistent way from a statistical perspective, but not in a case by case basis.

RESUMEN

El objeto principal de esta tesis es el estudio teórico de la competencia por recursos entre muchas especies. Esto se logra usando el "modelo de almacenamiento de nutrientes" para algas. Este es un modelo muy importante en la ecología del plancton y en el campo de la estequiometría ecológica. Desafortunadamente, hasta ahora los estudios han considerado la interacción de apenas unas pocas especies, en contraste con las muchísimas que se presentan en comunidades naturales.

Gracias a métodos analíticos y numéricos, podemos concluir que la competencia entre muchas especies con almacenamiento de nutrientes presenta una dinámica muy variada y compleja que incluye oscilaciones, caos, y la coexistencia de muchas especies sobre pocos recursos. En gran parte, las diferentes dinámicas son la consecuencia de trueques específicos en los patrones de consumo de las especies, lo cual también sucede en modelos menos realistas de competencia por recursos. Además, la comparación con otros modelos muestra que existen reglas generales que gobiernan la dinámica competitiva, y que tales reglas son independientes de los detalles microscópicos. Este resultado robusto esta en linea con la perspectiva de nichos de la ecología de comunidades, donde la diversidad es el resultado de las propiedades de las especies. Empero, al añadir mas detalles mecanísticos, como el almacenamiento, nuestra capacidad de predecir se hace cada vez mas difícil, por no decir inútil, dado que las variaciones mas pequeñas en los parámetros biológicos pueden llevar a la coexistencia estable, coexistencia alejada del equilibrio, caos, o la exclusión competitiva. Todo esto implica que las comunidades competitivas se comportan de una manera consistente desde una perspectiva estadística, pero no en casos particulares.

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[1] Theoretical Biology Group

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[2] Laughing Out Loud

[3] From the Holy Trinity: CareX, Mamamini (furniture) and Aldi (food).

PREFACE

This dissertation is the result of a PhD project that was part of the research program "The emergence of biocomplexity: a steady state between physical and biotic evolution?". This program was initiated by Prof. H. Olff (Community and Conservation Ecology Group) and Prof. F.J. Weissing (Theoretical Biology Group) and funded by the Computational Life Sciences initiative of the Dutch Science Foundation (NWO). The main goal of the program was to identify emergent properties in complex ecosystems and to understand these properties on the basis of interactions at lower levels of organization. The working hypothesis was that despite their inherent complexity, populations and communities must reflect the restrictions imposed by physico-chemical laws, which affect all ecological and evolutionary processes. Hopefully, these effects can to a large extent be captured by relatively simple and general functional relationships, for example scaling laws.

The research program was divided in two projects. The first project focused on the ecological implications of spatial complexity, such as the spatial patterns induced by the feedback between the distributions of resources and their consumers. I was in charge of the second project, aimed at unraveling the ecological implications of compositional complexity, i.e. the intricacies induced by the fact that typically a huge number of species interact in even simple ecosystems. This involved studying the dynamics of multi-species interactions, in particular resource competition. Throughout I neglected the complications of spatial complexity (which were covered by the first project) and focused on well mixed environments.

A major problem to be faced by a multi-species approach is the large number of model parameters. Not surprisingly, the dynamics of multi-species interaction strongly reflects the assumptions on these parameters (e.g. Huisman et al., 2001). To arrive at general insights, it is therefore crucial to have a good underpinning for the choice of parameters, preferably by deriving these parameters from general underlying principles, like physical and chemical laws or physiological and stoichiometric constraints. However, such principles can only be applied in mechanistic models of ecological interactions, where all parameters have a clear-cut interpretation in terms of a priori measurable biological quantities. As a first step, I therefore decided to base my modeling strategy not on the semi-mechanistic models that are typically being used in this field, but on the class of storage models, which is more firmly rooted in physiology and stoichiometry. Although this class of models is inherently more complicated than the traditional ones, I hoped that the increased complexity could later be reduced by the incorporation of simplifying physiological and stoichiometric principles.

Before thinking of such simplification, I first had to get firm insights into storage models and, in particular, into storage models of interspecific competition. It turned out that the analysis of these models is even more intricate than anticipated. In the end, I spent most of my thesis work on the analysis of multi-species competition in the presence of resource storage. The results are documented in this thesis, and I hope that I can convince the reader that these models are worth a study of their own. This thesis will demonstrate that multi-species resource competition, with and without storage, is governed by a few general rules that seem quite robust and not dependent on modeling details. Time did not permit to attack the more general problem of the implications of compositional complexity in contexts beyond competition for abiotic resources like mineral nutrients or light. In the final chapter of this thesis (‘Afterthoughts’) I will speculate a bit whether, and to what extent, my insights on resource competition can be extrapolated to more general ecological scenarios.

1

INTRODUCTION

1.1 ECOLOGICAL COMMUNITIES

Ecological communities are complex systems, consisting of many components at different levels of organization (individuals, populations, guilds). The components of a community interact in multiple, often non-linear ways, across different temporal and spatial scales. Yet, despite this complexity, communities display a number of consistent emergent features, like patterns in the structure of food webs, biomass and energy pyramids, species-abundance distributions, productivity patterns, to name a few (Begon et al., 2006).

Most ecological models ignore this complexity by focusing on highly simplified systems with few components and little or no spatial structure. This is not surprising, because complex ecological scenarios are difficult to model in a realistic way; a comprehensive analysis of complex models is often not feasible; and the results of the analysis can often not be extrapolated and, hence, does not lead to general insights. As a consequence, ecological theory has to face a major problem: only relatively simple scenarios can be analyzed in a robust and comprehensive manner, but it is far from obvious whether, and to what extent, the conclusions from simple scenarios can be extrapolated to the complexity of real ecosystems.

One possible way to address this problem consists in abstracting the complexities at each level of organization into emergent properties, expressed as universal relationships or rules. Then we could use these rules to justify a reduction in the number of degrees of freedom at higher levels of organization, making their analysis easier. This is, for example, the approach taken by the Metabolic Theory of Ecology (Brown et al., 2004), which is based on the assumption that the complexities of individual metabolism can be summarized in simple equations (a combination of Kleiber's law and the Arrhenius equation), and that these metabolic principles can be expanded to obtain equally simple equations describing all kinds of biological rates, such as rates of increase, mortality and energy flow. Another example is the field of Ecological Stoichiometry (Sterner and Elser, 2002), which attempts to explain individual composition (and, subsequently, population and ecosystem structure) on the basis of compositional (stoichiometric) rules governing the chemical transformation of resources into energy and biomass.

The idea that simple laws governing processes at lower levels of organization can help to understand the complexity at higher levels of organization inspired the initiation of this thesis. However, when I started to incorporate the simplest physiological assumptions in models of competitive interactions, I soon had to realize that already the simplest scenario of 2-species competition presented highly intricate technical problems. During the analysis, it turned out that solving these problems is both ecologically relevant and mathematically rewarding and, hence, worth a study in itself. I therefore decided to dedicate my thesis to unveil the rules governing the dynamics of multispecies competition in models that explicitly address the physiology of resource storage.

1.2 COMPETITION

Figure 1.1 shows a detailed representation of a real food web. The web is structured as a series of trophic levels corresponding to vertical layers. This vertical axis of inter-

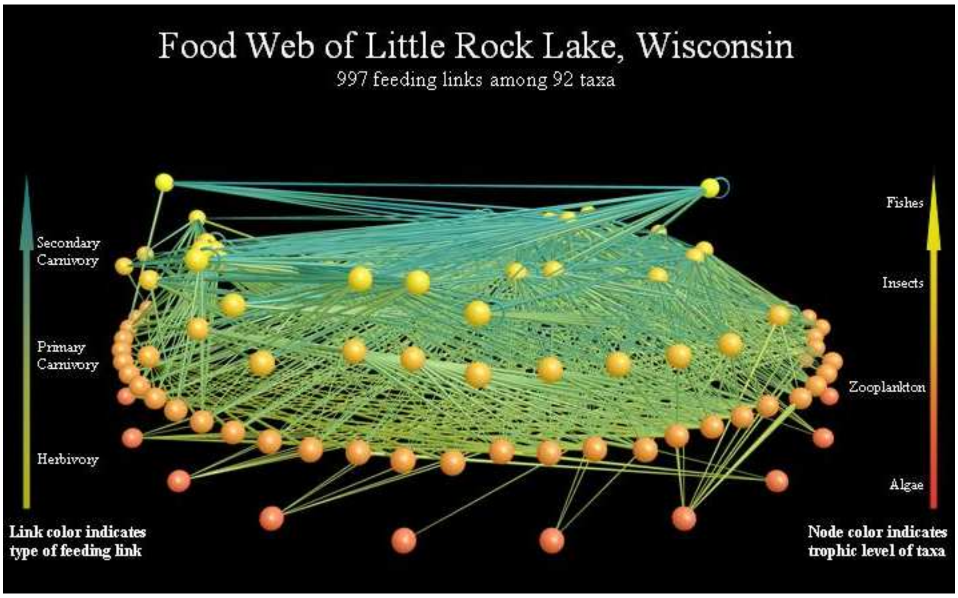

Figure 1.1: Food web of an aquatic ecosystem studied by Martinez (1991).

action, the sequence of consumer-resource interactions, is the subject of many theories of community organization (Hairston et al., 1960; Carpenter et al., 1985; Cohen et al., 1990; Williams and Martinez, 2000). But the same food web also illustrates the existence of another important axis of interaction: many species belonging to a trophic level share common resources, and the finiteness of such resources leads to competition. Competition is experienced by the species mainly in two ways. As implied by the food web diagram, species interact indirectly through the exploitation of resources that are important for their competitors; we call this form of interaction exploitative competition or resource competition. Organisms can also fight more directly for the access to resources, either through physical contact, like in many animals, or by poisoning each other (allelopathy) as some plants do. In the latter case we talk about interference competition. Whatever the mechanism, because of its potential to determine which and how many species can coexist in a community (Begon et al., 2006), competition is considered a fundamental process shaping the structure and functioning of ecological systems at all levels of organization (Grover, 1997).

1.2.1 *The Lotka-Volterra approach*

Broadly speaking, competition can be defined as an interaction in which the survival and reproduction of individuals is negatively affected by the presence of other individuals. Traditionally, ecological theory approaches competition from its effects on populations. For a long time, competitive interactions were modeled by means of Lotka-Volterra equations (Lotka, 1925; Volterra, 1926), which in case of two species take the form:

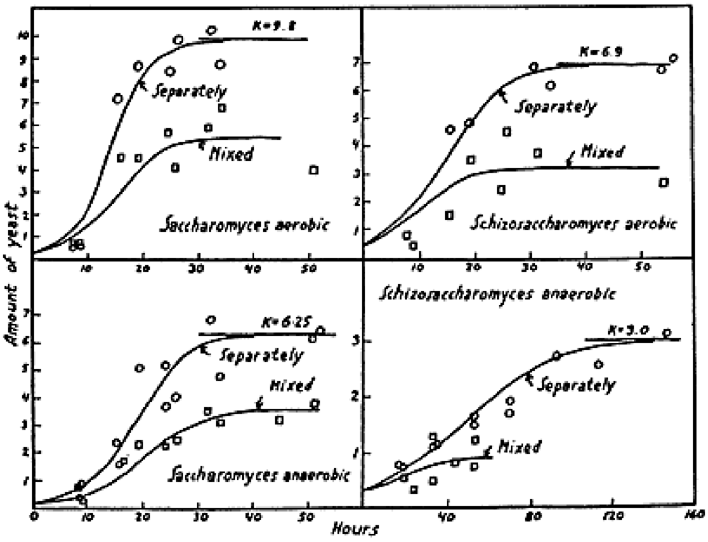

Figure 1.2: Competition between the yeast *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* under aerobic and anaerobic conditions. If the species grow separately, they attain stable population densities. If they are mixed, competition causes both species to grow slower and to attain lower equilibrium densities (if they coexist as in this experiment). The growth curves were fitted according to the Lotka-Volterra model (1.1). Taken from Gause (1934).

$$\begin{aligned} \frac{dN_1}{dt} &= N_1\{r_1 - a_{11}N_1 - a_{12}N_2\} \\ \frac{dN_2}{dt} &= N_2\{r_2 - a_{22}N_2 - a_{21}N_1\} \end{aligned} \tag{1.1}$$

Here N_i is the population density of species $i = 1, 2$. In the absence of its competitor, the dynamics of each species follows the logistic model, where r_i is the intrinsic growth rate, i.e. the net *per capita* growth rate at low populations densities, when competition is negligible. As the population density increases, intra-specific competition slows down the rate of growth until an equilibrium density or "carrying capacity" is achieved (Fig. 1.2). In the presence of the other species, the growth rate also slows down due to inter-specific competition, and the final density ends below the carrying capacity. The intensity of competition is assumed to be proportional to the species densities, and the proportionality constant is called the *competition coefficient*. Thus, the intra-specific competition coefficient a_{ii} measures the effect of species i on itself, and the inter-specific competition coefficient a_{ik}measures the effect of species k on species i.

According to standard Lotka-Volterra theory, competition has four distinct outcomes: 1) species 1 always outcompetes species 2, 2) species 2 always outcompetes species 1, 3) depending on the initial conditions either species 1 or species 2 drives its competitor to extinction, and 4) both species coexist. In all these cases, the system reaches an equilibrium state, and complex dynamics like oscillations do not occur. Stable coexistence of the two species requires that $a_{11}a_{22} > a_{12}a_{21}$, which can be interpreted as: intra-specific competition is stronger than inter-specific competition (Gilpin and Justice, 1972; Case, 2000). One of the major drawbacks of Lotka-Volterra theory is that it is not mechanistic, in the sense that the competition coefficients can not be derived from first principles. As a consequence, Lotka-Volterra models are not predictive: in order to predict the outcome of competition, we need to know the competition coefficients, but the competition coefficients can only be derived from the observed trajectory of competition.

1.2.2 *Resource Competition models*

In many cases competitors do not interact by coming in direct contact. Instead, they affect each other indirectly by exploiting common resources, like nutrients, light or other organisms (e.g. in Fig. 1.1). One of the most studied scenarios involves competition between two species for two resources, according to the following model:

$$\begin{aligned}
\frac{dN_1}{dt} &= N_1\{\mu_1(R_1, R_2) - m_1\} \\
\frac{dN_1}{dt} &= N_2\{\mu_2(R_1, R_2) - m_2\} \\
\frac{dR_1}{dt} &= D(S_1 - R_1) - f_{11}N_1 - f_{12}N_2 \\
\frac{dR_2}{dt} &= D(S_2 - R_2) - f_{21}N_1 - f_{22}N_2
\end{aligned} \tag{1.2}$$

where N_i is again the density of species i, while R_j is the concentration of resource j. $\mu_i(R_1, R_2)$ denotes the resource dependent *per capita* growth of species i, m_i is the *per capita* loss rate of species i due to mortality and other causes (assumed to be constant), and f_{ji} is the per capita consumption rate of resource j by species i. The resources are supplied from an external source with a flow rate D and a supply concentration S_j, and in the absence of the consumers they disappear from the system at the same flow rate.

According to this model, the possible outcome of resource competition is comparable to that of the Lotka-Volterra model: 1) species 1 wins, 2) species 2 wins, 3) both species coexist, or 4) depending on the initial conditions, one of the two species wins. Again, the competitive dynamics will always lead to equilibrium, and the condition for coexistence can be interpreted by saying that intra-specific competition has to be stronger than inter-specific competition (Chapter 5). In contrast to Lotka-Volterra theory, however, the outcome of competition can now be predicted from first principles of consumer-resource interactions. For example, we can grow each species alone in monoculture, determine their resource requirements and consumption characteristics, and then use this information to produce *a priori* predictions concerning the environmental circumstances allowing both species to coexist (Fig. 1.3).

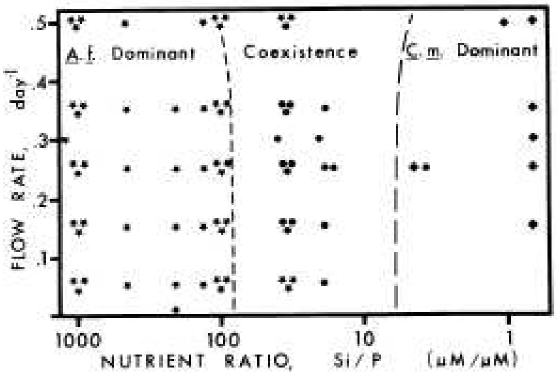

Figure 1.3: Competition between the algae *Asterionella formosa* (A.f.) and *Cyclotella meneghiniana* (C.m.) for two mineral resources, silica (Si) and phosphorous (P). The resource competition equations (1.2) can be used to predict the resource supply ratios ($S_1/S_2 = \text{Si/P}$) for which A.f. wins (left region), C.m. wins (right region), or both species coexist (middle region). These predictions can be contrasted with the results of experiments in which A.f. wins (★), C.m. wins (♦), or both coexist (●). Taken from Tilman (1977).

1.3 MULTISPECIES COMPETITION

It is well known that predator-prey interactions can be dynamically complex, often leading to oscillations and chaos. In fact, the textbook examples for oscillations in ecological systems are generated by predator-prey interactions, like the lynx-hare cycles (Begon et al., 2006) or the oscillations in Gause's (1934) laboratory experiments. On the other hand, it is a common perception that that competitive interactions lead to much simpler dynamics, typically leading to an equilibrium state (e.g. Fig. 1.2, Gause (1934); Tilman (1977)).

This perception is perhaps caused by the fact that most theoretical and empirical studies have considered the special case of two-species competition, where indeed only equilibrium outcomes are possible. As soon as more than two species are competing with each other, the situation may be fundamentally different. An extensive body of theory indicates that already in the case of only three species competitive interactions can generate complex non-equilibrium dynamics, like oscillations and chaos May and Leonard (1975); Gilpin (1975); Hofbauer and Sigmund (1988); Zeeman (1990); Huisman and Weissing (1999). In case of resource competition, the competitive dynamics is the result of trade-offs in resource requirements and consumption patterns (Huisman and Weissing, 2001; Huisman et al., 2001). Qualitatively, the outcome of competition can be predicted by the following "rules of thumb" (Huisman and Weissing, 2001):

1. If each species tends to consume most of the resources for which it has the highest requirements, the system will tend to equilibrium where as many species will coexist as there are limiting resources.

2. If each species tends to consume most of the resources for which it has the lowest requirements, competitive exclusion is to be expected. It depends on the initial conditions which species will outcompete all its competitors.

3. If each species tends to consume most of the resources for which it has intermediate requirements, competitive oscillations are to be expected. Even in a homogeneous environment, many more species can stably coexist than there are limiting resources.

Competitive oscillations have been proposed as a possible solution of the "paradox of the plankton" (Hutchinson, 1961), the observation that hundreds of algal species can coexist on a handful of mineral resources. Whether this is indeed the case is, however, not yet clear. In my thesis I will consider one potential problem, namely the fact that the resource competition model 1.2 is not really realistic when applied to algal competition. By assuming that algal growth is directly related to the external resource concentrations R_j, the model neglects important aspects of algal physiology. It is much more realistic to assume that algal growth reflects the concentrations of stored nutrients, while nutrient uptake is largely independent of algal growth (Ducobu et al., 1998). For this reason, competition models including resource storage have been developed (Droop, 1973; Turpin, 1988; Grover, 1997), which include both the physiology of resource uptake and the physiology of algal growth in a coherent framework. These storage models are the focus of my thesis.

It is not immediately obvious if storage models promote oscillations. On the one hand, such models contain many more variables and more non-linearities than standard competition models. This makes them good candidates for displaying complex dynamics. On the other hand, the delays caused by the decoupling of uptake and growth might have the effect of buffering and suppressing oscillations (Huisman and Weissing, 2001).

Unfortunately, the study of resource storage models has been restricted to very simple cases: a single species growing on a single resource (Lange and Oyarzun, 1992; Oyarzun and Lange, 1994), a single species growing on several limiting resources (Legovic and Cruzado, 1997; de Leenheer et al., 2006), many species competing for a single resource (Smith and Waltman, 1994), and two species competing for two resources (Turpin, 1988; Li and Smith, 2007). This restriction is not surprising, since the computational and mathematical study becomes extremely difficult even for low-dimensional scenarios. Yet, progress is needed in this field, since storage models are at center stage in some major new developments in ecological theory, most notably the field of ecological stoichiometry (Sterner and Elser, 2002; Klausmeier et al., 2008). They may also be crucial for the Metabolic Theory of Ecology, since they allow insights into the upscaling of metabolic principles from the individual to the population and even ecosystem level (Hall et al., 2008).

1.4 THIS THESIS

The primary focus of this thesis is the study of multispecies resource competition in systems where resource uptake is decoupled from resource-limited growth. I try to get some general insights into the dynamics of such storage models (also called 'quota models') and to answer the question whether, and to what extent, the dynamics and the competitive outcome in storage models differs from those of the more classical models of multispecies competition.

Chapter 2 reports on an extensive simulation study, where the dynamics of competition in a storage model is systematically compared with that of a 'corresponding' model without storage. As explained above, the dynamics of competition in the model without storage can be captured by a few rules of thumb that are based on the relationship between resource requirements and resource consumption. In such simple models, resource requirements and resource uptake relate to the model parameters in simple and straightforward way. The situation is much more complicated in storage models, which include many more variables (the quotas) and model parameters. Resource requirements and resource uptake can again be characterized by the same type of parameters, but these are now derived parameters with an intricate relationship to the basic parameters of the storage model. Moreover, there is no longer a 1-1 relationship between the basic model parameters and the pattern of resource requirements and resource uptake. While each such pattern fully determines the dynamics and outcome of competition in a model without storage, there are infinitely many versions of a storage model leading to an identical pattern. It is therefore not self-evident that the rules of thumb concerning requirements and uptake extend to storage models. Do storage models exhibit the same qualitative behaviors as model without storage, in only reflecting the pattern of resource requirements and uptake? Or does it matter how these patterns are generated by the interaction between resource consumption and the quota dynamics? The answers to these questions are of general relevance, since they provide important clues about the robustness of the results derived in classical resource competition theory.

In case of multispecies models, simulations such as those presented in Chapter 2 have the disadvantage that even with large efforts only a small fraction of the parameter range can be investigated. To get the full picture, analytical results are required. **Chapter 3** is an attempt to perform a mathematical analysis of storage models, with a focus on the classification of equilibria and their stability. Until now, results are only available for low-dimensional special cases (a single species growing on m resources; n species competing for a single resource; two species competing for two resources). I take on the more difficult task of characterizing equilibria and their stability for the general case of n species competing for m resources, which is characterized by a system of $n + m + n \times m$ differential equations. Some progress will be booked along two different lines. First, the stability problem is decomposed into more manageable parts by distinguishing between external stability (i.e., stability against the invasion of new species) and internal stability (i.e., stability against perturbations of the set of coexisting species). Second, the jacobian matrix characterizing internal stability will be decomposed into block matrices, whose properties can be related to stability. One of the main questions of this chapter is whether the results of the simulation study in Chapter 2 are confirmed (and perhaps generalized) by the mathematical analysis.

Chapter 4 reveal finer details about the global dynamics of the multispecies storage model, which are very difficult to identify under brute force simulation (Chapter 2), or by the exhausting analysis of all equilibria (Chapter 3). This is done by tracking (numerically) the transitions in the stability of all equilibria as the consumption parameters vary along a continuum (bifurcation and continuation analysis), for a storage model of three species competing for three resources. In order to reduce the number of parameters to an essential minimum, an assumption of cyclic symmetry with respect to the consumption and growth is made. This makes very easy to prove the existence of multiple limit cycles and unstable limit cycles, which are also present in simpler models of multispecies competition. Although the assumption of cyclic symmetric does not manifest in the real world, such ideal scenario belongs to the more general non-symmetric case. Thus, one has to be prepared to see the same complex dynamics in mode general scenarios.

My work on Chapters 2, 3 and 4, made me realize that the multispecies storage model displays similar dynamics as other models which are less mechanistic, or which lack any mechanism at all. For this reason **Chapter 5** reviews the equilibrium and stability properties of three competition models: the Lotka-Volterra model (non-mechanistic), the resource competition model without storage (mechanistic), and the resource competition model with storage (more mechanistic). The chapter starts by treating the simple scenarios of competition between two species (and two resources), and discussing to which extent the non-mechanistic and mechanistic models can be related to each other. The multispecies scenario is considered later, by addressing the rules for the existence of community equilibria and stability. Such rules are the same for all the three models, independently of their microscopic details, and they can be given simple geometric interpretations. A important common feature in all three models, is the big jump in complexity that occurs from the two-species to the three-species scenario, and in resource competition from the two-resources to the three-resources scenario.

Chapter 6 departs strongly from the primary focus on resource competition. There I study the indirect effects between competing plants, which arise as a consequence of their interactions with the organisms of the soil community. The soil community is a combination of plant parasites, consumers, symbionts, etc. The feedback, positive or negative, that the plants receive from the interaction with the soil have the potential to modify the outcomes of plant competition. This model is not mechanistic at all (is just a modification of the two-species Lotka-Volterra model 1.1), but it highlights the importance of considering the effects of other trophic levels. By means of graphical methods and invasion analysis, it is possible to obtain a rather complete description of the global dynamics for this system. An interesting feature of the model is that it allows competitive oscillations between two species, in contrast with the minimum of three species required in standard models. Also, the model allows for multiple coexistence equilibria between two species, in contrast with the classical Lotka-Volterra model, which only allows one coexistence equilibrium between two species.

Finally in **Chapter 7**, I start reviewing the most important results from the previous chapters, before placing them in a wider context. In this thesis, I focused on purely competitive systems, such that the interactions inside the trophic levels above or below the competitors do not represent any influence at all (but we can see Chapter 6 as an exception). Thus, I feel compelled to speculate about the dynamics of multispecies competition under more realistic contexts, where the species belong to a food web. In a food web, competitive interactions take place simultaneously with predator-prey interactions. Knowing that both types of interactions can generate oscillations, it remains an open question which kind of dynamics would result from the coupling of predator-prey and competitive oscillations. In the rest of the chapter, I try to return to the original problem of understanding emergent properties of ecosystems. I outline some preliminary attempts at integrating resource competition theory into the Metabolic Theory of Ecology (MTE). In doing so, it becomes evident that ecosystem level properties are sensitive to many mechanistic details, with the potential to obscure patterns predicted by the MTE.

2

NONEQUILIBRIUM COEXISTENCE IN A COMPETITION MODEL WITH RESOURCE STORAGE

Tomás A. Revilla and Franz J. Weissing

Resource competition theory predicts that, in equilibrium, the number of coexisting species cannot exceed the number of limiting resources. In some competition models, however, competitive interactions may result in nonequilibrium dynamics, allowing the coexistence of many species on few resources. The relevance of these findings is still unclear, since some assumptions of the underlying models are unrealistic. Most importantly, these models assume that individual growth directly reflects the availability of external resources, whereas real organisms can store resources, thereby decoupling their growth from external fluctuations. Here we study the effects of resource storage by extending the well-known Droop model to the context of multiple species and multiple resources. We demonstrate that the extended Droop model shows virtually the same complex dynamics as models without storage. Depending on the model parameters, one may obtain competitive exclusion, stable equilibrium coexistence, periodic and non-periodic oscillations, and chaos. Again, nonequilibrium dynamics allows for the coexistence of many species on few resources. We discuss our findings in the light of earlier work on resource competition, highlighting the role of luxury consumption, trade-offs in competitive abilities and ecological stoichiometry.

Keywords: *Resource competition, Monod model, Droop model, resource uptake, oscillations and chaos, supersaturation, trade-offs, ecological stoichiometry, Redfield ratios, luxury consumption.*

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2.1 INTRODUCTION

Many resource competition models have the property that – in a homogeneous environment and at equilibrium – the number of coexisting species is limited by the number of limiting resources (Grover, 1997). As noticed already by Hutchinson (1961) this creates the paradox of how to explain the coexistence of many species on a small number of resources. Traditional attempts to resolve the paradox tend to invoke spatial heterogeneity or externally imposed fluctuations (e.g. seasonal variation in nutrient supply or oscillations induced by predator-prey or host-parasite interactions) in order to create the nonequilibrium conditions required to maintain high levels of biodiversity (Hutchinson, 1961; Armstrong and McGehee, 1980).

More recently, Huisman and Weissing (1999, 2001, 2002) demonstrated that even in a homogeneous and constant environment multispecies competition does not necessarily lead to equilibrium. In fact, the competition process itself may generate oscillations and chaos. Such nonequilibrium conditions allow 'supersaturation' (Schippers et al., 2001), i.e. the coexistence of many more species than there are limiting resources. It crucially depends on the relationship between resource requirements and resource consumption patterns whether competition leads to equilibrium or to ongoing fluctuations (Huisman and Weissing, 2001; Huisman et al., 2001). If species tend to consume most of the resources for which they have low resource requirements, competitive exclusion will result where the initial conditions decide upon who will win the competition. If species tend to consume most of those resources for which they have high resource requirements, then equilibrium coexistence is to be expected, where the number of species does not exceed the number of resources. Finally, oscillations and supersaturation are to be expected if species tend to consume most of those resources for which they have intermediate requirements. These results are supported by mathematical analysis (Huisman and Weissing, 2001; Li, 2001; Li and Smith, 2003) and numerical simulations (Huisman et al., 2001).

The conclusions of Huisman and Weissing were based on the Monod model, which is one of the standard models of resource competition theory (León and Tumpson, 1975; Tilman, 1982; Grover, 1997). However, this model employs some unrealistic assumptions, making it difficult to judge the empirical relevance of the above predictions. Most importantly, the model assumes that individual growth reflects the external availability of resources, whereas many organisms are able to store resources and hence are more dependent on their individual internal resource content, called quota. Much recent work on multiple nutrient limitation (Legovic and Cruzado, 1997; Klausmeier et al., 2004b), dynamic energy budgets (Kooijman, 2000) and ecological stoichiometry in phytoplankton (Klausmeier et al., 2004a) shows the importance of a more mechanistic description of resource uptake, internal resource storage, and quota-dependent growth. The so-called quota models describe the dynamics of resource acquisition and population growth separately and they often provide a better description of competition than models without storage, in particular in fluctuating environments (Grover, 1997; Ducobu et al., 1998). On the other hand, quota models contain many more parameters and dynamic variables, making their analysis much more difficult. It is therefore not surprising that quota models have never been as popular as Lotka-Volterra models or Monod-type of models for resource competition.

Still it is important to investigate whether the conclusions of classical resource competition theory are robust with respect to plausible extensions of the underlying models, e.g. by taking storage and quota-dependent growth into account. In particular, it is by no means self-evident that the results of Huisman and Weissing still apply in the presence of nutrient storage. One might argue that storage will diminish the effects of external resource shortage and therefore help to protect numerically abundant species against invaders. Since repeated invasions are crucial for competition-induced oscillations and supersaturation, one might conjecture that nonequilibrium conditions are of minor importance in quota models. On the other hand, quota models have more degrees of freedom, they contain more nonlinearities, and they incorporate implicit time delays caused by the separation of uptake and growth. Since all these factors favour nonequilibrium conditions, one might conjecture that just quota models have a higher potential for oscillations and supersaturation. To settle this issue, we here study the Droop model (Droop, 1973; Tilman, 1977; Legovic and Cruzado, 1997; Grover, 1997), which is currently viewed as the standard quota model of resource competition. By means of a simulation approach, we ask the question whether and to what extent the conclusions of Huisman and Weissing (2001) are affected by nutrient storage. Is it, for example, more or less likely that oscillations and supersaturation do occur in the presence of nutrient storage?

2.2 MODELS AND DEFINITIONS

2.2.1 *The Multispecies Monod model*

Huisman and Weissing (1999, 2001) studied the multispecies extension of a classical resource competition model (León and Tumpson, 1975; Tilman, 1982) where the densities N_i (individuals per volume) of n species and the concentrations R_j (mass per volume) of k resources are governed by a system of ordinary differential equations:

$$\frac{dN_i}{dt} = N_i(\mu_i(R_1, \dots, R_k) - m_i) \tag{2.1a}$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, \dots, R_k)N_i \tag{2.1b}$$

where D is the resource flow rate, S_j is the input concentration of resource j, and c_{ji} the fixed content of resource j in species i (mass per individual). In this system, the specific growth rate of species i ($(1/N_i)dN_i/dt$) is given by the difference between the specific growth rate μ_i and the specific mortality rate m_i. Mortality rates are assumed to be constant, while the growth rates are functions of the (external) levels of resources $R_1, \dots, R_k$. Usually μ_i is assumed to be given by a combination of Monod's (1950) equation and Liebig's (1840) law of the minimum:

$$\mu_i(R_1, \dots, R_k) = r_i \min_j \left(\frac{R_j}{H_{ji} + R_j} \right) \tag{2.2}$$

where r_i is the maximal specific growth rate of species *i* under resource saturation, and H_{ji} is the half-saturation constant of resource j for species i. For brevity, we will call the system defined by (2.1) and (2.2) the *Monod model*. The properties of this system are well known (e.g. Tilman 1982; Huisman and Weissing 2001). To a large extent they depend on the resource supply point $\mathbf{S} = (S_1, \ldots, S_k)$, the consumption vectors $\mathbf{c}_i = (c_{1i}, \ldots, c_{ki})$ and the minimal resource requirements $\mathbf{R}_i^* = (R_{1i}^*, \ldots, R_{ki}^*)$ of the various species. Here, the resource requirement R_{ji}^* of species *i* with respect to resource j is that concentration of resource j for which mortality is just balanced by growth ($m_i = \mu_i$), given that all other resources are present in excess. In brief, Huisman and Weissing (2001) arrived at the following conclusions:

1. At equilibrium, each species is limited by a different resource. Accordingly, no more species can coexist than there are limiting resources.
2. If each species tends to consume most of that resource for which it has the lowest requirement (i.e., the lowest R_{ji}^*), species-poor equilibrium systems are to be expected where a single competitor excludes all others.
3. If each species tends to consume least of that resource for which it has the lowest requirement, then saturated equilibrium systems are to be expected, where the number of coexisting species corresponds to the number of limiting resources.
4. If species tend to consume most of the resources for which they have intermediate requirements, then oscillations and chaos allowing supersaturation (i.e. the coexistence of more species than limiting resources) are to be expected.

2.2.2 *The Multispecies Droop model*

In the Monod model, all species are assumed to have fixed resource contents (c_{ji}) and species growth is directly dependent on the external resource concentrations. In case of micro-organisms (e.g. phytoplankton), for which the Monod model was designed, it is more plausible to assume that the internal resource content can fluctuate (e.g. due to storage) and that growth more reflects *internal* resource concentrations than external resource availabilities. To model this, we use an extension of the variable stores model of Droop (1973) to n consumers and k resources. This model considers a third set of variables in addition to the species and resources: the internal resource content or *quota* Q_{ji} of resource j for species i. The quota is the variable equivalent of the fixed resource content c_{ji} in the Monod model, both having units of mass of resource per individual. The dynamical equations are:

$$\frac{dN_i}{dt} = N_i(\mu_i(Q_{1i}, \ldots, Q_{ki}) - m_i) \tag{2.3a}$$

$$\frac{dQ_{ji}}{dt} = f_{ji}(R_j) - \mu_i(Q_{1i}, \ldots, Q_{ki})Q_{ji} \tag{2.3b}$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} f_{ji}(R_j)N_i \tag{2.3c}$$

Notice that the equations for population growth (2.3a) correspond to equations (2.1a) of the Monod model, with the sole difference that the growth functions μ_i do not depend on external resource concentrations but on internal quotas. The resource equations (2.3c) correspond to equations (2.1b) of the Monod model, but now the specific resource uptake is described by functions $f_{ji}(R_j)$ rather than fixed consumption vectors. Equations (2.3b) characterizes the quota dynamics, which is governed by the resource uptake per individual (i.e. $f_{ji}(R_j)$) and dilution of quota due to growth and/or reproduction (accounted for by the term $\mu_i Q_{ji}$).

Following Tilman (1977) and Legovic and Cruzado (1997) we assume that the growth rate μ_i is governed by a combination of Liebig's law of the minimum and Droop's (1973) formula relating growth and quotas:

$$\mu_i(Q_{1i}, \ldots, Q_{ki}) = r_i \min_j \left(1 - \frac{q_{ji}}{Q_{ji}}\right) \tag{2.4}$$

r_i is the maximum growth rate under quota saturation and q_{ji} the minimum subsistence quota for resource j: for $Q_{ji} > q_{ji}$ the growth rate is positive, but it is set to zero if $Q_{ji} < q_{ji}$. According to equation (2.4) at any given moment the growth of species *i* depends only on the nutrient having the smallest internal content relative to the subsistence quota.

Uptake of resources from the external medium is assumed to be an increasing and saturating function of the external resource concentration:

$$f_{ji}(R_j) = \frac{\nu_{ji} R_j}{K_{ji} + R_j} \tag{2.5}$$

where ν_{ji} and K_{ji} are the maximum uptake rate and the uptake half-saturation constant for resource j by species i, respectively.

For brevity, we will call the system defined by (2.3, 2.4, 2.5) the *Droop model* for the rest of the paper.

At first sight, the Monod and the Droop model seem to share many properties. It is, however, important to be aware of some crucial differences:

1. Although the dependence of μ_i on R_j for the Monod model (2.2) and f_{ji} on R_j for the Droop model (2.5) are topologically identical functions, they describe different (though related) processes. In fact, f_{ji} can be given the same kind of mechanistic underpinning (based on handling time arguments) as a "functional response" of Holling type II (Aksnes and Egge, 1991). In contrast, the Monod terms in (2.2) correspond to a "numerical response" of consumer density towards changes in resource availability. Since metabolism is much more complex than resource uptake there is at present no general and simple theory providing a mechanistic underpinning for the numerical response. Accordingly, the Monod-type numerical response (2.2) in the Monod model and the Droop-type numerical response (2.4) in the Droop model both represent empirical relationships that are not yet linked to underlying mechanisms.

2. Although there is an obvious correspondence between some of the variables and parameters of the two models, the relationship between the models is less straightforward than one might think. For example, the parameter r_i corresponds to maximum growth rates in both models. Still there is an important difference. In the Monod model r_i corresponds to the growth rate of species *i* achieved asymptotically when

all resources are overabundant. In the Droop model this is not the case. Here an infinite availability of all resources saturates the uptake but not the growth rate. Even if uptake rates are maximal, the quotas do not exceed some limit values, leading to growth rates μ_i that can be substantially smaller than r_i.

3. For the reason indicated above, the simpler Monod model is not just a special case of the more complex Droop model. Burmaster (1979) derived a mapping between both models, but it only holds for the characterization of the community equilibrium in case of a single consumer growing on a single resource. In case of more than one resource the relationship between the models is rather intricate, even if the quota dynamics is rather fast and quotas are at a quasi-steady state all the time.

2.2.3 *Resource requirements and consumption patterns*

As indicated above, the dynamics of the Monod model is governed to a large extent by the relation between resource requirements and resource consumption patterns. We therefore start by defining the same concepts for the Droop model. In contrast to the Monod model, we now have to distinguish between external and internal resource requirements, while the consumption pattern of a species is no longer characterized by a fixed consumption vector.

The *internal requirement* Q^*_{ji} of species *i* for resource *j* is defined as the quota Q_{ji} for which mortality is just balanced by growth ($m_i = \mu_i$), given that the quota of all other resources are not limiting growth. In view of eq. (2.3a) and (2.4) Q^*_{ji} is given by:

$$Q^*_{ji} = r_i q_{ji} / (r_i - m_i) \tag{2.6}$$

We can now define the *external requirement* R^*_{ji} of species i for resource j as that resource concentration R_j just allowing to achieve the quota Q^*_{ji}, given that the quota of all other resources are not limiting growth. R^*_{ji} is obtained by setting (2.3b) equal to zero, given that $\mu_i = m_i$ and $Q_{ji} = Q^*_{ji}$. This implies $f_{ji}(R^*_{ji}) = m_i Q^*_{ji}$ or equivalently:

$$R^*_{ji} = \frac{K_{ji} m_i Q^*_{ji}}{\nu_{ji} - m_i Q^*_{ji}} \tag{2.7}$$

As in the Monod model, the parameter R^*_{ji} summarizes the competitive ability of species i for a given resource j. Whenever the resource concentration R_j is below R^*_{ji}, species i will decline. Hence if competition occurs for a single resource only, the species with the lowest requirement will exclude all the others (Smith and Waltman, 1994) which is known as the R^*-rule (Grover, 1997).

In resource space the set of external resource requirements R^*_{ji} define the nullcline (or zero net growth isocline) of species i: $R_j > R^*_{ji}$ implies that $\mu_i > m_i$ and species i can grow; while i decreases for $R_j < R^*_{ji}$. In case of two resources, the resource space (R_1, R_2) is two-dimensional, and the nullclines are L-shaped, indicative of a sharp switch in the identity of the limiting resource (Fig. 2.1A). This concept can be extended to higher dimensional resource spaces $(R_1 \dots, R_k)$ where the planes $R_j = R^*_{ji}$ define the nullclines.

The *consumption vector* (or *consumption pattern*) of species i is given by *i*'s specific consumption rates $f_{ji}(R_j)$ of the different resources. In the Monod model the consumption vector of species i is given by $\mathbf{c}_i = (c_{1i}, \ldots, c_{ki})$ and hence independent of the resource availabilities. In the Droop model, however, the direction of the consumption vector $\mathbf{f}_i(\mathbf{R}) = (f_{1i}(R_1), \ldots, f_{ki}(R_k))$ strongly reflects the external resource concentrations. Figure 2.1A illustrates this change in the direction of the consumption vectors in a two dimensional resource space. If we keep resource 1 fixed at its requirement ($R_1 = R^*_{1i}$) and if we increase the level of resource 2 above its requirement ($R_2 > R^*_{2i}$) then the component of the consumption vector corresponding to resource 2 increases with respect to the one of resource 1. The same applies mutatis mutandis for changes in resource 1. This behavior is associated with the accumulation of higher levels of non-limiting resources at equilibrium, a phenomenon known as *luxury consumption* (Grover, 1997).

2.2.4 *Community equilibrium*

A Droop system is at equilibrium if all rate equations (2.3a,2.3b,2.3c) are equal to zero: $dN_i/dt = dQ_{ji}/dt = dR_j/dt = 0$. Dynamic variables at equilibrium will be indicated by a hat (^). An equilibrium will be called a *community equilibrium* if $n \geqslant 2, k \geqslant 2$ and all dynamical variables are positive $\hat{N}_i > 0$, $\hat{Q}_{ji} > 0$, $\hat{R}_j > 0$. Such a state, stable or not, exists if the following conditions are met:

First, the nullclines of all coexisting species have to intersect in a single point in resource space (see Fig.2.1B). This implies that at most *k* species can coexist at equilibrium, since generically more than k nullclines will not have a common intersection point in *k*-dimensional resource space. Let us therefore assume from now on that $n = k$. Moreover, all n nullclines can only intersect if each species is limited by a different resource (see Fig. 2.1B). Let us therefore assume that species 1 is limited by resource 1, species 2 by resource 2, and so on. Then the equilibrium in resource space is given by:

$$\hat{\mathbf{R}} = (\hat{R}_1, \ldots, \hat{R}_n) = (R^*_{11}, \ldots, R^*_{nn}) \tag{2.8}$$

Second, the common intersection point in resource space must be attainable. This is only possible if the resource supply point $\mathbf{S} = (S_1, \ldots, S_n)$ is located in the positive cone that is attached at the resource equilibrium $\hat{\mathbf{R}}$ and spanned by the consumption vectors $\hat{\mathbf{f}}_i = \mathbf{f}_i(\hat{\mathbf{R}}) = (f_{1i}(R^*_{11}), \ldots, f_{ni}(R^*_{nn}))$ at this equilibrium (see Huisman and Weissing 2001 for a detailed justification). Figure 2.1B visualizes this cone as a wedge in a two-dimensional resource space.

The special case of two species competing for two resources has for the Droop model been studied graphically by Turpin (1988). This is depicted in Figure 2.1B, where each species consumes comparatively more of the resource for which it has the highest requirement, a situation leading to stable coexistence. If, on the other hand, each species consumes more of the resource most required by the other species (corresponding to the situation where the two consumption vectors $\hat{\mathbf{f}}_1$ and $\hat{\mathbf{f}}_2$ in Fig. 2.1B were interchanged), competitive exclusion will result where the winner may depend on the initial conditions. Hence for $n = k = 2$ the graphical analysis is very similar to that of the simpler Monod model. Notice, however, that the slopes of consumption vectors are fixed in the Monod model, whereas they are dependent on the position in resource space in the Droop model (as illustrated in Fig. 2.1A).

Notice further that the equilibrium values $\hat{R}_j$ and $\hat{Q}_{ji}$ are in general not equal to resource requirements R^*_{ji} and Q^*_{ji}. The "star values" are consumer properties that are derived under the assumption that the given resource j is limiting. In contrast the "hat values" are system properties reflecting the state of the system at equilibrium. Star and hat values only coincide for those resources that happen to be limiting at the community equilibrium, i.e. $\hat{R}_i = R^*_{ii}$ and $\hat{Q}_{ii} = Q^*_{ii}$. For the non-limiting resources ($j \neq i$) we have instead $\hat{R}_j > R^*_{ji}, \hat{Q}_{ji} > Q^*_{ji}$, corresponding to luxury consumption.

2.3 RESULTS

In a separate attempt, we show how the local stability of the community equilibrium can be characterized analytically (Revilla & Weissing, submitted). Because of the high dimensionality of the Droop model, already a local analysis is difficult, although it turns out that – as in the Monod model – the consumption patterns at equilibrium $\mathbf{f}_i(\hat{\mathbf{R}})$ plays a crucial role. We have little hope that global and nonequilibrium dynamics of the Droop model can be characterized analytically. Therefore we see no alternative than to rely on numerical simulations.

To get a representative picture of the dynamics, we performed tens of thousands simulations, each covering an extensive period of time. Details about parameters choice, initializations and the numerical integration technique are given in Appendix A. The parameters used in our figures are given in Appendix B. In the majority of simulations we focused on chemostat-like conditions where $m_i = D$. Moreover we usually set $r_i = r$ for all species. See the discussion for a justification of these assumptions.

2.3.1 *Competition for two resources*

In the Monod model, competition for two resources always results in the convergence of the system to a stable equilibrium where at most two species can stably coexist (Huisman and Weissing, 2001). Oscillations do never occur. To check whether the same holds true for the Droop model, we ran extensive simulations of two species competing for two resources. Without exception, we found the same three dynamical scenarios that are well-known from the Monod model:

1. Species 1 always wins when it is the better competitor for both resources (i.e. $R^*_{11} < R^*_{12}$ and $R^*_{21} < R^*_{22}$); species 2 always wins when the opposite holds true (i.e. $R^*_{12} < R^*_{11}$ and $R^*_{22} < R^*_{21}$).
2. The two species stably coexist at equilibrium if the nullclines intersect and at the intersection point each species consumes most of the resource for which it has the highest requirement (i.e. Fig. 2.1B).
3. Either species 1 or species 2 wins (depending on the initial condition) if the nullclines intersect and each species consumes at the intersection point most of the resource for which it has the lowest requirement (i.e Fig. 2.1B, but with $\hat{\mathbf{f}}_1$ and $\hat{\mathbf{f}}_2$ interchanged).

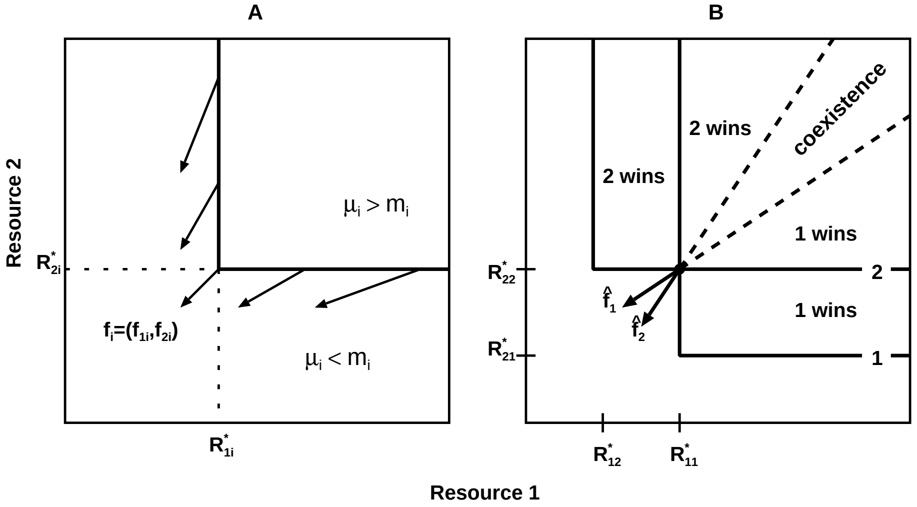

Figure 2.1: Two-dimensional resource space illustrating competition for two limiting resources. (A) For each species *i* an L-shaped nullcline divides the resource space into an area where net growth occurs ($\mu_i > m_i$) and an area where species *i* does decline ($\mu_i < m_i$). The nullcline is determined by the minimal resource requirements R^*_{1i} and R^*_{2i}. The consumption vector $\mathbf{f}_i = \mathbf{f}_i(R_1, R_2)$ of species *i* depends on the resource concentrations. The slope of $\mathbf{f}_i$ increases along the vertical segment of the nullcline and decreases along the horizontal segment. (B) A two species community equilibrium exists if the two nullclines cross and the supply point falls inside the wedge defined by the consumption vectors $\hat{\mathbf{f}}_1$ and $\hat{\mathbf{f}}_2$ of the two species at the intersection point. If each species consumes most of the resource limiting its own growth (the configuration shown here), the community equilibrium is stable.

In all simulations, the system approached a steady state, and oscillations did not occur. This conclusion does not depend on the chemostat assumption ($m_i = D$) or the equality of the r_i-values.

2.3.2 *Competition for three resources*

Also in case of more than two resources, the dynamics of competition strongly depends on the relationship between resource requirements and consumption patterns. However, a full characterization of the system behaviour seems a forbidding task. In fact, there are $(k!)^{2k}$ qualitatively different configurations of resource requirements and consumption patterns (Huisman and Weissing, 2001), giving a huge number (46656) already for $n = k = 3$. Huisman and Weissing therefore restricted their analysis to some important special cases. In case of three resources they were able to derive clear-cut predictions for the following three scenarios:

1. Each species consumes most of the resource for which it has the highest requirement. Prediction: stable equilibrium coexistence.
2. Each species consumes most of the resource for which it has the intermediate requirement. Prediction: species oscillations.
3. Each species consumes most of the resource for which it has the lowest requirement. Prediction: competitive exclusion where the winner depends on the initial condition.

In case of the Droop model there are even more degrees of freedom since the consumption patterns are not fixed but variable. The three scenarios above can, however, be implemented by focusing on the consumption vectors $\hat{\mathbf{f}}_i = \mathbf{f}_i(\hat{\mathbf{R}})$ at equilibrium (see Appendix A). The three scenarios and the predictions based on the Monod model are summarized in Table 2.1.

Figure 2.2 shows some simulations of the Droop model whose outcome is fully in line with the predictions derived on basis of the Monod model. When all species consume most of the resource for which they have the highest requirements, the three species coexist stably at equilibrium (Fig.2.2A). The same result was obtained by all 100000 simulations for scenario 1. When all species consumes least of the resource for which they have highest requirements, one of the three species outcompetes the other two (Fig.2.2B). In all simulations based on scenario 3 we similarly obtained competitive exclusion with the winner depending on the initial conditions.

Nonequilibrium outcomes were obtained for scenario 2, where each species consumes most of the resource for which it has intermediate requirements. We obtained regular limit cycles with a constant period as in Figure 2.2C or oscillations with increasing period as in Figure 2.2D. The latter type corresponds to a heteroclinic orbit connecting the three monoculture equilibria.

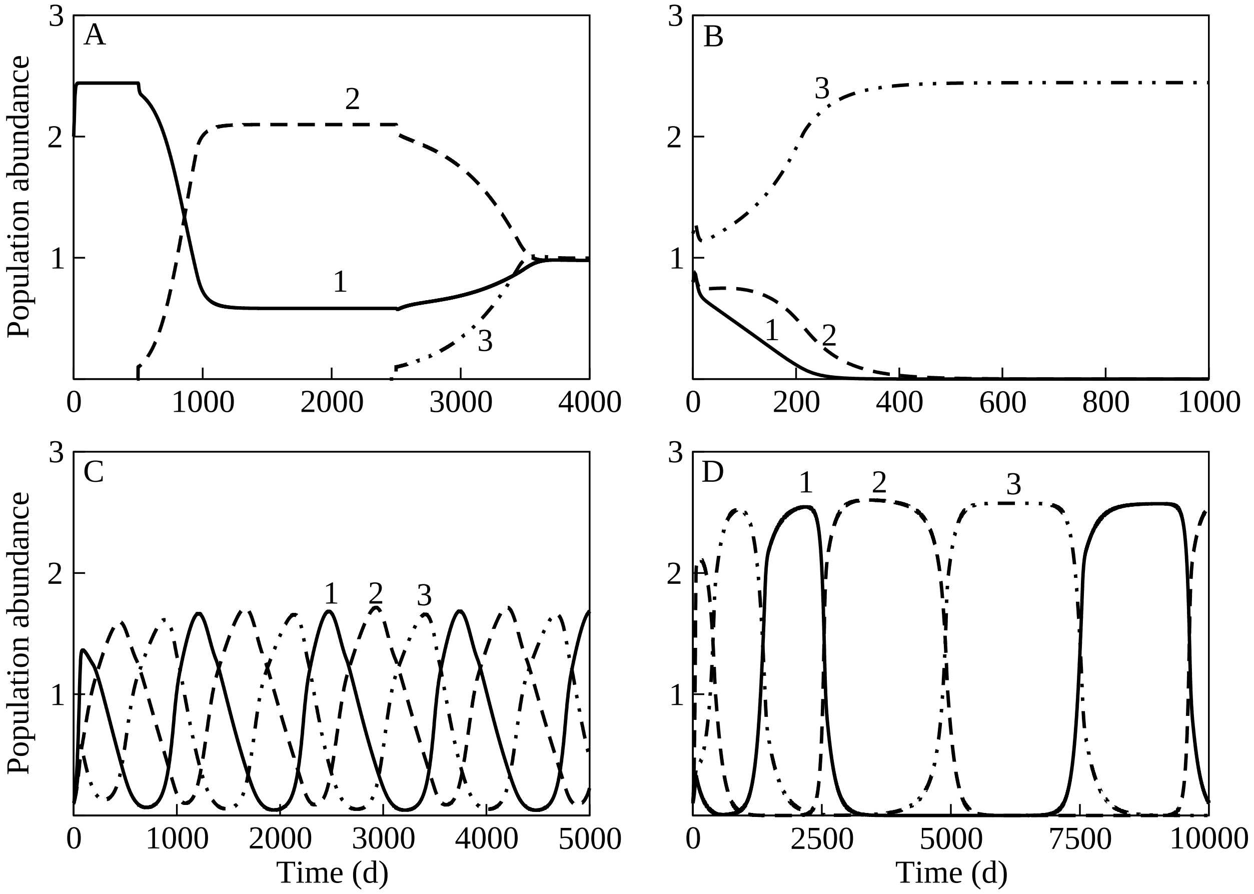

Figure 2.2: Three species competing for three resources. (A) Equilibrium coexistence: species 2 invades the monoculture of species 1, the resulting two species equilibrium is invaded by species 3 and the resulting three species equilibrium is stable. (B) Competitive exclusion: here the initial condition favors species 3. (C) Species oscillations: convergence to a limit cycle. (D) Species oscillations of increasing period; convergence to a heteroclinic cycle.

Requirements	*scenario 1*	*scenario 2*	*scenario 3*
$R^*_{11} > R^*_{12} > R^*_{13}$	$\hat{f}_{11} > \hat{f}_{12} > \hat{f}_{13}$	$\hat{f}_{12} > \hat{f}_{13} > \hat{f}_{11}$	$\hat{f}_{13} > \hat{f}_{12} > \hat{f}_{11}$
$R^*_{22} > R^*_{23} > R^*_{21}$	$\hat{f}_{22} > \hat{f}_{23} > \hat{f}_{21}$	$\hat{f}_{23} > \hat{f}_{21} > \hat{f}_{22}$	$\hat{f}_{21} > \hat{f}_{23} > \hat{f}_{22}$
$R^*_{33} > R^*_{31} > R^*_{32}$	$\hat{f}_{33} > \hat{f}_{31} > \hat{f}_{32}$	$\hat{f}_{31} > \hat{f}_{32} > \hat{f}_{33}$	$\hat{f}_{32} > \hat{f}_{31} > \hat{f}_{33}$
Prediction	equilibrium coexistence	oscillations	exclusion

Table 2.1: The dynamics of competition for 3 resources strongly depends on the relationship between resource requirements (quantified by R^*-values) and consumption patterns (quantified by the elements of the consumption vectors at equilibrium $\hat{f}_{ji} = f_{ji}(\hat{R}_j)$). For a cyclic configuration of resource requirements (where in all cases species *i* has the highest requirement for resource *i*), the table shows three different configurations of consumption patterns and the outcome predicted on basis of the Monod model. In the first scenario species *i* consumes most of resource for which it has the highest requirement; in the second scenario all species consume most of the resource for which it has the intermediate requirement; and in the third scenario each of them consumes most of the resource for which its requirement is the lowest.

Figure 2.3 illustrates that the competition induced oscillations are somewhat different than those of the Monod model. In this figure the dynamics of a Droop model (left panels) are compared with those of the "corresponding" Monod model, i.e. a Monod model with the same community equilibrium, the same external resource requirements R^*_{ji} and the same consumption patterns $\mathbf{c}_i = \frac{1}{m_i}\mathbf{f}_i(\hat{\mathbf{R}}) = \frac{1}{D}\mathbf{f}_i(\hat{\mathbf{R}})$. In line with many similar simulations, the Monod model displays a much higher oscillation frequency (notice the time scale). Apart from this, the oscillations of external resource concentrations and species densities look rather similar in both models, despite oscillations of the resource contents in the Droop model (in the Monod model the resource contents are constant by definition). However, in the Droop model the pattern of oscillations tends to be somewhat more complex at the resource level and somewhat less complex at the level of species densities. Interestingly, the oscillations of consumer densities are more pronounced than in the Monod model, despite of the (presumably) buffering effect of nutrient storage.

To investigate whether the outcomes in Figures 2.2C, 2.2D and 2.3 are representative, we again ran many simulations. In 20-25% of all cases (depending on the search window in parameter space) we obtained regular oscillations as in Figure 2.2C, where all species stayed well above zero in density. In about 60% of all cases we obtained either oscillations involving very low species densities ($<10^{-4}$) or heteroclinic cycles as in Figure 2.2D. In a heteroclinic cycle the system stays close to a monoculture equilibrium for increasingly long periods of time, once in a while rapidly switching from one monoculture to another. Hence for long periods of time two of the three species have very low densities. Accordingly, in a real-world system such a situation would lead to the extinction of two of the three

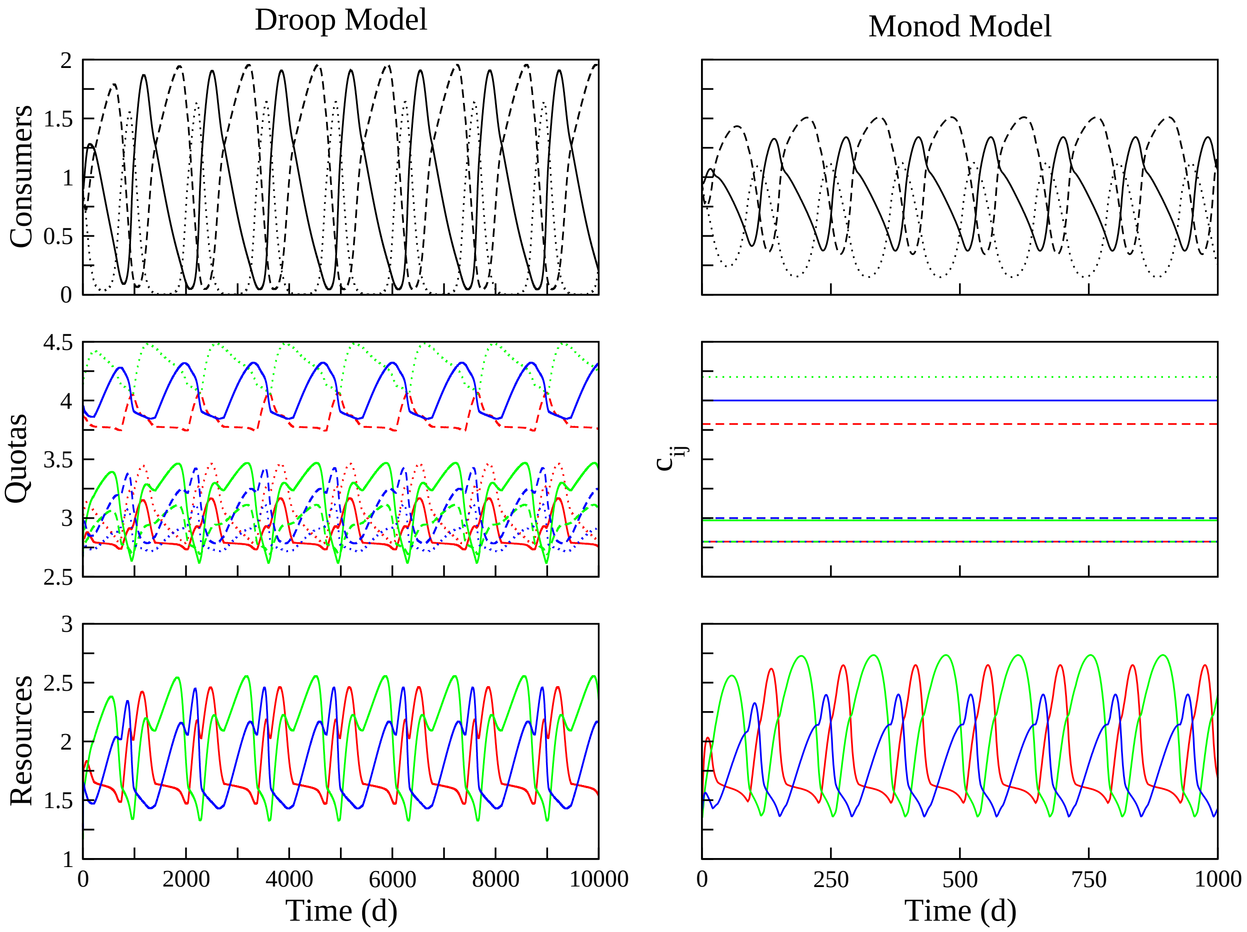

Figure 2.3: Dynamics of consumers, quotas and resources for a Droop model and an equivalent Monod model, i.e. a model with the same resource requirements, quotas and uptake rates as the Droop model has at equilibrium. Resources are indicated by colors (1: red, 2: green, 3: blue) and consumers by line patterns (1: solid, 2: dash, 3: dots). For the Monod model, the fixed resource contents c_{ji} are shown for comparison with the quotas Q_{ji}.

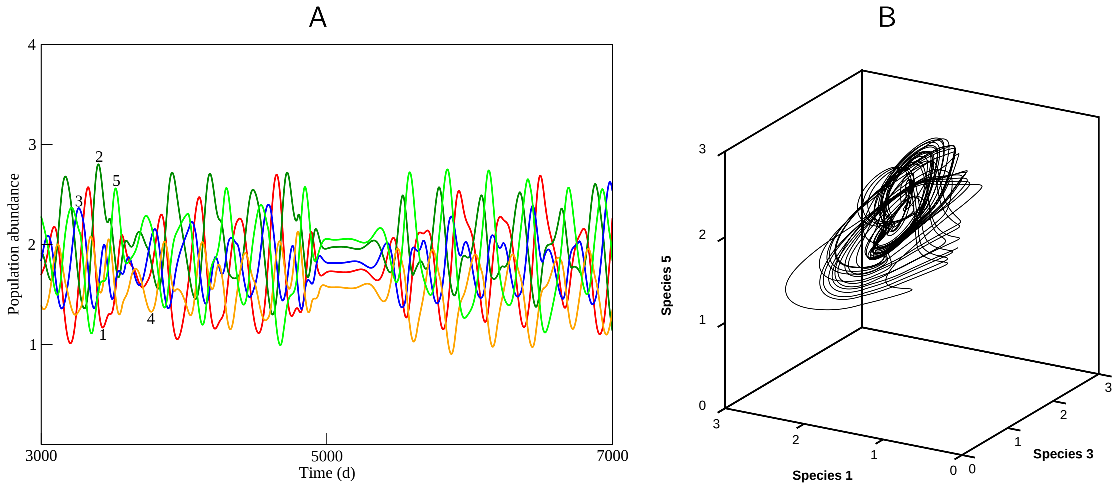

Figure 2.4: Competitive chaos for five species competing for five resources. (A) Time series illustrating how an apparently stable period is followed by violent fluctuations. (B) The chaotic attractor for the same series plotted for species 1, 3 and 5 for t = 10000 - 20000.

species, corresponding to competitive exclusion. In contrast with the Monod model, we also obtained "theoretical competitive exclusion" in 15-20% of our simulations. In these cases, the system converged to an asymptotically stable monoculture equilibrium. To understand this, notice that the scenarios in Table 2.1 are only valid at the community equilibrium. In contrast to the Monod model, the hierarchy of consumption patterns may change in time, leading, for example, to a switch from the "Rock-Scissors-Paper" scenario 2 to a scenario favoring competitive exclusion. In conclusion, nutrient storage and luxury consumption change the rules of the game, making oscillations (slightly) less likely than in the Monod model.

2.3.3 *Competition for more than three resources*

With the same reservations as in the case $n = k = 3$, the results of Huisman and Weissing (2001) seem to extend to more than three resources. With four species and four resources (results not shown) our simulations revealed stable equilibrium coexistence if at equilibrium each species consumes most of the resource for which it has the highest requirement; and competitive exclusion if each species consumes most of the resource for which it has the lowest requirement. We also found oscillations with either constant or increasing period when consumption is higher on resources for which the requirements are intermediate. In some cases, as in Huisman and Weissing (2001), if each species consumes most of the resource for which it has the second-highest requirement, one species pair displaces the other species pair; the winning pair depending on the initial conditions.

With five species competing for five resources competitive oscillations with switching partners occur if each species consumes most of the resource for which it has the second-highest requirement. But if each species consumes most of the resource for which it has the intermediate requirement, the system can generate chaos. In Figure 2.4 we show one of these chaotic time series, which displays an apparent period of stabilization followed by violent fluctuations again. For a given set of physiological and environmental parameters the system may have alternative attractors. This is exemplified by Figure 2.5, where the system may – depending on the initial conditions – end up in a limit cycle, a heteroclinic cycle or a non-periodic attractor.

2.3.4 *More species than resources: supersaturation*

In light of the previous results the question arises whether, as in the Monod model, internally generated nonequilibrium conditions allow supersaturation, i.e. the coexistence of more species than the number of resources (Huisman and Weissing, 1999). The answer is yes. Figure 2.6 shows oscillatory coexistence of four, five, and six species on three resources. These oscillations can have low or high amplitudes. Figure 2.6A is particularly interesting, here the invasion of a fourth species actually leads to a reduction in the amplitude of oscillations, making the system look more "equilibrium-like".

2.4 DISCUSSION

Storage-based models proved able to display as rich dynamics as their constant resource content counterparts (e.g. the Monod model). This is a new confirmation that multispecies competition can display sustained oscillations, with no need of externally imposed fluctuations. The mechanism is the same in both models: non-transitivity in competitive dominance (Huisman and Weissing, 2001). If species dominance relationships are not transitive (A beats B, B beats C, but C beats A) the community equilibrium is unstable, so that oscillations or chaos occur. Moreover many if not all of the boundary equilibria of the community are unstable, preventing species from going extinct and promoting high diversity and supersaturation (Fig. 2.6). It is worth to notice that a variety of modeling approaches (May and Leonard, 1975; Gilpin, 1975; Huisman and Weissing, 1999; Laird and Schamp, 2006) point towards the general conclusion that non-transitivity in competitive hierarchy promotes coexistence, or alternatively, delays competitive exclusion, enhancing biodiversity.

Mathematical analysis of the Monod model (Huisman and Weissing, 2001; Li, 2001) revealed that the stability of the community equilibrium is crucially dependent on the consumption pattern, i.e. the matrix of consumption terms c_{ji}. In a separate paper (Revilla and Weissing, submitted), we show analytically that the same is true for storage models in general. In line with a recent study of Li and Smith (2007), who perform a global analysis for the special case $n = k = 2$, we arrive at the conclusion that the dynamic behaviour of both types of model is qualitatively very similar close to equilibrium.

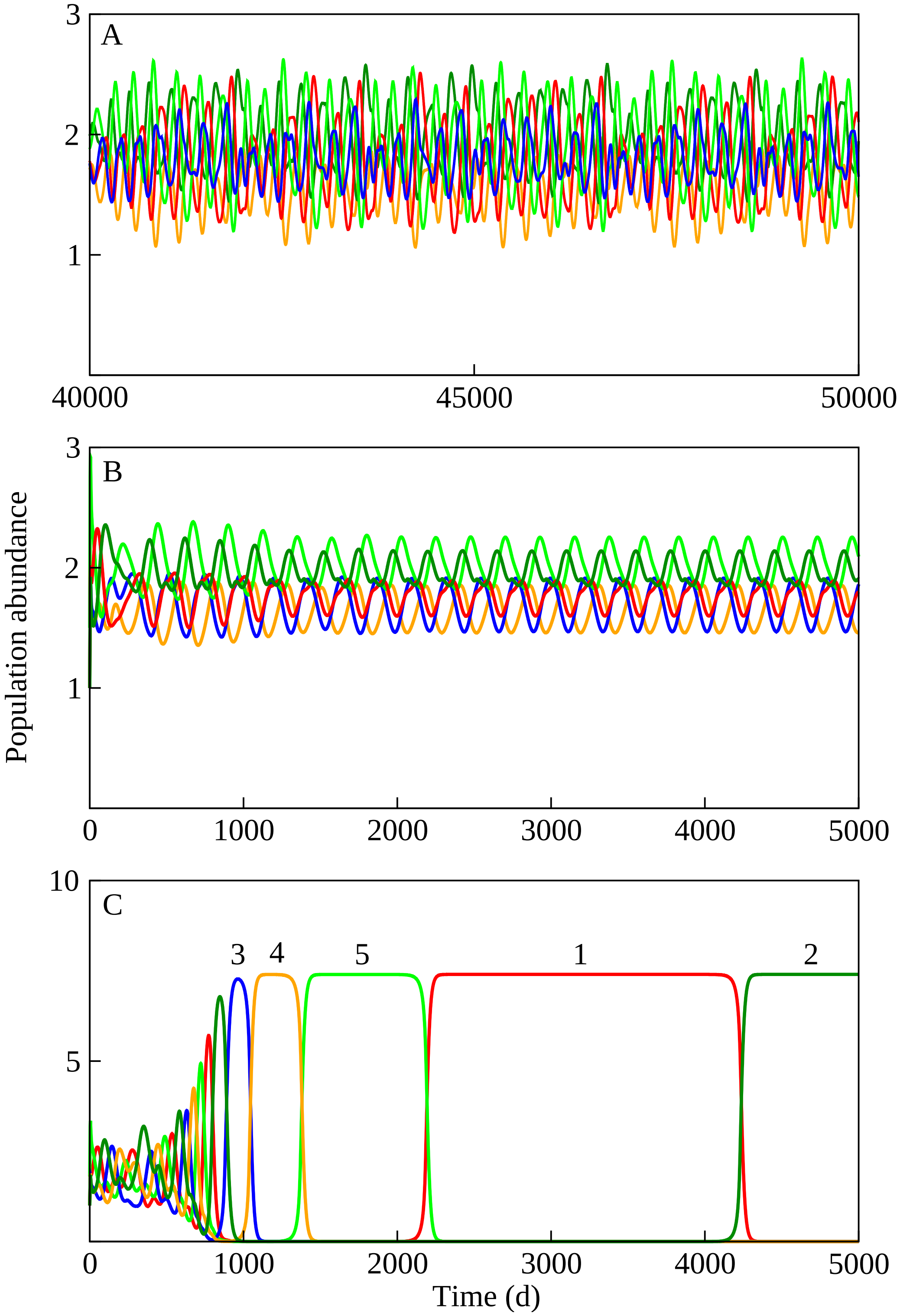

Figure 2.5: Coexisting attractors in case of five species competing for five resources. For a given set of parameters each graph corresponds to a different initial condition for the fifth species. (A) $N_5(0) = 0.9$: non-periodic oscillations. (B) $N_5(0) = 1.5$: limit cycle. (C) $N_5(0) = 1.8$: heteroclinic cycle.

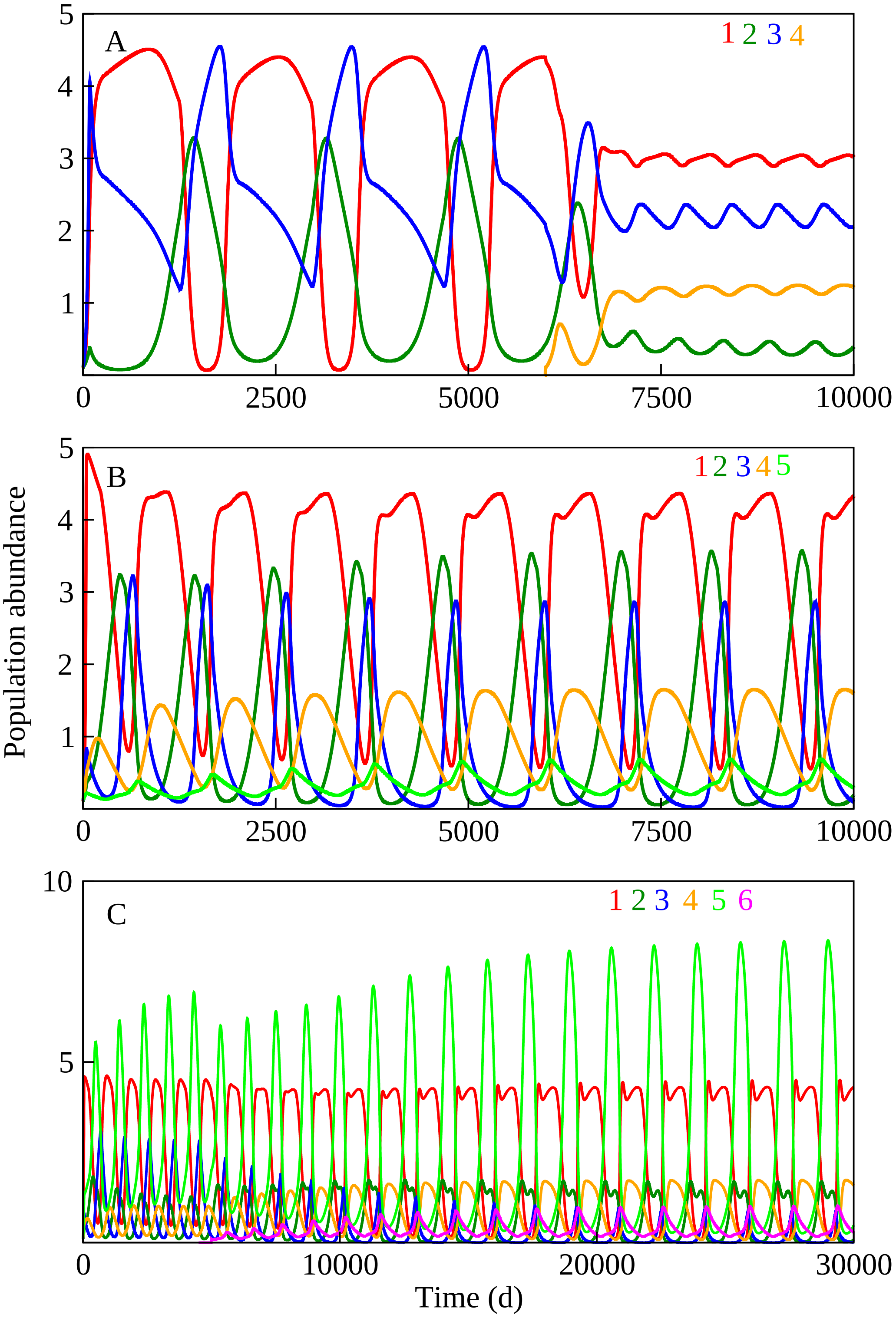

Figure 2.6: Nonequilibrium coexistence of 4, 5 and 6 species on three limiting resources. (A) High amplitude oscillations of three species allows the invasion of a fourth species (introduced at $t = 6000$). The system ends up displaying low amplitude oscillations. (B) Oscillations of five species competing for three resources. (C) Oscillations of six species competing for three resources (species 6 invades at $t = 5000$).

Still there are important differences between both types of model. Most importantly, the consumption terms in the Droop model are no longer fixed but functions $f_{ji}(R_j)$ of the external resource concentrations. Accordingly, it is not possible to separate resource requirements and consumption patterns, as in the Monod model. In the Monod model, the positive cone in resource space allowing stable coexistence (like the wedge in Fig. 2.1B), looks the same irrespective of the position of the resource equilibrium $\hat{\mathbf{R}}$. In the Droop model, luxury consumption of non-limiting resources has the effect that the corresponding cone (spanned by the consumption vectors $f_{ji}(R)$) gets smaller and smaller when the resource equilibrium $\hat{\mathbf{R}}$ is approached from the direction of the resource supply point. Accordingly, luxury consumption results in a decrease of the zone of stable coexistence. Thus, the multispecies quota models seems to be more likely to end up displaying unstable community equilibria. When the community equilibrium is unstable the resulting dynamics could be nonequilibrium coexistence or competitive exclusion.

According to our simulations, the Droop model has a lower tendency for oscillations than the Monod model, because the consumption pattern at equilibrium may change as the system evolves, as well as the identity of the resource that causes growth limitation for a given species. Theoretically, such changes might allow oscillations in cases where such oscillations cannot occur in the Monod model. We never encountered a simulation corresponding to this possibility, perhaps because we focused on the cases $k = 3, 4$ and 5. There is however, another potential mechanism that may cause oscillations in models with nutrient storage. In fact, damped oscillations occur in the single-species Droop model if the mortality rate m is large enough when compared to the flow rate D (Clodong and Blasius, 2004), this will never happen if $m = D$ (Lange and Oyarzun, 1992; Oyarzun and Lange, 1994; Legovic and Cruzado, 1997). It was for this reason that we made the chemostat assumption, since we were mainly interested in competition-induced oscillations. Since we ran only few simulations with $m_i > D$, it is an open problem whether or not such fluctuations of physiological origin could interact synergisticaly with competitive-induced oscillations, enhancing the chances of nonequilibrium coexistence.

Toward a realistic theory of trade-offs

We have seen that the occurrence of nonequilibrium dynamics strongly depends on trade-offs between resource requirements and consumption rates. In the context of the Monod model, it is difficult to develop a mechanistic theory of such trade-offs, since already the underlying growth equation (2.2) (corresponding to a numerical response) lacks a mechanistic underpinning. In contrast, the uptake function (2.5) (corresponding to a functional response of Holling (1959) type II) of the Droop model can be justified mechanistically in terms of physiological and environmental factors (e.g., transporter properties, cell size, medium viscosity, temperature).

For example, Aksnes and Egge (1991) have shown that the maximum uptake rate ν_{ji} for a given nutrient is directly proportional to the number n_{ji} of nutrient-specific transporters. If each transporter occupies an area a_{ji} on the surface of the cell membrane, a natural constraint arises, since $\sum a_{ji} n_{ji} \leqslant A_i$, where A_i denotes the total surface available. If we further assume that surface area scales with cell mass w_i with a certain allometric exponent

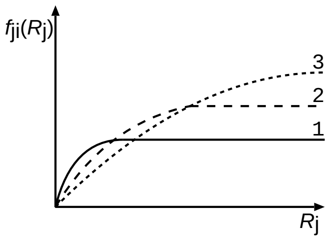

Figure 2.7: Change in uptake hierarchies due to mechanistic constraints. If the maximum uptake rate ν_{ji} and the half-saturation constant K_{ji} are positively correlated, as predicted by mechanistic theory, the resource uptake functions of three species can easily cross. As a consequence the ranking of the species with respect to resource uptake (as in Table 2.1) changes with the resource concentration.

ρ (i.e. $A_i \propto w_i^\rho$), we get an allometric constraint for the maximum uptake rates of the form $\sum a_{ji}\nu_{ji} \leqslant kw_i^\rho$. Thus, raising the maximum uptake ν_{ji} for resource j may be associated by a decrease in the maximum uptake of other resources, unless the cell size is increased too. An increase in cell size would in turn have other metabolic costs, reflected as increased threshold requirements q_{ji}.

To illustrate the use of a mechanistic interpretation of trade-offs, consider the following argument. For the second scenario in Table 2.1 we obtained competitive exclusion in a considerable number of cases where an equivalent Monod model would predict oscillations. When we looked at these cases in detail, it turned out that the ν_{ji} and K_{ji} yielded uptake functions that cross each other, like in Figure 2.7. This means that the consumption hierarchies can change as the system evolves, leading, for example, to a hierarchy inducing competitive exclusion. A situation as in Figure 2.7 can easily arise if the parameters $\nu_{ji}$and K_{ji} happen to be positively related. This is precisely what the model of Aksnes and Egge predicts, since both ν_{ji} and K_{ji} are proportional to the handling time needed to pass a nutrient molecule through the membrane. In our simulations, we unintendedly also introduced a positive correlation among ν_{ji} and K_{ji} (see Appendix A). Accordingly, we encountered a relatively large number of situations were the rules of the competitive game at equilibrium change drastically when moving away from equilibrium. If ν_{ji} and K_{ji} were negatively correlated instead, the consumption hierarchies of Table 2.1 are more likely remain stable, as in the Monod model.

Stoichiometry

For both the Monod and the Droop model oscillations can only occur if species differ in their resource requirements and in their resource uptake characteristics in a specific and contrasting way (e.g. scenario 2 in Table 2.1). In nature, variation in resource contents and requirements occur within the limits allowed by the stoichiometry of the underlying biochemical reactions. One may therefore wonder whether our theoretical considerations are compatible with such stoichiometric constraints.

First, one might think that species cannot differ too much in their hierarchy of resource requirements R^*_{ji} or in their hierarchy of quotas at equilibrium $\hat{Q}_{ji}$. It is, for example, well known that organisms cannot have a lower content (grams or moles) of carbon (C) than their contents of nitrogen (N) or phosphorous (P), no matter how flexible the variable quotas are. For algae, the canonical stoichiometric reference are the Redfield (1958) ratios for atomic composition, C:N:P = 106:16:1. However, recent work (Legovic and Cruzado, 1997; Klausmeier et al., 2004a,b) indicates that Redfield ratios are not cast in stone but actually quite variable. Due to this flexibility, it is not unrealistic that each resource has a different hierarchy across species with respect to either resource contents or resource requirements. This is illustrated by the following table, showing for three species resource contents coming close to Redfield ratios:

	Species 1	Species 2	Species 3
C	1045	**1060**	1053
N	165	160	**171**
P	**11**	10	9
C:N:P	95:15:1	106:16:1	117:19:1

In this example species 1 has the highest content of P, species 2 of C and species 3 of N. Similarly, we can build any hierarchy for resource requirements. We can conclude that stoichiometric principles like the Redfield ratios only imposes mild constraints on the hierarchies of requirements and quotas.

Second, one might think that – even if hierarchies differ between species – for each given species the hierarchy of resource requirements should roughly match the hierarchy of resource consumption. In fact, one might argue that scenario 1 in Table 2.1 is much more likely than the other two scenarios: according to equation (2.7) external (R^*_{ji}) and internal (Q^*_{ji}) requirements are positively related, implying, that the hierarchy of R^*- and Q^*-values are not to be different. Because of $\hat{f}_{ji} = m_i \hat{Q}_{ji}$, the hierarchy of uptake patterns $\hat{f}_{ji}$ should roughly match the hierarchy of equilibrium quotas $\hat{Q}_{ji}$, at least if the m_i are not too different (as in a chemostat, where $m_i = D$). Doesn't this not imply that the hierarchies of R^*-values should correspond to the hierarchy of $\hat{f}$-values, as in scenario 1 of Table 2.1? The answer is no. First, luxury consumption causes a mismatch between Q^*_{ji} and $\hat{Q}_{ji}$, implying that the relationship between R^*_{ji} and $\hat{Q}_{ji}$ is far from obvious. Second, already the relationship between R^*_{ji} and Q^*_{ji} is not really obvious, since the parameters ν_{ji} and K_{ji} in equation (2.7) are both species and resource specific. According to theories like those of Aksnes and Egge (1991) these parameters depend on many details that are not related with the rules of internal metabolism or the stoichiometry underlying biochemical reactions. Accordingly, we do not see a reason for stoichiometry to prevent specific patterns of resource requirements and resource consumption.

Conclusion

Our simulations show that multispecies resource competition models with storage dynamics like the Droop model can display the competitive oscillations that are common in other models (May and Leonard, 1975; Gilpin, 1975; Huisman and Weissing, 1999). In addition they can also generate coexistence of more species than the number of resources. The mechanism behind the oscillations is the sequence of replacements of species due to the lack of absolute winners in the total ensemble of species as in the "Rock-Scissors-Paper" game, a condition that results from trade-offs between resource requirements and consumption patterns. The implicit delay by which a species responds to resource fluctuations in the external medium does neither cause nor enhance these oscillations. In fact, it retards the oscillations considerably, leading to periods that are one or more orders of magnitude longer than those in corresponding models without storage. Moreover, in a considerable percentage of cases oscillations do not occur in models with storage, while they are to be expected on basis of the corresponding models without storage. This discrepancy is caused by luxury consumption that may destroy the intransitivity causing oscillations (as in the Rock-Scissors-Paper game) as soon as the system is sufficiently far from equilibrium. Storage models are considerably more complex than purely phenomenological models like the Lotka-Volterra models or less detailed semi-mechanistic models like the Monod model. But physiological models accounting for storage have the big advantage that the all-important trade-offs can be given a much better interpretation.

ACKNOWLEDGMENTS

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APPENDIX A: SIMULATION DETAILS

The multi-species Droop model (2.3,2.4,2.5) contains a large number of parameters and, hence, has many degrees of freedom: the maximum growth rates r_i and the mortality rates m_i of the n species; the minimum subsistence quotas q_{ji}; the maximum uptake rates v_{ji} and the half saturation constants for uptake K_{ji}; the flow rate D and the resource supply rates S_j. It can be shown analytically (Revilla and Weissing, submitted) that the dynamics of the Droop model depends crucially on the ranking of the species with respect to resource requirements R^*_{ji} and consumption patterns $\hat{f}_{ji}$ at equilibrium (see Table 2.1). For this reason we wanted to consider different scenarios regarding resource requirements and consumption. To this end, we started by imposing a certain sign pattern of the R^*_{ji} values and on the matrix $\hat{f}_{ji} = f_{ji}(\hat{R}_j)$ as in Table 2.1. To achieve such patterns the model parameters were chosen by a "reverse engineering" approach along the lines indicated below:

1. We set the flow rate D, maximum growth rates r_i and the mortality rates m_i. In most simulations, all r_i were equal: $r_i = r$ and all mortality rates were set equal to D (see the text for a motivation).

2. Resource requirements were randomly chosen from an interval (R^*_{low}, R^*_{high}) and arranged to form a matrix R^*_{ji} with the structure depicted in Table 2.1. Subsequently, the resource levels at equilibrium are set by $\hat{R}_j = R^*_{jj}$.

3. Consumption rates at equilibrium were randomly chosen from an interval $(\hat{f}_{low}, \hat{f}_{high})$ and arranged to give a $\hat{f}_{ji}$ matrix with a given hierarchy as in Table 2.1.

4. The half saturation constants K_{ji} were chosen at random, with the sole restriction that $K_{ji} > 0$.

5. The maximum uptake rates ν_{ji} were determined from eqn (2.5): $\nu_{ji} = (1 + K_{ji}/\hat{R}_j)\hat{f}_{ji}$ where $\hat{R}_j = R^*_{jj}$. Notice that this results in a positive correlation between the parameters ν_{ji} and K_{ji}, leading to resource uptake functions $f_{ji}(R_j)$ that tend to intersect as in Fig. 2.7.

6. Internal resource requirements are obtained from (2.7) as $Q^*_{ji} = \nu_{ji}R^*_{ji}/m_i(K_{ji} + R^*_{ji})$.

7. The minimum subsistence quotas are now obtained from (2.6) as $q_{ji} = (1 - m_i/r_i)Q^*_{ji}$.

8. Positive equilibrium densities $\hat{N}_i$ were chosen at random.

9. The supply rates S_j were obtained by setting the right-hand side of eqn (2.3c) equal to zero: $S_j = \hat{R}_j + (1/D)\sum \hat{f}_{ji}\hat{N}_j$.

The alternative approach of starting by choosing all parameters at random has two disadvantages. First, many combinations would result in a system without community equilibrium or a system where the community equilibrium is not attainable. In our approach steps 2, 8 and 9 guarantee that a community equilibrium exists and that the supply point fall inside the wedge in Fig. 2.1B, implying that the community equilibrium can be reached. Second, and more importantly, the huge number ($(k!)^{2k}$) of qualitatively different configurations of resource requirements and consumption patterns implies that any new set of parameter combinations would lead to a system falling into a new category. Accordingly an astronomic number of simulations would be required in order to draw any general conclusion on the system dynamics.

The system was initialized at the community equilibrium plus a random perturbation on the resources, i.e. $N_i(0) = \hat{N}_i$, $Q_{ji}(0) = \hat{Q}_{ji}$, $R_j(0) = \hat{R}_j + \varepsilon_j$. For each scenario, we replicated the above procedure 10000 to 50000 times, and we performed the corresponding numerical integration for $t = 10000$ to 50000 days.

Numerical integration was performed in the C programming language (source code at `http://www.esapubs.org/archive/ecol/E089/050/`) using the 4th order Runge-Kutta solver from the GNU Scientific Library (`http://www.gnu.org/software/gsl/`). Each time unit of the simulation (day) is fractioned into 1000 time steps by default unless adaptive step size control takes place with absolute error tolerance of 10^{-6}. The minimum operator of (2.4) is evaluated for each single time step. We checked the robustness of the numerical procedure by rerunning a large number of simulations with different time steps and error tolerances, and by replacing the minimum operator in (2.4) by a differentiable function.

APPENDIX B: PARAMETER VALUES

Parameter values are listed in the following order:

1. Flow rate D, maximum growth rate r and resource supplies S_j.
2. The parameters K_{ji}, ν_{ji} and q_{ji} are given by three matrices $\mathbf{K}, \mathbf{V}$ and $\mathbf{Q}$, where the rows indicate resources and columns indicate species.
3. Initial conditions for the species densities. If the species is a late invader, the time of invasion is placed between parentheses.

Figure 2.2:
$D = 0.50, r = 1, S_1 = S_2 = S_3 = 10$

	A			B			C			D		
K	0.47	0.66	0.73	0.43	0.21	0.24	0.43	0.21	0.24	0.47	0.75	0.84
	0.41	0.78	0.21	0.29	0.52	0.25	0.29	0.52	0.25	0.10	0.56	0.51
	0.16	0.82	0.16	0.41	0.31	0.46	0.41	0.31	0.46	0.54	0.43	0.21
V	2.17	2.09	1.43	1.88	1.57	2.28	1.76	2.25	1.71	1.28	2.45	2.24
	1.24	2.48	1.68	2.34	1.96	1.61	1.75	1.83	2.29	1.59	1.33	2.21
	1.64	1.48	1.86	1.74	2.37	1.91	2.49	1.78	1.78	2.24	1.88	1.12
Q	1.70	1.45	0.83	1.50	1.38	1.84	1.40	1.97	1.38	1.00	1.63	1.22
	0.88	1.71	1.48	1.82	1.50	1.38	1.36	1.40	1.97	1.44	1.00	1.65
	1.48	0.81	1.70	1.36	1.80	1.50	1.95	1.35	1.40	1.65	1.32	1.00

Initial conditions: A: $N_1 = 2, N_2(t = 500) = 0.1, N_3(t = 2500) = 0.1$; B: $N_1 = 0.8, N_2 = 0.8, N_3 = 1.2$; C: $N_1 = 0.1, N_2 = 0.1, N_3 = 0.1$; D: $N_1 = 0.1, N_2 = 0.11, N_3 = 0.12$

Figure 2.3:
$D = 0.5, r = 1, S_1 = S_2 = S_3 = 10$
The first column corresponds to a Droop model with species parameters:

K			**V**			**Q**		
0.96	0.28	0.96	2.21	2.22	2.35	1.40	1.88	1.20
1.07	0.72	0.32	2.44	2.00	2.49	1.18	1.40	2.04
0.60	0.84	0.86	2.71	2.25	2.11	1.93	1.21	1.40

The second column corresponds to a Monod model that results in the same community equilibrium as the Droop model $(\hat{N}_i, \hat{Q}_{ji} = c_{ji}, \hat{R}_j)$:

H			**C**		
1.67	1.58	1.00	2.80	3.80	3.00
1.01	1.69	1.44	2.98	2.80	4.20
1.48	0.97	1.70	4.00	3.00	2.80

Initial conditions: are set equal to the species equilibrium values $N_1 = 1.03, N_2 = 0.99, N_3 = 1.00$ in both cases.

Figure 2.4:
$D = 0.25, r = 1, S_1 = 8, S_2 = 12, S_3 = 14, S_4 = 9, S_5 = 10$

K					V					Q				
1.51	1.50	1.80	0.50	1.60	1.52	1.50	2.80	1.50	1.50	0.51	0.47	0.86	0.38	0.30
1.60	1.51	1.50	1.70	0.50	1.50	1.52	1.50	2.80	1.50	0.30	0.51	0.47	0.86	0.38
0.50	1.60	1.50	1.50	1.71	1.50	1.50	1.53	1.50	2.80	0.38	0.30	0.51	0.47	0.86
1.70	0.50	1.60	1.51	1.50	2.80	1.50	1.50	1.51	1.50	0.86	0.38	0.30	0.50	0.47
1.50	1.70	0.50	1.60	1.51	1.50	2.80	1.50	1.50	1.51	0.47	0.86	0.38	0.30	0.50

Initial conditions: $N_1 = 0.1, N_2 = 0.11, N_3 = 0.12, N_4 = 0.13, N_5 = 0.14$

Figure 2.5:
$D = 0.25, r = 1, S_1 = 8, S_2 = 12, S_3 = 14, S_4 = 9, S_5 = 10$

K					V					Q				
1.51	1.50	1.80	0.50	1.60	1.38	1.36	2.55	1.36	1.36	0.51	0.47	0.86	0.38	0.30
1.60	1.51	1.51	1.70	0.50	1.36	1.38	1.36	2.55	1.36	0.30	0.51	0.47	0.86	0.38
0.50	1.60	1.50	1.15	1.71	1.36	1.36	1.39	1.36	2.55	0.38	0.30	0.51	0.47	0.86
1.70	0.50	1.60	1.51	1.50	2.55	1.36	1.36	1.37	1.36	0.86	0.38	0.30	0.50	0.47
1.50	1.70	0.50	1.60	1.51	1.36	2.55	1.36	1.36	1.37	0.47	0.86	0.38	0.30	0.50

Initial conditions: $N_1 = N_2 = N_3 = N_4 = 1$ but in A: $N_5 = 0.9$; B: $N_5 = 1.5$; C: $N_5 = 1.8$

Figure 2.6:
$D = 0.25, r = 1, S_1 = 6, S_2 = 10, S_3 = 14$

	A				B					C: insert *i*=5 in B(*)
K	0.11	0.02	0.08	0.15	0.22	0.26	0.24	0.07	0.05	0.06
	0.05	0.13	0.08	0.04	0.25	0.33	0.23	0.10	0.01	0.12
	0.07	0.01	0.13	0.16	0.26	0.01	0.10	0.35	0.04	0.06
V	0.21	0.30	0.20	0.57	0.26	0.49	0.27	0.48	0.09	0.14
	0.37	0.44	0.49	0.45	0.56	0.63	0.67	0.52	0.71	0.27
	0.67	0.41	0.56	0.95	0.98	0.42	0.51	1.26	0.63	0.28
Q	0.48	0.83	0.33	1.20	0.47	0.79	0.24	1.20	0.23	0.28
	0.73	0.95	1.17	1.14	0.47	0.95	1.14	1.09	2.01	0.60
	1.65	1.14	1.20	1.39	1.55	1.10	1.18	1.16	1.68	0.56

Initial conditions: A: $N_1 = 0.1, N_2 = 0.11, N_3 = 0.12, N_4(6000) = 0.1$; B: $N_1 = 0.1, N_2 = 0.11, N_3 = 0.12, N_4 = 0.13, N_5 = 0.14$; C: $N_1 = 0.1, N_2 = 0.11, N_3 = 0.12, N_4 = 0.13, N_5 = 0.14, N_6(5000) = 0.1$ (*: Insert this column between columns 5 and 6 in part B).

3

THE DYNAMICS OF MULTISPECIES COMPETITION WITH NUTRIENT STORAGE

Tomás A. Revilla and Franz J. Weissing

Multispecies competition can display a rich dynamic behavior, including non equilibrium coexistence. In this article we show that multispecies nutrient storage models can be used to explain these dynamics, in the same way as less realistic models do, and one should expect: coexistence when species consume most of those resources for which they have high requirements, competitive exclusion when species consume most of those resources for which they have low requirements, and oscillations when species consume most of those resources for which they have intermediate requirements. Although both simpler and complex resource competition models share many properties, we also found that predictability under nutrient storage is more difficult to asses because the rules of the competitive game, stated as relationships between resource requirements and consumption characteristics, are not rigid ones but instead dependent on the continuous feedback between the species and the environment.

Keywords: *resource competition, storage, quota, equilibrium, internal stability, external stability, oscillations.*

3.1 INTRODUCTION

Resource competition theory (Tilman, 1982; Grover, 1997) is well supported by mathematical models. These models describe the dynamics of competing populations and their resources explicitly. In one of the most common formulations, the interaction of two species competing for two abiotic resources is modeled using the following set of ordinary differential equations:

$$\begin{aligned} \frac{dN_i}{dt} &= (\mu_i(R_1, R_2) - m_i)N_i \\ \frac{dR_j}{dt} &= D(S_j - R_j) - \sum_i c_{ji}\mu_i(R_1, R_2)N_i \end{aligned} \tag{3.1}$$

in which N_i represents the population density of species $i = 1, 2$ and R_j is the concentration of resource $j = 1, 2$. The net growth of species i is the result of the balance between its specific growth rate μ_i, which is an increasing function of the resource concentrations, and its specific mortality rate m_i which is constant. c_{ji} is the content of resource j per species i, and is also a proportionate measure of the consumption impact of species i on resource j. In the absence of consumers, resources follow a linear dynamics, where D is the turnover rate, and S_j the supply concentration.

Basic insight on the dynamics of competition can be achieved by means graphical approaches (León and Tumpson, 1975; Tilman, 1980, 1982), combining the following elements:

RESOURCE REQUIREMENTS: described by the nullclines $\mu_i(R_1, R_2) = m_i$, i.e. lines in the plane R_1R_2 indicating resource combinations for which the net growth of species i is zero.

CONSUMPTION VECTORS: $\mathbf{f}_i = (c_{1i}\mu_i, c_{2i}\mu_i)$, which describe the consumption pattern of species i.

SUPPLY POINT: $\mathbf{S} = (S_1, S_2)$, the steady state condition of the resources in the absence of the consumers.

The main results from the graphical approach are summarized in Figure 3.1. In principle, all the necessary elements, like growth rates, resource contents and resource turnover rates, can be measured or controlled in the laboratory (Tilman, 1977), before the species actually interact. This makes resource competition theory a predictive theory, in contrast with the Lotka-Volterra approach which is phenomenological and not predictive Grover (1997).

However, the reality is that the instantaneous growth of a population does not respond to the level of resources in the environment, i.e. the specific growth rate μ_i is not a direct function of R_i. Instead, the growth rate responds to the internal resource contents or quotas (Droop, 1973), that is, the variable amount of resources that individuals are able to take from the external environment. This has important implications, specially for competition among microorganisms like bacteria and algae (Ducobu et al., 1998). The corresponding *nutrient storage models* are more complex, since they consider a new set of variables, the nutrient quotas. In case of two species and two resources, we must consider four quotas

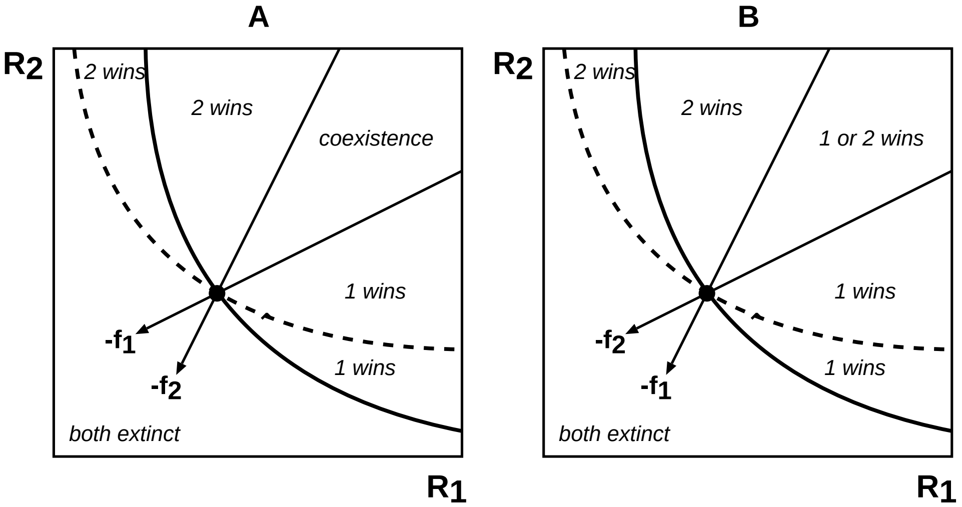


Figure 3.1: In standard resource competition theory, the outcomes of competition between two species for two resources depend on the geometry of nullclines (solid curve for species 1, dashed for species 2), the consumption vectors $\mathbf{f}_i$, and the position of the resource supply point $\mathbf{S}$ in the resource plane R_1R_2. A community equilibrium exists only for supply points located in the "wedge" or "conic" shaped region formed by the projections of consumption vectors at the nullcline intersection, otherwise species 1 or 2 always wins, or both go extinct. (A) If the community equilibrium exists, it will be stable if each species consume a high proportion of its most limiting resource, as indicated by the slopes of the consumption vectors (species 1 and 2 are more limited by resources 1 and 2 respectively). (B) But if each species consume a high proportion of the most limiting resource of its competitor, the community equilibrium will be unstable, and either species 1 or 2 wins depending on the initial conditions. If the nullclines never cross (not shown here) a community equilibrium is not possible at all, and the species whose nullcline is closer to the origin always wins the competition.

(of two resources per species), in addition to the two species densities and the two resource concentrations; this leave us with eight differential equations. And in general, for n species and m resources there are $n \times m$ quotas, for a total $n + m + n \times m$ differential equations. Whereas in classical models the number of variables increase additively with the number of species and resources, in storage models they increase in a multiplicative way. Naturally, the number of parameters that control the dynamics also increases.

Only recently, the scenario of two species and two resources has been fully studied analytically (Li and Smith, 2007), but for a particular class of storage models and under chemostat conditions ($m_i = D$). In addition, the mathematics involved (monotone dynamical systems Smith, 1995) is far from the grasp of most biologists. The graphical approach, which is much more useful for shaping our intuition, has been seldom applied (Turpin, 1988; Hall et al., 2008), and limited to conditions prevailing in chemostats. However, it is not immediately obvious that the graphical approach is applicable to storage models. On the one hand, like in standard models, the resource supplies and the consumption vectors are defined in the resource planes. On the other hand, the growth rates are not dependent on the external resources, and thus, the species nullclines cannot be defined in the resource planes. In addition, it is known that under non-chemostat conditions ($m_i > D$) the transient behavior of simple quota models can be different from that in chemostat conditions (Clodong and Blasius, 2004).

In this article we make a systematic analysis of a simple but generic model of competition that includes resource storage. We discuss to what extent resource requirements, consumption patterns and resource supplies still govern the dynamics of the competitive system. We explore to what extent the graphical approach can be applied to storage based models, and the link between the graphical approach and the stability of equilibria. Finally, the insights gained from the graphical approach are applied to higher dimensional scenarios, illustrating the advantages and also the limitations.

3.2 THE MODEL

The model discussed in this article is a multiple species and multiple resources extension of the nutrient storage, or quota model for microorganisms (Droop, 1973; Grover, 1997). It describes the competition among n species with population densities N_i ($i = 1, \dots, n$) for m essential resources with densities R_j ($j = 1, \dots, m$). Its main distinction with standard models is that it follows the dynamics of the *quota* Q_{ji} *of resource j in species i*, i.e. the variable content of resource j in an individual of species i:

$$\frac{dN_i}{dt} = (\mu_i(Q_{1i}, \dots, Q_{mi}) - m_i)N_i \tag{3.2a}$$

$$\frac{dQ_{ji}}{dt} = f_{ji}(R_j) - \mu_i(Q_{1i}, \dots, Q_{mi})Q_{ji} \tag{3.2b}$$

$$\frac{dR_j}{dt} = \phi_j(R_j) - \sum_{i=1}^{n} f_{ji}(R_j)N_i \tag{3.2c}$$

Some equations in this model resemble the equations of the standard model in the introduction (3.1). However, in the storage model the specific growth rate of species i is a

Function	Generic Properties	Special case
Growth rate $\mu_i(Q_{1i}, \ldots, Q_{mi})$	$\partial\mu_i/\partial Q_{ji} \geqslant 0$ for all j $\mu_i = 0$ if $Q_{ji} = 0$ for at least one *j*	Droop-Liebig growth $\mu_i = r_i \min\left(1 - \frac{q_{ji}}{Q_{ji}}\right)$
Resource consumption $f_{ji}(R_j)$	$df_{ji}/dR_j > 0$ $f_{ji}(0) = 0$	Holling type II uptake $f_{ji}(R_j) = \frac{\nu_{ji} R_j}{K_{ji} + R_j}$
Resource turnover $\phi_j(R_j)$	$d\phi_j/dR_j < 0$ $\phi_j(S_j) = 0$ for $S_j > 0$	Chemostat turnover $\phi_j(R_j) = D(S_j - R_j)$

Table 3.1: Generic assumptions on the competition model with resource storage and a special case implementation used in some examples.

function of the resource quotas $\mu_i(Q_{1i}, \ldots, Q_{mi})$ instead of the external resources R_j. The specific growth rate m_i is, as before, constant. The quota dynamics is determined by *resource uptake* at rate $f_{ji}(R_j)$ and "dilution by growth" (Grover, 1997), i.e. the distribution of quotas among offspring in the case of reproduction. Since dilution is coupled to reproduction, the dilution term is typically assumed to be proportional to the specific growth rate (Grover, 1997). In the absence of consumers, the resource dynamics is governed by a turnover rate $\phi_j(R_j)$. In the presence of consumers. resources are depleted by consumption where $f_{ji}(R_j)N_i$ corresponds to the uptake of resource j by the population of species i.

In the following sections we will discuss the assumptions made on the functions μ_i, f_{ji} and ϕ_j. All assumptions are summarized in Table 3.1.

3.2.1 *Growth rate*

The contents of the various resources in an individual of species i is characterized by a quota vector $\mathbf{Q}_i = (Q_{1i}, \ldots, Q_{mi})$. The set of all possible quota vectors will be called the *quota space* of species i. We assume that the rate $\mu_i(\mathbf{Q}_i)$ is a non-decreasing function of the quotas. Since resources are essential, the growth rate $\mu_i(\mathbf{Q}_i)$ is zero if the quota of at least one resource is zero. We will only consider species where $\mu_i(\mathbf{Q}_i) > m_i$ for at least some $\mathbf{Q}_i$.

Special case. For simplicity, resource competition theory often focuses on *perfectly essential resources*, that is on a situation where the lack of one resource cannot be compensated by the overabundance of another resource. In such a case, the specific growth rate μ_i follows Liebig's law of the minimum (Von Liebig, 1840; Tilman, 1977, 1982; Grover, 1997):

$$\mu_i(Q_{1i} \ldots, Q_{mi}) = \min(\mu_{1i}(Q_{1i}), \ldots, \mu_{mi}(Q_{mi})) \tag{3.3}$$

where μ_{ji} is the growth rate of species i when only resource j is limiting (i.e. all other quotas have a very high level). If the growth rate is given by (3.3), growth is determined by only a single resource at any time, the so called *limiting resource*.

In most studies, the functions μ_{ji} are modeled explicitly using Droop's (1973) empirical formula:

$$\mu_{ji}(Q_{ji}) = r_i \left(1 - \frac{q_{ji}}{Q_{ji}}\right) \tag{3.4}$$

Here r_i is the maximum specific growth rate (which does not depend on j), and q_{ji} is a threshold level such that for $0 \leqslant Q_{ji} \leqslant q_{ji}$ the growth is assumed to be zero.

3.2.2 *Resource consumption*

The *specific consumption or uptake rate* f_{ji} of resource j by species i is a continuous increasing function of the resource concentration R_j. Obviously, the uptake should be zero if the resource is absent: $f_{ji}(0) = 0$. The consumption pattern of species i can be characterized by its *consumption vector* $\mathbf{f}_i = \mathbf{f}_i(\mathbf{R}) = (f_{1i}(R_1), \dots, f_{mi}(R_m))$, where $\mathbf{R} = (R_1, \dots, R_m)$ is the *resource vector*. As illustrated in Figure 3.2B and 3.2D, consumption vectors can be symbolized by arrows in *resource space* (the set of all possible resource vectors). The overall consumption pattern of the community can be described by a *consumption matrix* $\mathbf{F} = \mathbf{F}(\mathbf{R}) = (f_{ji}(R_j))_{j,i}$, that is a matrix the columns of which are given by the consumption vectors of the species.

It is also acknowledged that resource uptake is also a negative function of the quotas, i.e. $\partial f_{ji}/\partial Q_{ji} < 0$ Morel (1987). We decided not to consider this fact, because it involves a great deal of mathematical complication. Nevertheless, in the final discussion we justify why our main results are not affected by this omission.

Special case. Most studies assume that consumption rates follow a Holling type II functional response, where ν_{ji} is the maximum uptake rate of resource j and K_{ji} is a half-saturation constant:

$$f_{ji}(R_j) = \frac{\nu_{ji} R_j}{K_{ji} + R_j} \tag{3.5}$$

In contrast to Droop's purely phenomenological formula (3.4), the uptake function (3.5) can be given a mechanistic interpretation (Aksnes and Egge, 1991).

3.2.3 *Resource turnover*

We assumed the *turnover rate* ϕ_j of resource j is a continuous decreasing function of R_j. In the absence of consumers, resource j attains a steady state concentration $R_j = S_j$, at which $\phi_j(S_j) = 0$. The turnover dynamics is characterized by *resource turnover vectors* $\mathbf{\Phi}(\mathbf{R}) = (\phi_1(R_1), \dots, \phi_m(R_m))$, which correspond to arrows in resource space shown in Figure 3.2B and 3.2D (Grover, 1997). The turnover vector is zero at the *resource supply point* $\mathbf{S} = (S_1, \dots, S_m)$.

Special case. The simplest model for ϕ_j is the linear function

$$\phi_j = D(S_j - R_j) \tag{3.6}$$

where D is the resource flow rate. This form of turnover dynamics can be realized in chemostats, and it is a good approximation for many aquatic systems (Grover, 1997).

3.3 RESOURCE REQUIREMENTS

The species dynamics depends directly on the amount of stored resources Q_{ji}: low quotas result in $\mu_i < m_i$ and high quotas in $\mu_i > m_i$. Thus, there is a boundary in quota space where $\mu_i = m_i$. As the actual values of Q_{ji} are determined by the consumption dynamics (3.2b), μ_i depends indirectly on R_j: if resources in the environment are scarce, quotas will eventually decrease, leading to $\mu_i < m_i$; if resources are overabundant, quotas will eventually increase, leading to $\mu_i > m_i$. Accordingly, there is a boundary for species i in the space of external resources, which determines resource combinations leading to net growth or decrease in the long term. In this section we characterize these boundaries. in other words minimum resource requirements for growth, in quota space and in resource space.

3.3.1 *General case*

The *nullcline of species i* $\mathbf{Q}_i^0$, is a $(m-1)$-dimensional surface in m-dimensional quota space. It corresponds to those quota vectors $\mathbf{Q}_i$ for which

$$\mu_i(\mathbf{Q}_i) = m_i \tag{3.7}$$

In the case of two resources, the nullcline of species i is a 1-dimensional surface (a line) in a 2-dimensional quota space, as in Figure 3.2A. For quota vectors below the nullcline, species i will decline ($\mu_i < m_i$), for quota vectors above the nullcline it will grow ($\mu_i > m_i$).

Let us assume for the moment that the system is at a positive equilibrium, i.e. with $N_i, Q_{ji}, R_j > 0$. In this case $\mu_i = m_i$, thus the quotas of species i lie on $\mathbf{Q}_i^0$. As $\dot{Q}_{ji} = f_{ji}(R_j) - m_i Q_{ji} = 0$ in (3.2b), each quota Q_{ji} is associated to a particular resource concentration R_{ji}. Using this relationship, we can map the nullcline $\mathbf{Q}_i^0$ in quota space to a $(m-1)$-dimensional surface $\mathbf{R}_i^0 : \mu_i(\mathbf{f}_i(\mathbf{R})/m_i) = m_i$ in resource space. We call this boundary a *quasi-nullcline* in resource space, since $\mu_i < m_i$ below $\mathbf{R}_i^0$ and $\mu_i > m_i$ above $\mathbf{R}_i^0$.

We would like to stress that $\mathbf{R}_i^0$ is not a nullcline in the technical sense of the word, since the relations $\mu_i < m_i$, $\mu_i = m_i$ and $\mu_i > m_i$ only hold under under the equilibrium assumption made above. Since the specific growth rate μ_i depends on the quotas (and not on the external resource concentrations), $\mu_i(\mathbf{Q}_i)$ can be large even for small resource concentrations R_i, due to storage in the past. However, for a resource vector below $\mathbf{R}_i^0$, the quota $\mathbf{Q}_i$ will *eventually* drop below $\mathbf{Q}_i^0$, leading to the decline of species i. Similarly, for resources vector above, quotas will eventually increase to values above $\mathbf{Q}_i^0$, allowing population growth.

The nullclines in quota species and quasi-nullclines in resource space are illustrated in Figure 3.2. The nullcline $\mathbf{Q}_i^0$ belongs to the "private" quota space of species i, thus it cannot be used to predict the outcomes of competition, which takes place in the "public" space of external resources. We can only make predictions about competition by considering the geometry of quasi-nullclines $\mathbf{R}_i^0$.

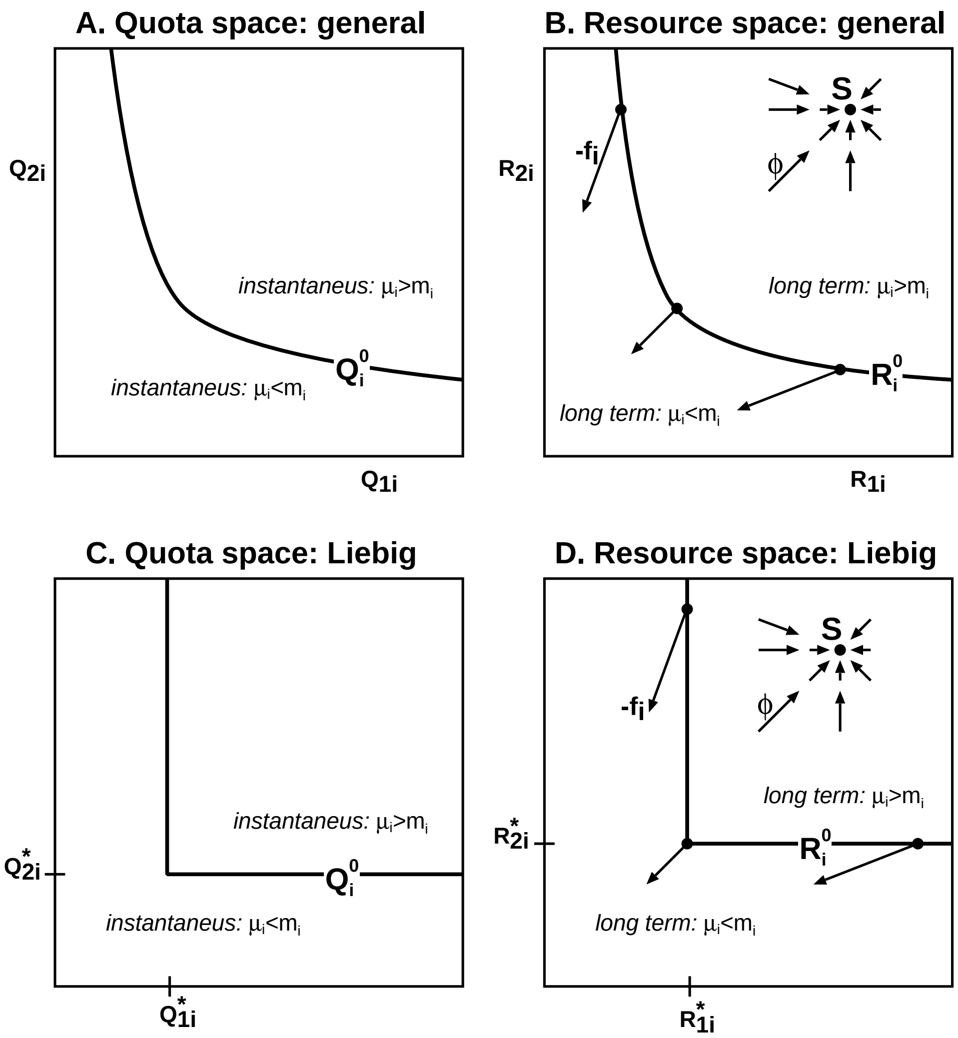


Figure 3.2: Quota space (A,C) and external resource space (B,D) for two essential resources. The nullcline $\mathbf{Q}_i^0$ separates the quota space into regions of positive net growth ($\mu_i > m_i$ above the nullcline) and negative net growth ($\mu_i < m_i$ below the nullcline). The quasi-nullcline $\mathbf{R}_i^0$ separates resource space in regions for which the net growth rate is positive or negative, but in the long term. In the special case of Liebig's law (C,D), the nullclines are specified by quota requirements Q^*_{ji} and the quasi-nullclines the external resource requirements R^*_{ji}. Nullclines are most easily derived for quota space. External resource space has the advantage that it allows the simultaneous representation of the resource turnover vector field $\boldsymbol{\Phi}$ (pointing towards the resource supply point $\mathbf{S}$) and the resource-dependent consumption vectors $\mathbf{f}_i$. Note that the consumption vectors tend to align with the resource R_j axis if R_j is increasing while keeping all other resource concentrations fixed.

3.3.2 *Liebig's law*

In the special case of Liebig's law (3.3), nullclines and quasi-nullclines have a particularly simple description in terms of m minimal requirements for Q_{ji} (respectively R_j).

The *internal resource (or quota) requirement* of resource j for species i is that quota $Q_{ji} = Q^*_{ji}$ for which the specific growth rate is balanced by the specific loss rate, given that the other resources are not limiting growth

$$\mu_{ji}(Q^*_{ji}) - m_i = 0 \tag{3.8}$$

Figure 3.2C illustrates how the vector $\mathbf{Q}^*_i = (Q^*_{1i}, Q^*_{2i})$ determines the L-shaped nullcline in quota space for the special case of two resources. This basic principle extends to higher dimensions $(m > 2)$.

The *external resource requirement* of resource j for species i is that resource concentration $R_j = R^*_{ji}$ just allowing to achieve the quota Q^*_{ji} given that the quotas of all other resources are not limiting. In view of (3.2b), R^*_{ji} is implicitly given by

$$f_{ji}(R^*_{ji}) - m_i Q^*_{ji} = 0 \tag{3.9}$$

Figure 3.2D shows (for $m = 2$) how the vector $\mathbf{R}^*_i = (R^*_{1i}, R^*_{2i})$ determines the L-shaped quasi-nullcline of species i in external resource space. Again, this result extends to any number of resources $(m > 2)$.

Special case. If μ_{ji} and f_{ji} are specified by (3.4) and (3.5), Q^*_{ji} and R^*_{ji} are given by

$$Q^*_{ji} = \frac{r_i q_{ji}}{r_i - m_i} \tag{3.10}$$

$$R^*_{ji} = \frac{K_{ji} m_i Q^*_{ji}}{\nu_{ji} - m_i Q^*_{ji}} = \frac{K_{ji} m_i r_i q_{ji}}{\nu_{ji}(r_i - m_i) - m_i r_i q_{ji}} \tag{3.11}$$

3.4 EQUILIBRIA

In general, our model has many equilibrium points. With the exception of the trivial case (all $N_i = 0$) the feasibility of an equilibrium requires certain conditions regarding resource requirements and consumption. In this section we will demonstrate that this conditions have a clear representation in the geometry of the quasi-nullclines, consumption vectors and resource supply vectors.

3.4.1 *General case*

For *n* species, a positive equilibrium ($dN_i/dt = dQ_{ji}/dt = dR_j/dt = 0$ for all $N_i > 0$) requires all resource equilibrium concentrations $\hat{R}_j$ to be part of all the quasi-nullclines. In other words the quasi-nullclines of all species in external resource space must intersect in a common *resource equilibrium vector*

$$\hat{\mathbf{R}} = (\hat{R}_1, \ldots, \hat{R}_m)$$

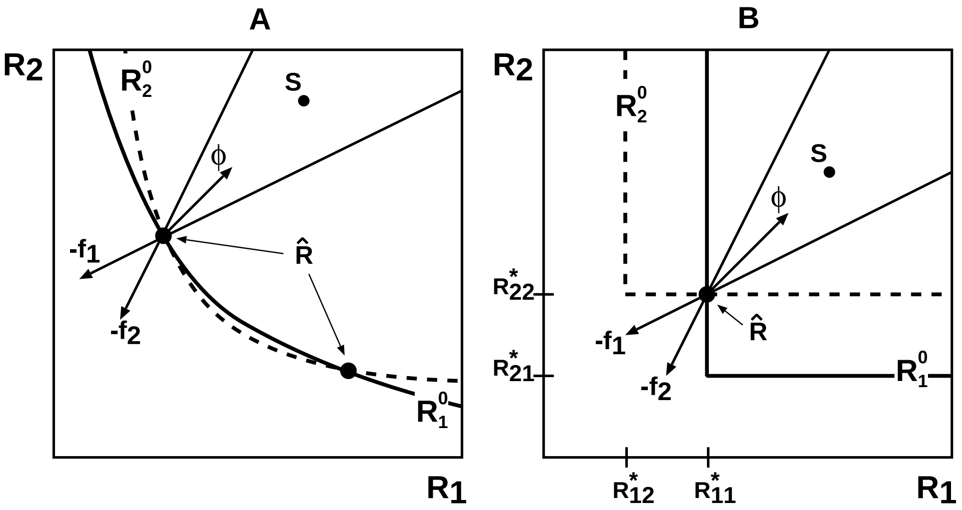


Figure 3.3: (A) Nullclines and their intersection points ($\hat{\mathbf{R}}$) for two species competing for two essential resources. If resource turnover is described by the chemostat equation, a two-species equilibrium is feasible only if the supply point (or the resource turnover vector $\hat{\mathbf{\Phi}}$) lies in the cone formed by the species consumption vectors at $\hat{\mathbf{R}}$. (B) For perfectly essential resources, nullclines can only intersect at a single point. The consumption vectors at the intersection point define locations of the supply points for which the two species can coexist, and for which one species excludes the other.

In generic cases, the intersection of the n $(m-1)$-dimensional quasi-nullclines will be a set of dimension $m-n$. If the number of species equals the number of resources $(m=n)$, the quasi-nullclines will intersect (if they intersect at all) in one or several points (0-dimensional), as illustrated in Figure 3.3A. The intersection will typically be lines (1-dimensional) for $m = n+1$ (e.g. two species competing for three resources), surfaces (2-dimensional) for $m = n+2$, and so on. If $m < n$ the intersection will in generic cases be empty. In other words: *at equilibrium the number of coexisting species does not exceed the number of resources* ($n \leqslant m$), which corresponds to the well known *Principle of Competitive Exclusion* (Grover, 1997).

For a given resource equilibrium vector $\hat{\mathbf{R}}$, the species equilibrium densities $\hat{N}_i$ are the solutions of a linear system of m equations in n unknowns that results from setting $dR_j/dt = 0$ in (3.2c):

$$\phi_j(\hat{R}_j) = \sum_{i=1}^{n} f_{ji}(\hat{R}_j)\hat{N}_i \tag{3.12}$$

In Appendix A we prove that this equation has a unique positive solution (all $\hat{N}_i > 0$) if and only if *the resource turnover vector* $\hat{\mathbf{\Phi}} = (\phi_1(\hat{R}_1), \ldots, \phi_m(\hat{R}_m))$ *falls in the cone spanned by the consumption vectors* $\hat{\mathbf{f}}_i = (f_{1i}(\hat{R}_1), \ldots, f_{mi}(\hat{R}_m))$ *of the species*. The same result was obtained earlier by Huisman and Weissing (2001), for the corresponding resource competition model without nutrient storage.

For the special case of a chemostat (3.6), this corresponds to the requirement that the resource supply point $\mathbf{S} = (S_1, \dots, S_m)$ falls into the cone that is formed by the n consumption vectors and attached to the resource equilibrium vector $\hat{\mathbf{R}}$, which appears as a "wedge" in Figure 3.3.

Once $\hat{\mathbf{R}}$ and $\hat{\mathbf{N}}$ are determined, the equilibrium quotas $\hat{\mathbf{Q}}$ are obtained by setting $dQ_{ji}/dt = 0$ in (3.2b)

$$\hat{Q}_{ji} = \frac{f_{ji}(\hat{R}_j)}{m_i} \tag{3.13}$$

The case of a monoculture $(m > n = 1)$ deserves special attention. In a monoculture the "cone" collapses into a semi-line, the slope of which is given by the consumption vector at $\hat{\mathbf{R}}$. Logically, this time $\hat{\mathbf{R}}$ cannot be a quasi-nullcline intersection (there is only one species!). Instead $\hat{\mathbf{R}}$ corresponds to the point in the quasi-nullcline where the consumption vector and the turnover vector are parallel. This fact will be extremely useful when exploring the stability of monocultures against invaders.

3.4.2 *Liebig's law*

Consider an equilibrium (a monoculture or a community) where species i is limited by resource j, thus $\mu_i(\hat{\mathbf{Q}}_i) = \mu_{ji}(\hat{Q}_{ji}) = m_i$. According to (3.8) the equilibrium level $\hat{Q}_{ji}$ corresponds to the quota requirement Q^*_{ji} of species i for j: $\hat{Q}_{ji} = Q^*_{ji}$. In view of equation (3.9), this implies $\hat{R}_j = R^*_{ji}$. In other words, *the equilibrium concentration* $\hat{R}_j$ *of resource* j *matches species* i *external resource requirement* R^*_{ji} *for the limiting resource* j.

In generic cases, different species will differ in their values R^*_{ji}. As a consequence, in a community equilibrium, each species i has the highest requirement (compared to others) for the resource j limiting its own growth. To see this, consider another species k with a higher requirement for resource j: $R^*_{jk} > R^*_{ji} = \hat{R}_j$. This, however, is impossible, since $R^*_{jk} > \hat{R}_j$ would imply that the external resources are below the quasi-nullcline of species k, which accordingly, decreases. In other words, species k cannot be in equilibrium with species i. Thus, *in a community equilibrium each species* i *has the highest requirement (compared to the other species) for the resource limiting its own growth.* The same result was obtained earlier by Huisman and Weissing (2001), for the corresponding resource competition model without nutrient storage.

Summarizing, in an equilibrium if species i is limited by resource j then $\hat{R}_j = R^*_{ji}$. If this happens to be a community equilibrium, then no other species $k \neq i$ has a higher requirement for that resource j, i.e. $R^*_{jk} < R^*_{ji} = \hat{R}_j$. Ergo, in a community equilibrium no other species but i determines the equilibrium level of resource j. In other words, there is a one-to-one relationship between n species and their n limiting resources.

Thus, given n species, without loss of generality we can label the resources in such a way that species i has the highest requirement for resource i, thus $\hat{R}_i = R^*_{ii}$. In particular for $m = n$ the resource equilibrium vector is

$$\hat{\mathbf{R}} = (\hat{R}_1, \dots, \hat{R}_i, \dots, \hat{R}_n) = (R^*_{11}, \dots, R^*_{ii}, \dots, R^*_{nn}) \tag{3.14}$$

If $m > n$, there will be $m - n$ resources in the $\hat{\mathbf{R}}$ vector that are non-limiting; by definition the equilibrium concentrations of such resources must higher than any of the species requirements ($\hat{R}_{j(non-limiting)} > R^*_{ji}$).

3.5 STABILITY

If n species are competing for m resources, the competitive dynamics is described by $n + m + n \times m = (n+1)(m+1) - 1$ differential equations. Because of the high number of dimensions, the stability of equilibria is difficult to characterize. The stability of an equilibrium $\hat{\mathbf{X}} = (\hat{\mathbf{N}}, \hat{\mathbf{Q}}, \hat{\mathbf{R}},)$ can be determined by investigating the eigenvalues of the corresponding jacobian matrix $\mathbf{J}(\hat{\mathbf{X}})$ (Murray, 2002). This is a difficult task, because already for $n = m = 2$, $\mathbf{J}(\hat{\mathbf{X}})$ is an 8×8 matrix, while it is a 15×15 matrix for $n = m = 3$. At the moment, only the chemostat scenario ($m_i = D$) for $m = n = 2$ has been analysed (Li and Smith, 2007), and it displays the same outcomes as standard competition models. More general results, however, are not available. In this section we give an overview of our partial stability analysis, relating the stability conditions to the resource consumption patterns at equilibrium, i.e. to the geometry of the consumption vectors. (the lenghty details of our analysis can be read in Appendix B).

3.5.1 *External vs internal stability*

Some progress can be made by distinguishing between *internal* and *external stability*. To this end, we distinguish between those species that are present at equilibrium (those i for which $\hat{N}_i > 0$) from those that are absent (those i for which $\hat{N}_i = 0$). The former will be called *resident species* and the latter *invader species*. By relabeling the n species, we can assume without loss of generality that the first n_k species $i = 1, \ldots, n_k$ are residents, while the last $n_l = n - n_k$ species are invaders. The concept of internal stability refers to the stability of $\hat{\mathbf{X}}$ with respect to small perturbations involving the community of resident species. External stability refers to the stability of $\hat{\mathbf{X}}$ with respect to the invasion of (a set) invader species that appear with low densities.

In Appendix B.1 we prove that: *the equilibrium $\hat{\mathbf{X}}$ is stable if and only if, it is both internally and externally stable.* Hence, a full stability analysis can be decomposed into the simpler task of considering the analysis (lower dimensional) of internal and external stability.

3.5.2 *External stability*

External stability is relatively easy to characterize. In fact, it suffices to address each of the n_l invader species in isolation. In Appendix B2. we prove that: *a community of n_k residents is externally stable if none of the n_l invaders is able to grow when rare.* To put this in graphical terms: the resident community is externally stable, if and only if the equilibrium level of resources $\hat{\mathbf{R}}$ set by the residents happens to be below the quasi-nullclines of all possible invaders.

The reader will immediately recall that instantaneous growth does not depend on external resources but on the quotas. It might happen that the invaders come very high quotas, so they initially grow even if $\hat{\mathbf{R}}$ lies below their quasi-nullclines. However, this does not invalidate the consequences of our claim: since they have very low densities, invaders cannot have a noticeable effect on external resource abundances, and simultaneously their quotas rapidly dilute following the initial growth. Thus, invaders are always doomed to extinction if $\hat{\mathbf{R}}$ lies below their quasi-nullclines. The most correct statement regarding external stability would be: *a community of* n_k *residents is externally stable if none of the* n_l *invaders can grow when rare in the long term*.

3.5.3 *Internal stability*

Internal stability is a much more challenging problem, because the variables of the resident populations are interdependent. The situation is somewhat simplified in case of Liebig's law of the minimum, since the growth rate of each species is only dependent on a single resource. As a consequence, the jacobian matrix has a simpler structure. In Appendix B.3, we show that this allows to deduce a simple but important stability requirement if resources are perfectly essential, *an equilibrium* $\hat{\mathbf{X}}$ *can only be internally asymptotically stable if the determinant of the consumption matrix* $\hat{\mathbf{F}}$ *of the resident species is positive*:

$$\det(\hat{\mathbf{F}}) > 0 \tag{3.15}$$

This determinant criterion has simple geometrical interpretations, for a single species, for two, and for many. In the trivial case of a resident community consisting of one species, i.e. a monoculture, the determinant is equal to the consumption rate of its limiting resource at equilibrium, which by definition is always positive. The internal stability requirement is always hold for monocultures. In Appendix B.4 we prove that in fact: *all monocultures are internally stable* (previously demonstrated by Legovic and Cruzado 1997, for $m_i = D$).

In the scenario of two species competing for two resources, if we label the species according to our convention in equation (3.14), the stability (3.15) requirement can be writen as:

$$\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.16}$$

in other words, the consumption vector species 2 is steeper than the consumption vector of species 1 (provided R_1 is the horizontal axis and R_2 the vertical axis) at the intersection point of the quasi-nullclines. Thus, for two species competing for two resources internal stability requires that at equilibrium: *each species consume comparatively more of the resource for which it has the highest requirement*.

In higher dimensions ($n = m > 2$), the geometrical interpretation of (3.15) is that the consumption vectors of the resident species are *positively oriented* (Weinstein, 2003) with respect to the external resource axes. For example, see that in Figure 3.4A, $\mathbf{f}_1$ tends to be "horizontal" like the R_1 axis, and $\mathbf{f}_2$ tends to be "vertical" like the R_2 axis: the vectors are positively oriented. In contrast, see that in Figure 3.4B, $\mathbf{f}_1$ is tends to be vertical and $\mathbf{f}_2$ tends to be horizontal: the vectors are negatively oriented. In higher dimensions, positive orientation means that $\mathbf{f}_i$ tends to be more "aligned" to the R_i axis than to any other axis. Thus, each species becomes associated with one resource (the one limiting its own growth), and we interpret condition (3.15) in words as follows: *stability requires that species tend to consume relatively more of those resources for which they have the highest requirements*.

Although conceptually interesting and computationally useful, the criterion (3.15) is (for more than two resources) by far not sufficient to characterize internal stability. In contrast, the invasion analysis, on which external stability is based, is relatively easy to perform. In the next section we show that invasion analysis can also give important clues concerning internal stability. In brief, a community equilibrium is often internally stable if all border equilibria are externally unstable. The latter corresponds to the concept of mutual invadibility: a set of species is expected to coexist stably if each species can invade any combination of resident species.

3.6 TWO LIMITING RESOURCES

In the introduction we said that the outcomes in competition models without storage is closely related to the geometry of nullclines, consumption vectors, and resource supply points. These elements have been considered in the study of the storage model of two species competing for two resources (Tilman, 1977; Turpin, 1988; Hall et al., 2008), but only for the special case of the chemostat, in which real mortalities m_i are replaced by the chemostat flow rate D.

In the last section we showed that in general, i.e. not just for the chemostat, both the existence of the community equilibrium and its internal stability, are strongly dependent on the properties of quasi-nullclines, supply points, and the consumption matrix (the "cone rule" and the "determinant rule"). However, a complete criterion of internal stability is still lacking. In this section, we will show that the consumption patterns at the community equilibrium, given by the matrix $\hat{\mathbf{F}}$, will tell us if the monocultures are externally stable against invasion. Thus, even if the graphical approach cannot address the full stability of the system, it can show whether or not two species competing for two resources can coexist.

First of all, If the quasi-nullclines never cross, the outcome of competition is trivial: the species with lowest requirements always wins the competition because it can to grow when the level of external resources are below the requirements of other species. So, from here onwards we will assume the nullclines always cross.

Let us then assume that the quasi-nullclines of species 1 and 2 cross, so an equilibrium will be possible for certain combinations of resource supplies S_1, S_2. Following our labeling convention (3.14), species 1 has the highest requirement for resource 1, and species 2 the highest for resource 2:

$$R^*_{11} > R^*_{12}, R^*_{22} > R^*_{21} \tag{3.17}$$

Hence the species quasi-nullclines cross at the resource equilibrium vector $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22})$, where species 1 is limited by resource 1 and species 2 is limited by resource 2. All these details appear in Figure 3.4. Now we proceed to use this graphical information in order to predict the outcomes of competition.

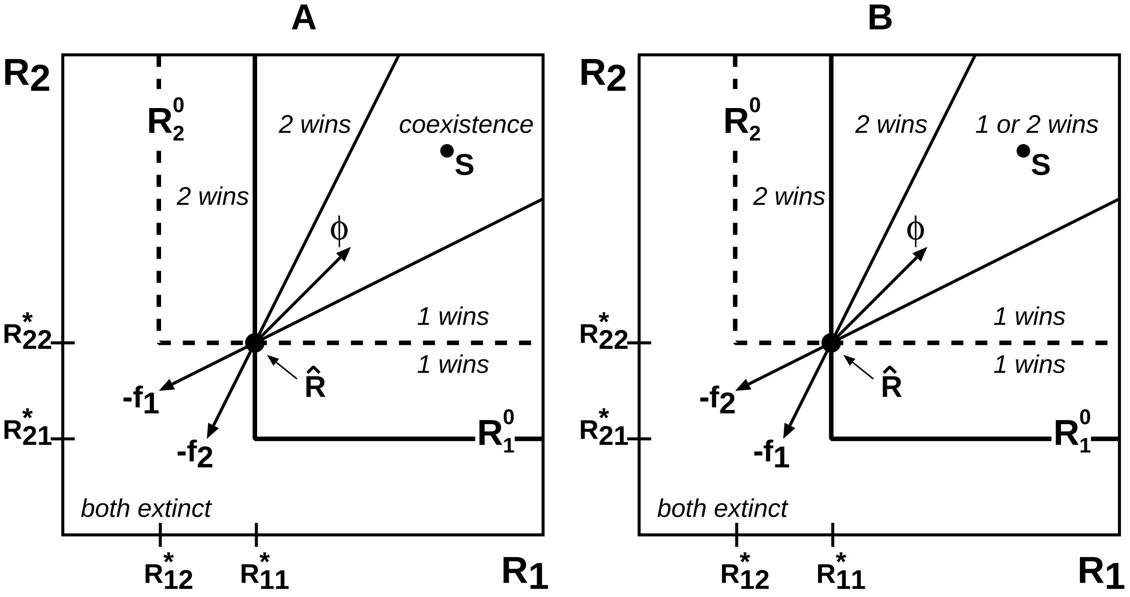


Figure 3.4: Outcomes of the competition between two species for two perfectly essential resources in the nutrient storage model. In contrast with the standard model (Fig. 3.1), the quasi-nullclines (solid for species 1, dashed for species 2) replace the nullclines in the space of external resources. See the main text for a detailed explanation.

(1) Coexistence. Let us assume that at the nullcline intersection the slopes of the consumption vectors and the resource turnover vector are related in the form shown in Figure 3.4A

$$\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} > \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.18}$$

i.e. the consumption vector of species 2 is steeper than the consumption vector of species 1, and the slope of the turnover vector lies in between. In consequence, by the "cone rule" a community equilibrium ($\hat{N}_1, \hat{N}_2 > 0$) exists, and by the "determinant rule", in the form of (3.16), we cannot rule out that this equilibrium is stable.

Now consider the following. First, according to (3.18) the slope of the consumption vector of species 1 is smaller than the slope of the turnover vector at $\hat{\mathbf{R}}$. Second, in the monoculture equilibrium of species 1, the slopes of these vectors must be equal, i.e. parallel, in a point $\tilde{\mathbf{R}} = (\tilde{R}_1, \tilde{R}_2)$ of the L-shaped quasi-nullcline of species 1. The relative position $\tilde{\mathbf{R}}$ in the quasi-nullcline of species 1 could be (see Fig. 3.4A):

- In the horizontal branch where $\tilde{R}_1 > R^*_{11}$ and $\tilde{R}_2 = R^*_{21}$. This means that $\tilde{R}_2 < R^*_{22}$. However, this cannot be true, because in such a point the slope of $\mathbf{f}_1$ is smaller than in $\hat{\mathbf{R}}$ and the slope of $\mathbf{\Phi}$ is much bigger (properties of consumption and turnover vectors, see Fig. 3.2).

- In the vertical branch where $\tilde{R}_1 = R^*_{11}$, and $\tilde{R}_2 < R^*_{22}$. This also must be ruled out, because it makes $\boldsymbol{\Phi}$ more steeper than $\mathbf{f}_1$, compared to the situation at the quasi-nullcline intersection.

- In the vertical branch where $\tilde{R}_1 = R^*_{11}$, and $\tilde{R}_2 > R^*_{22}$. This last alternative is correct, because only by raising R_2 above R^*_{22} we have that the slope of $\mathbf{f}_1$ increases and that of $\boldsymbol{\Phi}$ decreases, making both vectors parallel.

Thus, if the slopes of the consumption and turnover vectors at the quasi-nullcline intersection relate as in (3.16), we conclude that in the monoculture of species 1: $\tilde{R}_1 = R^*_{11}$ and $\tilde{R}_2 > R^*_{22}$. In consequence, the monoculture of species 1 is unstable against invasion. Mutatis mutandis, the same is true for the monoculture of species 2.

Thus, if at the community equilibrium *each species consumes comparatively more of its limiting resource*, then both monocultures are locally unstable and both species persist. A series arguments lead us to conjecture that such coexistence is stable. First, under conditions of parameter symmetry, the community equilibrium is in fact internally stable. Second, all simulations so far indicate that the configuration described by (3.18) always converges to stable equilibrium coexistence.

(2) Competitive exclusion. Let us assume that at the nullcline intersection the slopes of the species consumption vectors and the resource turnover vector are related in the form shown by Figure 3.4B

$$\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} < \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} < \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.19}$$

i.e. a configuration in which the slope of the consumption vectors is the opposite of that in (3.18). The slope of the turnover vector lies between that of both consumption vectors, thus the community equilibrium is feasible. However, this equilibrium is unstable because (3.19) contradicts (3.16). By comparing the slopes of consumption and turnover vectors in monocultures as before, we conclude that under (3.19) the monocultures are externally stable against invasion.

Thus, if at the community equilibrium *each species consumes comparatively less of its limiting resource*, then both monocultures are locally stable and both species exclude each other. Condition (3.19) describes a system where both monocultures are local attractors and the community equilibrium is a saddle point. Depending on the initial conditions either species 1 or species 2 exclude the other species and wins the competition.

Competitive dominance. The slopes of the consumption and resource turnover vectors at the quasi-nullcline intersection can also be related either as

$$\frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})}, \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.20}$$

or

$$\frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} < \frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})}, \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.21}$$

In both cases the slope of the turnover vector in higher or smaller that the slopes of both consumption vectors, thus by the “cone rule”, the community equilibrium is not feasible. Again, using the quasi-nullcline intersection as referencem and comparing the slopes of a single species against the turnover vector, we will conclude that in the first alternative (3.20) species 2 meets the invasion criterion but species 1 does not, thus species 2 always wins. The second alternative (3.21) is the opposite, species 2 is always excluded by species 1. In contrast with the mutual exclusion case, one species is always the winner, not depending on the initial conditions.

Although our analysis concerned perfectly essential resources (L-shaped quasi-nullclines), it is possible to show graphically that in general, if quasi-nullclines, consumption vectors and turnover vectors have the same geometries of Figure 3.4, the same predictions will be obtained. Thus, we conclude that for two species and two resources, the graphical methodology used for standard models without storage (Fig. 3.1) can be extrapolated to the nutrient storage model.

3.7 THREE LIMITING RESOURCES

In models without storage like in the introduction (3.1), there are only a few outcomes in case of two resources, while the dynamics of competition can be highly complex in case of three or more resources (Zhang, 1991; Huisman and Weissing, 1999, 2002; Baer et al., 2006). For $m = 2$, we have just seen that the number of outcomes is also rather limited for the storage model. On the other hand, with three or more resources, the dynamics of the storage model is as complex (Revilla and Weissing, 2008) as in standard models without storage.

One interesting result is the emergence of competitive oscillations as in the example of Figure 3.5A: three species take turns trying to exclude each other, as in the game of Rock-Scissors-Paper (RSP: Rock crushes Scissors, Scissors cuts Paper, Paper wraps Rock). Also interesting is the widespread occurrence of alternative states. Already for $m = n = 2$ we have alternative stable states, but they only concern monocultures, whereas in higher dimensions they can involve communities, as Figure 3.5B shows. In other words, even if coexistence is possible, it may not manifest for certain initial conditions.

Previous analysis of models without storage (Huisman and Weissing, 2001), indicate that the configuration of nullclines and consumption vectors play an important role in the origin of the complex dynamics of multispecies resource competition. The purpose of this section is to prove that this is also the case for nutrient storage models. Since the number of possible configurations for quasi-nullclines and consumption vectors for more than two species and resources is hopelessly high, we limit our exposition to some representative cases. We will only consider scenarios in which an equilibrium between three species always exists, i.e. the quasi-nullclines cross and the “cone rule” holds. For this community equilibrium, we consider a given arrangement of consumption vectors. Then, using the properties of the consumption and turnover vectors (see Fig. 3.2), will deduce if the two-species equilibria and the monocultures, are externally stable. This, along with the determinant rule (3.15), will give us a rather robust picture of the corresponding dynamics. Although this method-

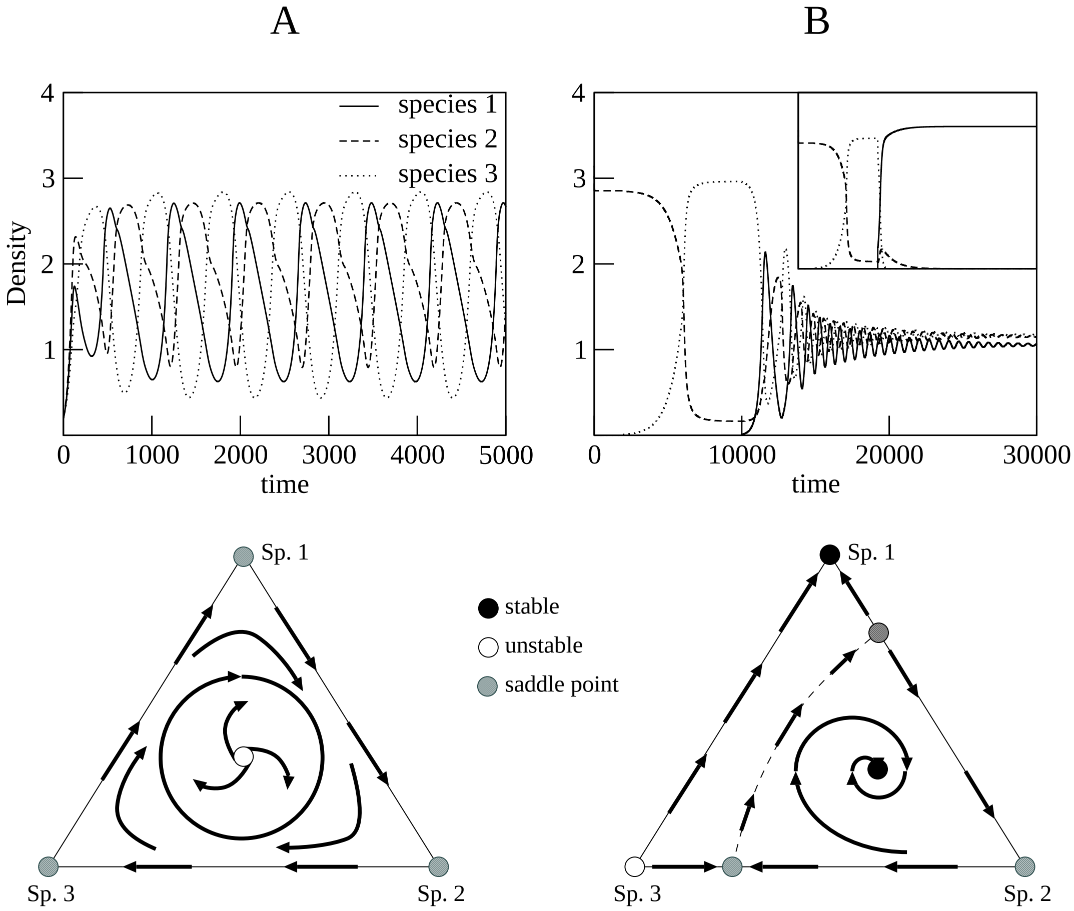


Figure 3.5: (A) Limit cycle of three species competing for three resources. (B) Alternative stable states: at time 10000 species 1 invades the community of species 2 and 3, the outcome can be coexistence or the extinction of species 2 and 3 (inset), depends on the initial density of the invader. The triangular graphs below each time plot represent the corresponding equilibria and their stability: monocultures are the vertices, two-species equilibria lie on the edges, and the three-species equilibrium is in the interior. For part A, the monocultures form a heteroclinic cycle around the unstable equilibria, this explains the oscillations. For part B, the three-species community and monoculture of species 1 are localy stable. If a small fraction of species 2 is replaced by species 1, the system coverges to coexistence. If a small fraction of species 3 is replaced by species 1, species 1 excludes both residents. The parameters for the simulations are in Appendix E.

ology can in principle be applied to any resource type, we will limit it to perfectly essential resources for the sake of simplicity.

To ensure that the quasi-nullclines cross, if each species must have the highest requirement for one resource. Without loss of generality, we follow our early convention (3.14) in which species i has the highest requirement for resource i. The other resource requirements $(R^*_{ji}, , j \neq i)$ could be related in other ways, tough. Thus, *with some loss of generality*, we will assume that external resource requirements are related in a cyclic fashion

$$\begin{aligned} R^*_{11} > R^*_{12} > R^*_{13} \\ R^*_{22} > R^*_{23} > R^*_{21} \\ R^*_{33} > R^*_{31} > R^*_{32} \end{aligned} \tag{3.22}$$

Thus, all quasi-nullclines intersect at $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22}, R^*_{33})$. We will examine under which conditions the species trio *(1)* coexist, *(2)* mutually exclude each other, or develop *(3)* competitive oscillations.

(1) Coexistence. Our results from the last section tell us that species 1 and 2 can invade each other if (3.18) holds. Then by symmetry, any monoculture can be invaded by any of the two invaders, if all the following inequalities hold at the nullcline intersection point $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22}, R^*_{33})$:

$$\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} > \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.23a}$$

$$\frac{f_{33}(R^*_{33})}{f_{13}(R^*_{11})} > \frac{\phi_3(R^*_{33})}{\phi_1(R^*_{11})} > \frac{f_{31}(R^*_{33})}{f_{11}(R^*_{11})} \tag{3.23b}$$

$$\frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})} > \frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} > \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})} \tag{3.23c}$$

Accordingly, all two-species equilibria exist. Using geometrical analysis in resource space, this arrangement (3.23) places the resource turnover vector in the cone formed by the consumption vectors at $\hat{\mathbf{R}}$, thus the three species community equilibrium $\hat{N}_1, \hat{N}_2, \hat{N}_3 > 0$ also exists. In Appendix C we prove that all two-species border equilibria are externally unstable, i.e. they can be invaded by the third species. Thus, if all inequalities in (3.23) hold and all species are always limited by the resource for which they have the highest requirement, then all monocultures and all two-species equilibria are externally unstable: no species can be excluded, thus all three species persist.

In Appendix D, we show that the consumption pattern (3.23) also met the internal stability requirement (3.15). However, we cannot simply rule out the possibility that the community equilibrium is indeed unstable, and that the three species may develop some form of non-equilibrium dynamics. The pattern of resource requirements (3.22), together with the consumption pattern (3.15), simply says that *coexistence through invasion is possible when each species tends to consume comparatively more of those resources for which it has the highest requirements*. Nothing more.

(2) Competitive exclusion. This time consider that all six inequalities in (3.23) are changed to:

$$\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} < \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} < \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \tag{3.24a}$$

$$\frac{f_{33}(R^*_{33})}{f_{13}(R^*_{11})} < \frac{\phi_3(R^*_{33})}{\phi_1(R^*_{11})} < \frac{f_{31}(R^*_{33})}{f_{11}(R^*_{11})} \tag{3.24b}$$

$$\frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})} < \frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} < \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})} \tag{3.24c}$$

This is likely to happen when each species consumes comparatively less of those resources for which it has the highest requirement.

As before, all two species equilibria and the three species equilibrium still exist, since the supply vector remains in the cone formed by the consumption vectors. All two-species equilibria have the same configuration of consumption and resource turnover vectors as in (3.19) or Figure 3.4B. Hence, they are internally unstable and all monocultures are in turn externally stable. If the monocultures cannot be invaded, this is because they leave a level of external resources that is below the quasi-nullclines of the invaders. In consequence, a two-species equilibrium leaves an even smaller amount of external resources: all two-species equilibria are externally stable, they cannot be invaded. Finally, in Appendix D we prove that the three-species equilibrium is internally unstable.

Summarizing, under (3.24) the two-species equilibria are saddle points (internally unstable, but externally stable), the community equilibrium is unstable, and all monocultures are stable. In consequence, depending on the initial conditions, the system evolves toward the monoculture of species 1, 2 or 3. Thus, *competitive exclusion will happen when each species tends to consume comparatively less of those resources for which it has the highest requirements.*

(3) Oscillations. Competitive oscillations can happen when the competitive hierarchy among species is intransitive. For three species this means that they relate as in a Rock-Scissors-Paper (RPS) game (Weissing, 1991). In such a game each species i can invade monoculture $j = i - 1$ and can be invaded by species $k = i + 1$ when in monoculture. For example species 1 can be invaded by species 2 but not by species 3, species 2 can be invaded by species 3 but not by species 1 and species 3 can be invaded by species 1 but not by species 2. According to our results for competitive dominance and given the scheme of resource requirements (3.22), this scenario can be generated by the following arrangement of turnover and consumption vector slopes:

$$\frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})}, \frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} \tag{3.25a}$$

$$\frac{\phi_1(R^*_{11})}{\phi_3(R^*_{33})} < \frac{f_{13}(R^*_{11})}{f_{33}(R^*_{33})}, \frac{f_{11}(R^*_{11})}{f_{31}(R^*_{33})} \tag{3.25b}$$

$$\frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} > \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})}, \frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})} \tag{3.25c}$$

For this configuration, one can show graphically that the turnover vector falls in the cone formed by the three consumption vectors at $\hat{\mathbf{R}}$, thus the three-species equilibrium exists. However, none of the two-species equilibria exists, (compare with inequalities (3.20)).

Summarizing, the consumption pattern (3.25) describes a situation of three monocultures connected by heteroclinic orbits, $1 \rightarrow 2 \rightarrow 3 \rightarrow 1$, surrounding a three-species equilibrium. If all species start with non-zero densities, they will oscillate. Because of the way in which they are written, we cannot use inequalities (3.25) to judge the stability of the three-species equilibrium. However, if the consumption vector slopes relate as in (3.23), the community equilibrium may be stable and oscillations will dampen out. But if the consumption vector slopes relate as in (3.24), the community equilibrium will be unstable (Appendix D) and the oscillations will persist.

When competitive oscillations do not damped out, they can develop into two types: limit cycles and heteroclinic cycles. This has important consequences. In the first case, oscillations attain uniform amplitude and period, thus the species can coexist provided that the minimum densities attained in these cycles are sufficiently far from zero, like in Figure 3.5A. In the second case however, population densities become closer and closer to zero for increasing periods on time. Under realistic scenarios, sooner or later one of the species will get extinct due to stochastic events, and the cycle will break, leaving one winner.

Bear in mind that our examination of *coexistence*, *exclusion* and *competitive cycles* was easy, because the cyclic arrangement of resource requirements like (3.22) is often sufficient to ensure that each species is limited by the same resource for all equilibria. This is not always the case, in nutrient storage models, and also for models without storage (Zhang, 1991). The fact that the orientation of the consumption vectors are resource dependent, is another reason by which resource limitation can differ among the different equilibria for the same species. Thus in general, it is in practice very difficult to predict the outcomes of competition for three or more resources based on the configuration of consumption and turnover vectors at the quasi-nullcline intersections. A good example is given by Figure 3.5B: the parameters for this simulation are such that species i has the highest requirement for resource i, and the consumption vectors at the intersection of the quasi-nullclines $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22}, R^*_{33})$ are related like in (3.25). The system display damped oscillations around the three-species equilibrium as predicted, but depending on the initial conditions, this equilibrium may be achievable or not.

3.8 DISCUSSION

The multispecies storage model behaves in a qualitatively similar way as the much simpler multispecies competition models without storage. Despite the increased complexity of the storage model because of the more state variables and parameters, the competitive dynamics mainly reflects the competitive hierarchy among the species, rather than microscopic (e.g. physiology) details causing these hierarchies. These hierarchies can be represented as orderings of resource requirements and consumption vectors, allowing us to apply the graphical analyses used for models without storage. In the case of two species and two resources, the outcomes of competition are the same as in classical resource competition models: coexistence, mutual exclusion and competitive dominance. For three species and three resources, graphical insights and local stability analysis reveals a strong match between the patterns of resource consumption and the global dynamics, i.e. the "rules of thumb" of multispecies resource competition (Huisman and Weissing, 1999, 2001, 2002):

(1) expect stable coexistence when species consume relatively much of those resources for which they have high requirements, (2) expect competitive exclusion when species consume relatively much of those resources for which they have low requirements, and (3) expect oscillations when species consume much of those resources for which they have intermediate requirements. These expectations are in line with our previous numerical exploration of the multispecies storage model (Revilla and Weissing, 2008).

It is important to stress the way in which we treat the graphical analysis: as a tool to judge external stability instead of internal stability. Only the computation of eigenvalues, a tough problem, can tell us if an equilibrium is internaly stable or not. We simply use a reference point, the quasi-nullcline crossing, and the geometric properties of turnover and consumption vectors (Fig. 3.2), to infer what is the state of the resources left by one species in monoculture. Then we ask: is that amount above the quasi-nullcline of the invader(s)? That is why the graphical approach works, it does not mater if we are considering nullclines (models without storage) or quasi-nullclines (with storage).

Although much of our results rely heavily on invasion and graphical analyses. this does not rest merit to our partial result concerning internal stability. The stability requirement, in the form of inequality (3.15), has a very simple but important interpretation: stable equilibrium coexistence requires that each species has a higher consumption impact for its most needed resources, rather than on the most needed resources of others. In other words, stable coexistence requires that *intraspecific competition is stronger than interspecific competition*, a general rule applicable from Lotka-Volterra type of models (Gilpin and Justice, 1972) to resource competition models (León and Tumpson, 1975). Thus, multispecies competition models seem to have common stability rules, independent of the amount (or lack) of mechanistic underpinning. It is interesting to see that this result is equally valid for chemostat $(m_i = D)$ and non-chemostat conditions. Unfortunately, this result is restricted to perfectly essential resources, i.e. Liebig's law.

It is well known that resource uptake slows down and eventually halts due to the accumulation of nutrients (Morel, 1987; Grover, 1997). This is modelled by decomposing $f_{ji}(R_j, Q_{ji})$ as the product of two monotone functions: $g_{ji}(R_j)$ which is monotonically increasing on R_j (as in the original $f_{ji}(R_j)$) and $h_{ji}(Q_{ji}) = u_{ji} - w_{ji}Q_{ji}$ which is linearly decreasing on Q_{ji}. We did not considered this level of realism, which would have made our analysis much more difficult. However our most important results, concerning equilibria, invasion and stability, still hold. This is because under the equilibrium condition, the quota dynamical equation becomes $g_{ji}(R_j)(u_{ji} - w_{ji}Q_{ji}) - m_i Q_{ji} = 0$, resulting in a positive relationship between R_j and Q_{ji}. Thus the nullcline in quota space can be mapped one-to-one into a quasi-nullcline in resource space as we did before. The same requirements for the existence of equilibria will follow, i.e. the crossing of quasi-nullclines and the "cone rule". Finally, in Appendix B.5 we show that both the external stability conditions, and the requirement for internal stability (3.15) still hold in the presence of quota dependent uptake.

Our graphical and analytical approaches covered simple cases, i.e. cyclical arrangements of resource requirements and consumption vectors. This leaves out an important number of scenarios, not covered by the rules of thumb (e.g. like in Fig. 3.5B). However, this problem is not exclusive of nutrient storage models. For example, in the much simpler Lotka-Volterra model, the number of possible outcomes is impressive just for three species (Zeeman, 1993, lists 33 different phase plots like those in Fig. 3.5). And in standard models of competition for three or more perfectly essential resources, the number of configurations for three species becomes very high, because pairs of species can display more than one coexistence equilibrium (Zhang, 1991). Thus, although competition models become complicated by the incorporation of mechanistic detail (storage in the present case), the dynamics becomes more complicated mainly because the dimensionality of the system increases.

Now, it is time to stress the differences between competition models with and without storage. In models without nutrient storage like (3.1), the resource requirements and the consumption rates relate with the model parameters in simple and direct ways. In these models the growth rates tipically follow the Monod (1950) equation, $\mu_{ji} = r_i R_j/(H_{ji} + R_j)$, making resource requirements proportional to the half-saturation constants for growth H_{ji}, and consumption rates proportional to fixed resource contents c_{ji} (Huisman and Weissing, 2001, 2002). This means that resource requirements and resource consumption can be treated independently. The story is very different for nutrient storage models. Resource requirements and the consumption rates relate with the model parameters in complex and non-linear ways, like in equations (3.9) and (3.5), and cannot be treated independently. In consequence, the small variation in a single parameter (e.g. q_{ji}, ν_{ji}, K_{ji}) can trigger important qualitative changes for all equilibria, compared with the variation a single parameter in models without storage. Now consider that the present model could be more complex: we did not include negative feedback in consumption rates (de Leenheer et al., 2006), and there must be trade-offs between parameters (Grover, 1991). Thus, prediction in terms of life-history parameters becomes unpractical, there are simply too many parameters and trade-offs.

Another important difference between models without storage and with storage can be easily appreciated in the graphical analysis. For models like (3.1) it is often the case that the consumption vectors have the same orientation at all points in resource space (but see Tilman (1982) for exceptions), thus the consumption pattern is the same at monocultures, two-species equilibria, three-species equilibria and so on. For the resource storage model, the orientation of the consumption vectors is different at all equilibria. In the case of two species and two resources this do not lead to important changes in the prediction of outcomes. In case of three or more species and resources, the situation can be radicaly different, because the limiting resource for a species can change among the different equilibria. In consequence, predictability becomes more localized: the structure of the consumption matrix at the quasi-nullcline intersection can tell us if the system has the tendency to approach the equilibrium or not, or to oscillate, but that will be often insufficient to inform us about the long term dynamics. For example, using simulation (Revilla and Weissing, 2008), we found that in a high number of cases where competitive oscillations where predicted, the oscillations did occur, but in the long term the system approached a monoculture. In these monocultures the limiting resources and the consumption patterns where different than in the three-species equilibrium. These changes are more easy to appreciate by means of bifurcation analysis (chapter 4).

APPENDIX A: EXISTENCE OF A COMMUNITY

In this appendix we proceed to prove the "cone rule": that a community equilibrium exists if the supply vector falls inside the positive cone formed by the consumption vectors. For this, let start by considering any matrix $\mathbf{A}$ with column vectors $\mathbf{a}_1, \dots \mathbf{a}_n$. The set

$$C = \{\sum_{i=1}^{n} \mathbf{a}_i x_i | x_i > 0\} \tag{3.26}$$

is the positive cone spanned by those vectors (Strang, 1988). Hence a vector $\mathbf{b}$ with m elements has a representation $\mathbf{b} = \sum_{i=1}^{n} \mathbf{a}_i x_i$, with $x_i > 0$ for all i, if and only if $\mathbf{b}$ belongs to the cone C. If we apply this to $\mathbf{b} = \hat{\mathbf{\Phi}}$, $\mathbf{A} = \hat{\mathbf{F}}$ and $x_i = \hat{N}_i$ (see equation 3.12 in the main text), we conclude that a community equilibrium with all $\hat{N}_i > 0$ does exists if and only if the $\hat{\mathbf{\Phi}}$ lies inside the positive cone formed by the columns of $\hat{\mathbf{F}}$.

APPENDIX B: LOCAL STABILITY OF EQUILIBRIA

As in the main text, we consider any community equilibrium $\hat{\mathbf{X}} = (\hat{\mathbf{N}}, \hat{\mathbf{Q}}, \hat{\mathbf{R}},)$ in which some or all possible n species are present. This equilibrium will be locally stable if and only if all the eigenvalues of the jacobian matrix $\mathbf{J}$ evaluated at $\hat{\mathbf{X}}$ have negative real parts (May, 1974). This jacobian matrix is

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \dot{\mathbf{R}}}{\partial \mathbf{R}} & \frac{\partial \dot{\mathbf{R}}}{\partial \mathbf{Q}} & \frac{\partial \dot{\mathbf{R}}}{\partial \mathbf{N}} \\ \frac{\partial \dot{\mathbf{Q}}}{\partial \mathbf{R}} & \frac{\partial \dot{\mathbf{Q}}}{\partial \mathbf{Q}} & \frac{\partial \dot{\mathbf{Q}}}{\partial \mathbf{N}} \\ \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{R}} & \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}} & \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{N}} \end{bmatrix} \tag{3.27}$$

where $\frac{\partial \dot{\mathbf{X}}}{\partial \mathbf{Y}} = \{\frac{\partial \dot{X}_x}{\partial Y_y}\}$, $X_x, Y_y = N_i, Q_{ji}, R_j$ are matrix blocks, and the dot on top is a shorthand for the time derivative $\dot{X}_x = dX_x/dt$. The jacobian has $m + n + m \times n$ rows and columns.

The eigenvalues of $\mathbf{J}$ are roots λ of the characteristic equation

$$\det(\mathbf{J} - \lambda \mathbf{I}) = 0 \tag{3.28}$$

where $\mathbf{I}$ is the identity matrix. The degree of (3.28) is equal to the number rows (or columns) of $\mathbf{J}$. Just in the simple scenario $n = m = 2$, this is an 8^{th} order equation, for which the application of analytical stability criteria is according May (1974) a pointless exercise (and so forth for $m, n \geqslant 2$).

B.1 External vs internal stability

Equation (3.28) can be factorized as two characteristic equations of lesser degree. This will allow an easier characterization of the stability conditions of the competitive system.

Our first step is to acknowledge that the community equilibrium represented by $\hat{\mathbf{X}}$ consists of a set $K = \{i = k | \hat{N}_k > 0\}$ of n_k resident species, and a set $L = \{i = l | \hat{N}_l > 0\}$ of n_l invader species. The total number of species, residents plus invaders is $n = n_k + n_l$.

The rows and columns containing the quotas and densities of the invaders can be moved to the bottom and to the right of the jacobian respectively, without any effect on the eigenvalues (the only rule is: move row r one position below, then move column c one position to the right). After such rearrangement, the jacobian has the following block structure

$$\mathbf{J} = \left[\begin{array}{ccc|cc} \frac{\partial\dot{R}}{\partial R} & \frac{\partial\dot{R}}{\partial Q_K} & \frac{\partial\dot{R}}{\partial N_K} & \frac{\partial\dot{R}}{\partial Q_L} & \frac{\partial\dot{R}}{\partial N_L} \\ \frac{\partial\dot{Q}_K}{\partial R} & \frac{\partial\dot{Q}_K}{\partial Q_K} & \frac{\partial\dot{Q}_K}{\partial N_K} & \frac{\partial\dot{Q}_K}{\partial Q_L} & \frac{\partial\dot{Q}_K}{\partial N_L} \\ \frac{\partial\dot{N}_K}{\partial R} & \frac{\partial\dot{N}_K}{\partial Q_K} & \frac{\partial\dot{N}_K}{\partial N_K} & \frac{\partial\dot{N}_K}{\partial Q_L} & \frac{\partial\dot{N}_K}{\partial N_L} \\ \hline \frac{\partial\dot{Q}_L}{\partial R} & \frac{\partial\dot{Q}_L}{\partial Q_K} & \frac{\partial\dot{Q}_L}{\partial N_K} & \frac{\partial\dot{Q}_L}{\partial Q_L} & \frac{\partial\dot{Q}_L}{\partial N_L} \\ \frac{\partial\dot{N}_L}{\partial R} & \frac{\partial\dot{N}_L}{\partial Q_K} & \frac{\partial\dot{N}_L}{\partial N_K} & \frac{\partial\dot{N}_L}{\partial Q_L} & \frac{\partial\dot{N}_L}{\partial N_L} \end{array}\right] = \left[\begin{array}{c|c} \mathbf{J_K} & \mathbf{M_1} \\ \hline \mathbf{M_2} & \mathbf{J_L} \end{array}\right] \tag{3.29}$$

The block $\mathbf{J_K}$ has $m + m \times n_k + n_k$ rows and columns. $\mathbf{J_K}$ has the same structure of the original jacobian in (3.27) and in fact it is a jacobian matrix of an equilibrium that only contains the resident species. On the other hand, the block $\mathbf{J_L}$ has $m \times n_l + n_l$ rows and columns. $\mathbf{J_L}$ only contains elements belonging to the invaders, and looks like the jacobian of a system lacking the differential equations of the resources. That is precisely the situation from the perspective of the invaders: they cannot affect the external resources.

There are many zero blocks in $\mathbf{J}$ that arise from the model definition: (1) external resources are not affected by quotas, quotas are not affected by species densities, and species densities are not affected by external resources; (2) densities and quotas are species specific; and (3) the residents are at equilibrium $\partial\dot{N}_k/\partial N_k = \hat{\mu}_k - m_k = 0$. Thus, the blocks of $\mathbf{J}$ have block structures

$$\mathbf{J_K} = \begin{bmatrix} \frac{\partial\dot{R}}{\partial R} & \mathbf{0} & \frac{\partial\dot{R}}{\partial N_K} \\ \frac{\partial\dot{Q}_K}{\partial R} & \frac{\partial\dot{Q}_K}{\partial Q_K} & \mathbf{0} \\ \mathbf{0} & \frac{\partial\dot{N}_K}{\partial Q_K} & \mathbf{0} \end{bmatrix}, \mathbf{J_L} = \begin{bmatrix} \frac{\partial\dot{Q}_L}{\partial Q_L} & \mathbf{0} \\ \frac{\partial\dot{N}_L}{\partial Q_L} & \frac{\partial\dot{N}_L}{\partial N_L} \end{bmatrix}, \mathbf{M_1} = \begin{bmatrix} \mathbf{0} & \frac{\partial\dot{R}}{\partial N_L} \\ \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix}, \mathbf{M_2} = \begin{bmatrix} \frac{\partial\dot{Q}_L}{\partial R} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{bmatrix} \tag{3.30}$$

The eigenvalues λ of the jacobian are the roots of the characteristic equation (3.28). Due to the special structure of the jacobian, i.e. (3.29) and (3.30), we can employ Schur's formula (Weinstein, 2003) and factorize the characteristic equation as

$$\det(\mathbf{J} - \lambda\mathbf{I}) = \det(\mathbf{J_K} - \lambda\mathbf{I}) \times \det(\mathbf{J_L} - \lambda\mathbf{I}) = 0 \tag{3.31}$$

i.e. a product of two characteristic equations. The eigenvalues of $\mathbf{J_K}$ determine the stability of $\hat{\mathbf{X}}$ with respect to small perturbations in the resident species, they say whether $\hat{\mathbf{X}}$ is *internally stable* or not. The eigenvalues of $\mathbf{J_L}$ determine the stability of $\hat{\mathbf{X}}$ against the introduction of invader species with very small densities, they say whether $\hat{\mathbf{X}}$ is *externally stable* or not.

According to equation (3.31) all the eigenvalues of $\mathbf{J}$ have negative real parts, if and only if, all eigenvalues of $\mathbf{J_K}$ and $\mathbf{J_L}$ separately, have negative real parts. Thus, *a community equilibrium* $\hat{\mathbf{X}}$ *is stable, if and only if, it is both externally and internally stable.*

B.2 External stability

$\mathbf{J_L}$ is a block triangular matrix, thus, its eigenvalues are those of $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ and $\frac{\partial \dot{\mathbf{N}}_\mathbf{L}}{\partial \mathbf{N_L}}$. Notice that the entries of $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ are of the form

$$\frac{\partial \dot{Q}_{jl}}{\partial Q_{il}} = -\hat{Q}_{jl}\frac{\partial \mu_l}{\partial Q_{il}} - \delta_{ji}\hat{\mu}_l$$

where δ_{ji} is Kroneker's delta ($\delta_{ji} = 1$ if $i = j$, $\delta_{ji} = 0$ if $j \neq i$), and $\hat{\mu}_l$ denotes the invader's specific growth rate evaluated at $\hat{\mathbf{X}}$. Accordingly, the characteristic equation of $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ can be rewritten as

$$\det\left(\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}} - \lambda \mathbf{I}\right) = \det(-\mathbf{E} - (\hat{\mu}_l + \lambda)\mathbf{I}) = 0 \tag{3.32}$$

where $\mathbf{E} = \mathbf{Q}_l \cdot \nabla\hat{\mu}_l$ is the scalar product of the invader's quota vector $\mathbf{Q}_l = (\hat{Q}_{1l}, \ldots, \hat{Q}_{ml})^T$, and the is the invader's gradient of its specific growth rate $\nabla\hat{\mu}_l = (\partial\mu_l/\partial Q_{1l}, \ldots, \partial\mu_l/\partial Q_{ml})$. $\mathbf{Q}_l$ is a $m \times 1$ column vector, and $\nabla\hat{\mu}_l$ is a $1 \times m$ row vector, thus $\mathbf{E}$ is a $m \times m$ matrix.

Now consider the following equation

$$\mathbf{E} \cdot \mathbf{Q}_l = \mathbf{Q}_l \cdot \nabla\hat{\mu}_l \cdot \mathbf{Q}_l \tag{3.33}$$

The scalar product $\nabla\hat{\mu}_l \cdot \mathbf{Q}_l$ in the right-hand-side has the same terms of $\mathbf{E}$, but in reverse order. Thus $\sigma = \nabla\hat{\mu}_l \cdot \mathbf{Q}_i$ is a 1×1 matrix, i.e. a scalar. Because $Q_l > 0$ and $\partial\mu_l/\partial Q_l \geqslant 0$, we conclude that $\sigma \geqslant 0$.

Equation (3.33) can be written as $\mathbf{E} \cdot \mathbf{Q}_l = \mathbf{Q}_l\sigma$, where $\mathbf{Q}_l$ and σ are respectively, an eigenvector and its associated eigenvalue, of $\mathbf{E}$. By definition, the other eigenvectors $\mathbf{x}$ are orthogonal with respect to $\mathbf{Q}_l$, i.e. $\mathbf{x} \in \mathbf{Q}_l^\perp$ with $\mathbf{Q}_l^\perp = \{\mathbf{x} | \mathbf{x} \cdot \mathbf{Q}_l = 0\}$. In consequence

$$\mathbf{x} \cdot \mathbf{E} = \mathbf{x} \cdot \mathbf{Q}_l \cdot \nabla\hat{\mu}_l = 0 \cdot \nabla\hat{\mu}_l = (0, \ldots, 0)$$

In other words, the eigenvalues associated with the other eigenvectors $\mathbf{x}$, of $\mathbf{E}$, are zero. Therefore, the eigenvalues of $\mathbf{E}$ are $(\sigma, \underbrace{0, \ldots, 0}_{m \times n_l - 1 \text{ times}})$. Going back to (3.32) the eigenvalues of $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ are $\lambda = (-\sigma - \hat{\mu}_l, \underbrace{-\hat{\mu}_l, \ldots, -\hat{\mu}_l}_{m \times n_l - 1 \text{ times}})$, and all of them are negative. The matrix $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ cannot tell us whether $\hat{\mathbf{X}}$ is externally stable or not.

Now, let us check the matrix $\frac{\partial \dot{\mathbf{N}}_\mathbf{L}}{\partial \mathbf{N_L}}$. Because dN_l/dt does not depend on other species densities but N_l, this matrix is diagonal, and its eigenvalues are the diagonal entries: $\lambda = \partial\dot{N}_l/\partial N_l = \hat{\mu}_l - m_l$, i.e. species l net specific rate of increase when rare. Since they can be positive or negative, only the eigenvalues of $\frac{\partial \dot{\mathbf{N}}_\mathbf{L}}{\partial \mathbf{N_L}}$ can tell us whether $\hat{\mathbf{X}}$ is externally stable or not: *a community equilibrium $\hat{\mathbf{X}}$ is externally stable if and only if none of the invaders can grow when rare.*

B.3 Internal stability

The characteristic equation of $\mathbf{J_K}$ is much more difficult to factorize, but we can obtain some results if resources follow Liebig's law. Following our convention that species *i* is limited by resource *i*, the quotas $\mathbf{Q_K}$ can be split into $\mathbf{Q}_=$ corresponding to the Q_{ii} and $\mathbf{Q}_{\neq}$ corresponding to the Q_{ji} ($j \neq i$). The same applies for the external resources **R**, where $\mathbf{R}_=$ corresponds to taking derivatives to or with respect to resources that are limiting, and $\mathbf{R}_{\neq}$ for the resources which do not cause limitation to any resident. $\mathbf{J_K}$ can be rearranged (by moving rows and columns as we before) as the following block-triangular matrix

$$\mathbf{J_K} = \left[\begin{array}{ccc|cc} \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{R}_=} & \mathbf{0} & \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{N}} & \mathbf{0} & \mathbf{0} \\ \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{R}_=} & \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{Q}_=} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}_=} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{R}_=} & \mathbf{0} & \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{N}} & \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \mathbf{0} \\ \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{R}_=} & \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{Q}_=} & \mathbf{0} & \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{Q}_{\neq}} \end{array}\right] = \left[\begin{array}{c|c} \mathbf{J}_1 & \mathbf{0} \\ \hline \mathbf{J}_3 & \mathbf{J}_2 \end{array}\right]$$

where the sub-blocks $\frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{R}_{\neq}} = \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{Q}_{\neq}} = \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}_{\neq}} = \mathbf{0}$ because $\mathbf{R}_{\neq}, \mathbf{Q}_{\neq}$ are correspond to non-limiting resources, and $\frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{R}_{\neq}} = \mathbf{0}$ because of the independence among external resources. Thus the eigenvalues of $\mathbf{J_K}$ at those of the block:

$$\mathbf{J}_1 = \begin{bmatrix} \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{R}_=} & \mathbf{0} & \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{N}} \\ \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{R}_=} & \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{Q}_=} & \mathbf{0} \\ \mathbf{0} & \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}_=} & \mathbf{0} \end{bmatrix} \tag{3.34}$$

together with those of

$$\mathbf{J}_2 = \begin{bmatrix} \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \mathbf{0} \\ \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{Q}_{\neq}} \end{bmatrix} \tag{3.35}$$

where $\mathbf{J}_1$ is of size $(2n_k + n_k^2) \times (2n_k + n_k^2)$ and $\mathbf{J}_2$ is of size $(m - n_k)(n_k + 1) \times (m_k - n)(n_k + 1)$.

First we look at $\mathbf{J}_2$. According to (3.2c) the small block $\frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{R}_{\neq}}$ is $(m - n_k) \times (m - n_k)$ and diagonal with

$$\frac{\partial \dot{R}_j}{\partial R_j} = \varphi(\hat{R}_j) - \sum_i \frac{\partial f_{ji}(R_j)}{\partial R_j} \hat{N}_i = -a_j < 0$$

and according to (3.2b) the dynamics of Q_{ji} is affected by Q_{ii} and Q_{ji} but not by the other quotas $\neq i, j$, thus $\frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{Q}_{\neq}}$is a $(m - n_k)n_k \times (m - n_k)n_k$ diagonal block with

$$\frac{\partial \dot{Q}_{ji}}{\partial Q_{ji}} = -\mu_i(\hat{Q}_{ii}) = -m_i$$

along its diagonal, $m-1$ times for resident. Thus, $\mathbf{J_2}$ is triangular and its characteristic equation is

$$\det(\mathbf{J}_2 - \lambda \mathbf{I}) = \prod_{j \neq i} (a_j + \lambda) \times \prod_{i} (m_i + \lambda)^{m-1} = 0 \tag{3.36}$$

which has all negative real roots. Thus the internal stability depends only on the eigenvalues of $\mathbf{J}_1$.

In $\mathbf{J}_1$ the small block $\frac{\partial \dot{\mathbf{R}}_{=}}{\partial \mathbf{N}}$ is $n_k \times n_k$ with elements $\frac{\partial \dot{R}_j}{\partial N_i} = -f_{ji}(\hat{R}_j)$. This is the negative of the consumption matrix at equilibrium $\hat{\mathbf{F}}$, but only for the limiting resources; in other words, with the with rows $j > n_k$ removed. The other four non-zero blocks of $\mathbf{J}_1$ are also of size $n_k \times n_k$ but they are all diagonal because:
$\frac{\partial \dot{\mathbf{R}}_{=}}{\partial \mathbf{R}_{=}}$: resource *i* cannot be affected by resources $\neq i$. The diagonal elements are

$$\frac{\partial \dot{R}_i}{\partial R_i} = \phi_i(\hat{R}_i) - \sum_k \frac{\partial f_{ik}(R_i)}{\partial R_i} \hat{N}_k = -a_i < 0 \tag{3.37}$$

$\frac{\partial \dot{\mathbf{Q}}_{=}}{\partial \mathbf{Q}_{=}}$: the quotas of one species cannot affect the quotas of another species. The diagonal elements are

$$\frac{\partial \dot{Q}_{ii}}{\partial Q_{ii}} = -\frac{\partial(\mu_i(Q_{ii})Q_{ii})}{\partial Q_{ii}} = -b_i < 0 \tag{3.38}$$

$\frac{\partial \dot{\mathbf{Q}}_{=}}{\partial \mathbf{R}_{=}}$: species *i* quota for resource *i* cannot be affected by external resources$\neq i$. Thus

$$\frac{\partial \dot{Q}_{ii}}{\partial R_i} = \frac{\partial f_{ii}(R_i)}{\partial R_i} = c_i > 0 \tag{3.39}$$

$\frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}_{=}}$: The growth of species *i* only depends on its quota for resource *i*. The diagonal elements are

$$\frac{\partial \dot{N}_i}{\partial Q_{ii}} = \frac{\partial \mu_i(Q_{ii})}{\partial Q_{ii}} \hat{N}_i = d_i > 0 \tag{3.40}$$

Thus the characteristic equation of $\mathbf{J}_1$ is

$$\det(\mathbf{J}_1 - \lambda \mathbf{I}) = \det \begin{bmatrix} \mathbf{A}(\lambda) & -\hat{\mathbf{F}} \\ \mathbf{B}(\lambda) & \mathbf{C}(\lambda) \end{bmatrix} = 0$$

$$\begin{aligned} \mathbf{A}(\lambda) &= \begin{bmatrix} -\mathrm{diag}(a_i + \lambda) & \mathbf{0} \end{bmatrix} \\ \mathbf{B}(\lambda) &= \begin{bmatrix} \mathrm{diag}(c_i) & -\mathrm{diag}(b_i + \lambda) \\ \mathbf{0} & \mathrm{diag}(d_i) \end{bmatrix} \\ \mathbf{C}(\lambda) &= \begin{bmatrix} \mathbf{0} \\ \mathrm{diag}(-\lambda) \end{bmatrix} \end{aligned}$$

and by application of Schur's formula:

$$\det(\mathbf{J}_1 - \lambda\mathbf{I}) = \det(\mathbf{B}(\lambda))\det(-\hat{\mathbf{F}} - \mathbf{A}(\lambda)\mathbf{B}(\lambda)^{-1}\mathbf{C}(\lambda)) = 0$$

$\det(\mathbf{B}(\lambda) = \prod_i c_i d_i > 0$, and Schur's complement $\mathbf{AB}^{-1}\mathbf{C}$ is a diagonal matrix:

$$\mathbf{A}(\lambda)\mathbf{B}(\lambda)^{-1}\mathbf{C}(\lambda) = \mathrm{diag}\left(\frac{\lambda(\lambda + a_i)(\lambda + b_i)}{c_i d_i}\right)$$

Accordingly, the eigenvalues of $\mathbf{J}_1$ are the solutions of the determinant equation:

$$\det(\hat{\mathbf{F}} + Z_i(\lambda)) = 0 \tag{3.41}$$
$$Z_i(\lambda) = \lambda(\lambda + a_i)(\lambda + b_i)/c_i d_i$$

where $Z_i(\lambda)$ is a polynomial of degree 3 in λ. The equilibrium is internally stable if all the roots of (3.41) have negative real parts.

We can prove that a necessary but not sufficient condition for the negativity of all the real parts of the roots of (3.41) is that

$$\det(\hat{\mathbf{F}}) > 0 \tag{3.42}$$

Proof. The polynomials $Z_i(\lambda)$ are zero at zero ($Z_i(0) = 0$) and they increase monotonically to infinity for $\lambda > 0$. From (3.41) we get that the equilibrium cannot be asymptotically stable if $\det(\hat{\mathbf{F}}) = 0$, since in that case $\lambda = 0$ would be an eigenvalue of the jacobian. Suppose that $\det(\hat{\mathbf{F}}) < 0$ and consider the function $\chi(\lambda) = \det(\hat{\mathbf{F}} + \mathrm{diag}(Z_i(\lambda)))$. Then $\chi(0) = \det(\hat{\mathbf{F}}) < 0$. If $\lambda > 0$ is big enough $\chi(\lambda)$ will be positive, since it is the determinant of a diagonally dominant matrix with a positive diagonal. Hence by continuity there exists a $\lambda_+ > 0$ that satisfies $\chi(\lambda_+) = 0$. In other words the jacobian has a positive eigenvalue λ_+ and $\hat{\mathbf{X}}$ cannot be stable.

B.4 Monocultures

The stability of monocultures in nutrient storage models has been analysed many times (Lange and Oyarzun, 1992; Oyarzun and Lange, 1994; Legovic and Cruzado, 1997; de Leenheer et al., 2006), but for the chemostat scenario, i.e. $\phi_j = D(S_J - R_J)$ and $m_i = D$. In case of one species and one resource, the monoculture can display damped oscillations around the equilibrium, when the mortality rate is high enough compared with the resource turnover rate (Clodong and Blasius, 2004). Thus, it is not immediatly clear if monocultures are stable under more general conditions.

In case of a monoculture $m > n = 1$, a positive equilibrium of a species i corresponds to the only point $\tilde{\mathbf{R}}$ in the quasi-nullcline of i, where according to (3.12) the consumption vector $\mathbf{f}_i$ and the turnover vector $\mathbf{\Phi}$ are parallel. In case of Liebig's law, this point $\tilde{\mathbf{R}}$ lies in one of the two branches of the L-shaped quasi-nullcline in Figure 3.3, or "hyper-planes" if $m > 2$, to be more general. Without loss of generality, let us assume that $\tilde{\mathbf{R}}$ lies in the $R_i = R^*_{ii}$ hyper-plane, thus the corresponding consumption vector is $\tilde{f}_i(\tilde{\mathbf{R}})$. This monoculture is internally stable if all the roots of the characteristic equation (3.41):

$$\tilde{f}_{ii} + \lambda(\lambda + a_i)(\lambda + b_i)/c_i d_i = 0$$

have negative real parts. In this equation $\tilde{f}_{ii}$ corresponds to the consumption matrix $\tilde{\mathbf{F}}$ in which the rows of the non-limiting resources have been removed, leaving us a single scalar: the consumption rate $\tilde{f}_{ii} = f_{ii}(R^*_{ii})$. All the coefficients of this polynomial have the same sign; thus all roots have negative real parts if and only if (Routh-Hurwitz criterion, May 1974, Appendix):

$$(a_i + b_i)a_i b_i > c_i d_i \tilde{f}_{ii} \tag{3.43}$$

Using the definitions of a, b, c, d in (3.37,3.38,3.39,3.40) respectively, and the fact that $\mu_i = m_i$ and $\tilde{f}_{ii} = m_i \tilde{Q}_{ii}$ at equilibrium, inequality (3.43) becomes

$$\left(-\frac{\partial \phi_i}{\partial R_i} + \frac{\partial f_{ii}}{\partial R_i}\tilde{N}_i + \underline{m_i} + \tilde{Q}_{ii}\frac{\partial \mu_i}{\partial Q_{ii}}\right)\left(-\frac{\partial \phi_i}{\partial R_i} + \underline{\frac{\partial f_{ii}}{\partial R_i}\tilde{N}_i}\right)\left(m_i + \underline{\tilde{Q}_{ii}\frac{\partial \mu_i}{\partial Q_{ii}}}\right) > \frac{\partial f_{ii}}{\partial R_i}\frac{\partial \mu_i}{\partial Q_{ii}}\tilde{N}_i m_i \tilde{Q}_{ii}$$

In the left-hand-side of this inequality we have all the terms (underlined) that appear as the product in the right-hand-side. Thus, if the left-hand-side is expanded, it will produce the product of the right-hand-side, plus other terms which are all positive (remember that $\partial \phi_i/\partial R_i < 0$). Thus, the left-hand-side is bigger than the right-hand-side and the stability requirement (3.43) is true. Conclusion: monocultures are internally stable.

B.5 Quota dependent uptake

Let us consider that the resource uptake f_{ji}, is a decreasing function of Q_{ji} (and no other quotas)

$$\frac{\partial f_{ji}}{\partial Q_{ji}} < 0 \tag{3.44}$$

and see how the stability requirements change.

According to appendix B.2, external stability depends on the eigenvalues of the matrix $\mathbf{J_L}$ in (3.30), and the eigenvalues of this matrix are are those of $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ and $\frac{\partial \dot{\mathbf{N}}_\mathbf{L}}{\partial \mathbf{N_L}}$. This time the entries of the diagonal block $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ become

$$\frac{\partial \dot{Q}_{jl}}{\partial Q_{il}} = -\hat{Q}_{jl}\frac{\partial \mu_l}{\partial Q_{il}} - \delta_{ji}\left(\hat{\mu}_l - \frac{\partial f_{jl}}{\partial Q_{il}}\right)$$

Because of (3.44), and following exactly the same procedures we conclude that all the eigenvalues of the $\frac{\partial \dot{\mathbf{Q}}_\mathbf{L}}{\partial \mathbf{Q_L}}$ are real and negative (they are the same negative eigenvalues plus the derivatives of uptake rates with respect to quotas, which are also negative). Thus, only the eigenvalues of $\frac{\partial \dot{\mathbf{N}}_\mathbf{L}}{\partial \mathbf{N_L}}$, for which the resource uptake does not play a role, will determine external stability. We conclude again that *a community is stable against invasion if and only if none of the invaders can grow when rare.*

According to appendix, B.3 internal stability depends on the eigenvalues of the matrices $\mathbf{J_1}$ (3.34) and $\mathbf{J_2}$ (3.35). With quota dependent uptake $\mathbf{J_1}$ changes into

$$\mathbf{J}_1 = \begin{bmatrix} \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{R}_=} & \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{Q}_=} & \frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{N}} \\ \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{R}_=} & \frac{\partial \dot{\mathbf{Q}}_=}{\partial \mathbf{Q}_=} & \mathbf{0} \\ \mathbf{0} & \frac{\partial \dot{\mathbf{N}}}{\partial \mathbf{Q}_=} & \mathbf{0} \end{bmatrix}$$

where the $n_k \times n_k$ block $\frac{\partial \dot{\mathbf{R}}_=}{\partial \mathbf{Q}_=}$ is a diagonal matrix with

$$e_i = -\frac{\partial f_{ii}}{\partial Q_{ii}} \hat{N}_i > 0$$

along its diagonal, all positive because of (3.44). Following the same steps as before, the characteristic equation of $\mathbf{J_1}$ is similar to (3.41), where the polynomial Z_i becomes

$$Z_i(\lambda) = \lambda\left(c_i e_i + (\lambda + a_i)(\lambda + b_i)\right)/c_i d_i$$

Since this polynomial is zero at $\lambda = 0$ and is monotonically incresing with λ, we will arrive to same internal stability requirement as before (3.42), in which $\det(\mathbf{F}) > 0$.

With respect to $\mathbf{J}_2$ we have

$$\mathbf{J}_2 = \begin{bmatrix} \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \frac{\partial \dot{\mathbf{R}}_{\neq}}{\partial \mathbf{Q}_{\neq}} \\ \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{R}_{\neq}} & \frac{\partial \dot{\mathbf{Q}}_{\neq}}{\partial \mathbf{Q}_{\neq}} \end{bmatrix}$$

which is not block-triangular anymore, and in consequence, there is not a simple way to determine if this matrix is stable or not. However, this uncertainty does not rest invalidate the internal stability requirement (3.42).

APPENDIX C: THREE-SPECIES COEXISTENCE THROUGH INVASION

As motivated in the main text let us assume that three species have resource requirements related as in (3.22):

$$\begin{array}{l} R^*_{11} > R^*_{12} > R^*_{13} \\ R^*_{22} > R^*_{23} > R^*_{21} \\ R^*_{33} > R^*_{31} > R^*_{32} \end{array} \tag{3.45}$$

so, the quasi-nullcline intersection point is $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22}, R^*_{33})$. We will prove that the consumption patterns (3.23), (3.24) and (3.25) at result in coexistence, competitive exclusion and oscillations, respectively.

(1) Coexistence. Let the slopes of the resource turnover vector and the consumption vectors be related according to (3.23):

$$\begin{array}{l} \frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} > \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})} \\ \frac{f_{33}(R^*_{33})}{f_{13}(R^*_{11})} > \frac{\phi_3(R^*_{33})}{\phi_1(R^*_{11})} > \frac{f_{31}(R^*_{33})}{f_{11}(R^*_{11})} \\ \frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})} > \frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} > \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})} \end{array} \tag{3.46}$$

The ordering of slopes (3.47) indicates that the turnover vector falls in the cone formed by the consumption vectors, not only at $\hat{\mathbf{R}}$, but also when this point is represented in all the resource planes R_1R_2, R_1R_3 and R_2R_3. In consequence, the three-species equilibrium, and all three two-species equilibria exist.

Let us examine the equilibrium of species 1 and 2. In view of the resource requirements, species 1 must be limited by resource 1 and species 2 by resource 2. The resource concentrations in this equilibrium will be: $R_1 = R^*_{11}$, $R_2 = R^*_{22}$ and $R_3 > R^*_{31}, R^*_{32}$ (we prove later that they cannot be limited by resource 3). Because species 1 and 2 display the same coexistence configuration of Figure 3.4A, they can invade each other. Appealing to symmetry, all species can invade any monoculture. What is left is to prove that any species can invade a two-species equilibrium.

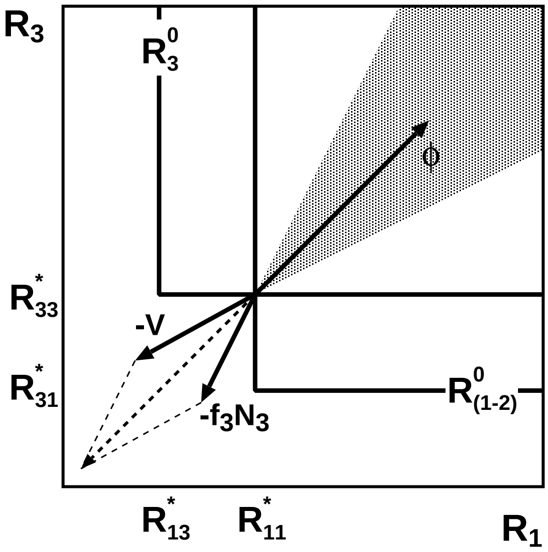
From the perspective of species 3, we can view species 1 and 2 as a single competitor called "1-2", that is limited by resources 1 and 2 simultaneously. This allow us to represent the interaction of species 3 against species "1-2", in the R_1R_3 plane. In such representation, the combined consumption rate of species 1 and 2 is given by

$$\mathbf{v} = \mathbf{f}_1 N_1 + \mathbf{f}_2 N_2$$

and the quasi-nullcline of "1-2" is the same as the quasi-nullcline of species 1, defined by R^*_{11} and R^*_{31} (because between species 1 and 2, those are the highest requirements for resources 1 and 3). The intersection of species "1-2" quasi-nullcline and that of species 3 occurs at the point $\hat{\mathbf{R}} = (R^*_{11}, R^*_{33})$. At this point, according to the resource equilibrium conditions (3.12), the following vector sum holds:

$$\mathbf{\Phi} = \mathbf{v} + \mathbf{f}_3 N_3$$

Now, according to (3.46) the slope of the turnover vector is smaller than the slope of the consumption vector of species 3 ($\frac{f_{33}(R^*_{33})}{f_{13}(R^*_{11})} > \frac{\phi_3(R^*_{33})}{\phi_1(R^*_{11})}$), at $\hat{\mathbf{R}}$. In consequence, the slope of $\mathbf{v}$ must be the smallest among the three vectors, as shown by the following diagram:



This diagram corresponds to the scenario of coexistence described in the main text, Figure 3.4A. Thus, the community of species 1 and 2, or "1-2", is unstable against invasion by species 3 (and since species 3 can invade, $R_3 > R^*_{33} > R^*_{31} > R^*_{32}$ in the equilibrium between species 1 and 2: our assumption that species 1 and 2 are not limited by resource 3 is correct). By symmetry, any species can invade a two-species equilibrium.

Since each species can invade any monoculture and two-species equilibria, all three species coexist.

(2) Competitive exclusion. The opposite outcome, exclusion, will result if the signs of all the inequalities are changed, like in (3.24):

$$\begin{aligned}
\frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})} &> \frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} > \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})}\\
\frac{f_{33}(R^*_{33})}{f_{13}(R^*_{11})} &> \frac{\phi_3(R^*_{33})}{\phi_1(R^*_{11})} > \frac{f_{31}(R^*_{33})}{f_{11}(R^*_{11})}\\
\frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})} &> \frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} > \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})}
\end{aligned} \tag{3.47}$$

In this case, we can repeat the previous analysis (species 3 against "1-2"), and we will find that the community of species 1 and 2 is externally stable against invasion by species 3, that the community of species 1 and 2 is internally unstable, and that the monocultures of species 1 and 2 are externally stable (e.g. like in Fig. 3.4B). In addition, Appendix D shows that the three species equilibrium is internally unstable. For such a pattern of resource consumption, the only stable states are the monocultures, thus coexistence is not possible.

(3) Oscillations. Finally, let us consider the inequalities in (3.25)

$$\begin{aligned}
\frac{\phi_2(R^*_{22})}{\phi_1(R^*_{11})} &> \frac{f_{21}(R^*_{22})}{f_{11}(R^*_{11})}, \frac{f_{22}(R^*_{22})}{f_{12}(R^*_{11})}\\
\frac{\phi_1(R^*_{11})}{\phi_3(R^*_{33})} &< \frac{f_{13}(R^*_{11})}{f_{33}(R^*_{33})}, \frac{f_{11}(R^*_{11})}{f_{31}(R^*_{33})}\\
\frac{\phi_3(R^*_{33})}{\phi_2(R^*_{22})} &> \frac{f_{32}(R^*_{33})}{f_{22}(R^*_{22})}, \frac{f_{33}(R^*_{33})}{f_{23}(R^*_{22})}
\end{aligned} \tag{3.48}$$

Due to the cyclic symmetry of the resource requirements and vector slopes, we are left with a system in which there cannot be any two-species equilibria, since the turnover vector falls outside the cone formed by the consumption vectors, for any species pair considered separately. In consequence, the only outcome between two species is competitive dominance: species 2 wins against 1, 1 wins against 3, and 3 wins against 2. Thus, there is a heteroclinic cycle connecting the three monocultures, and in consequence competitive oscillations are possible. As stated in the main text, such oscillations can dampen out, become limit cycles or heteroclinic cycles.

APPENDIX D: THREE SPECIES STABILITY

For $n = m = 3$, the characteristic equation for the internal equilibrium (3.41) can be expanded as

$$Z_1(\lambda)Z_2(\lambda)Z_3(\lambda) + \sum f^*_{ii}Z_j(\lambda)Z_k(\lambda) + \sum M_i Z_i(\lambda) + \det(\hat{\mathbf{F}}) = 0 \qquad (3.49)$$

where $f^*_{ji} = f_{ji}(R^*_{jj})$, and $M_i = f^*_{jj}f^*_{kk} - f^*_{jk}f^*_{kj}$ are the 2×2 minors along the diagonal of $\hat{\mathbf{F}}$. Since $Z_i(\lambda) = \lambda(\lambda + a_i)(\lambda + b_i)/c_i d_i$ are polynomials of degree 3 in the eigenvalues λ, the substitution of Z_1, Z_2 and Z_3 in (3.49) produces a characteristic equation of degree 9 in the eigenvalues.

According to the Routh-Hurwitz criterion, a necessary but not sufficient condition for stability is that all the coefficients of the characteristic equation have the same sign. On the one hand, in (3.49), the products $Z_1Z_2Z_3$ and $f^*_{ii}Z_jZ_k$ $(i \neq j \neq k)$ result in polynomials with positive coefficients, because by definition $a_i, b_i, c_i, d_i, f^*_{ii} > 0$ (Appendix B.3). On the other hand, M_i and $\hat{\mathbf{F}}$ can be positive or negative since they are determinants. Thus, whether or not all the coefficients of (3.49) have the same sign, depends on $\sum M_i$ and $\hat{\mathbf{F}}$, giving us two necessary but not sufficient conditions for stability:

- **criterion I:** $\sum M_i > 0$
- **criterion II:** $\det(\hat{\mathbf{F}}) > 0$

The positivity of $\hat{\mathbf{F}}$ has the biological interpretation that, in the internal equilibrium, the three species tend to consume most of the resources for which they have the highest requirements. The positivity of M_i has the same interpretation, but with respect to border equilibria involving two species. Now, let us see if we can use the above criteria to decide upon the stability, or instability, of equilibria displaying the consumption patterns proposed in the main text.

(1) Coexistence: By inspection of (3.46) we see that all $M_i > 0$, thus **criterion I** holds. The consumption ratios alone do not provide enough information to asses whether **criterion II** holds or not, because $\hat{\mathbf{F}}$ is a 3×3 matrix. However, if the consumption rates (not the slopes!) are arranged in the same way as the resource requirements (3.45), i.e. $f^*_{11} > f^*_{12} > f^*_{13}$, $f^*_{22} > f^*_{23} > f^*_{21}$, $f^*_{33} > f^*_{31} > f^*_{32}$, **criterion II** is fulfilled. Proof: consider the matrix $\mathbf{\Gamma}$ in which each row element of the matrix $\hat{\mathbf{F}}$ is divided by the smallest element in the row. The determinant of matrix $\mathbf{\Gamma}$ has the same sign as $\det(\hat{\mathbf{F}})$, since

$$\mathbf{\Gamma} = \frac{\hat{\mathbf{F}}}{f^*_{13}f^*_{21}f^*_{32}}$$

and from the order of the f^*_{ji} we note that $\mathbf{\Gamma}$ is of the form

$$\mathbf{\Gamma} = \begin{bmatrix} 1 + y_1 & 1 + x_1 & 1 \\ 1 & 1 + y_2 & 1 + x_2 \\ 1 + x_3 & 1 & 1 + y_3 \end{bmatrix}$$

where $y_i > x_i > 0$. Accordingly, the determinant of $\mathbf{\Gamma}$ can be written as

$$\det(\Gamma) = x_1x_2x_3 + x_1x_2 + x_1x_3 + x_2x_3 + y_1y_2y_3 + y_1(y_2 - x_2) + y_2(y_3 - x_3) + y_3(y_1 - x_1)$$

which is always positive. Thus, if the consumption rates are ordered in the same way as the resource requirements, $\det(\hat{\mathbf{F}})$ is positive and **criterion II** holds.

(2) Competitive exclusion: By inspection of (3.47) all $M_i < 0$, thus **criterion I** does not hold, the three species equilibrium is unstable.

(3) Oscillations: The arrangement in (3.48) does not indicate what could be the signs of M_i and $\hat{\mathbf{F}}$. If we assume the consumption vector slopes have the same order as in (3.47), then **criterion I** does not hold, the three species equilibrium is unstable (see *(2) Competitive exclusion*), and the oscillations will increase. But if the consumption ratios are arranged as in (3.46), then both **criterion I** and **II** may hold not (see *(1) Coexistence*), and the oscillations can either increase or decrease.

APPENDIX E: SIMULATIONS

The simulations in Figure 3.5 employ the special formulas in Table 3.1 (equations 3.4, 3.5 and 3.6) and Liebig's law (3.3). In part A the parameter values are: $D = 0.5, r_i = 1.2, m_i = 0.9$, $S_1 = 32.84, S_2 = 39.88, S_3 = 43.30$,

$$v_{ji} = \begin{bmatrix} 0.63 & 5.13 & 1.94 \\ 3.01 & 2.16 & 5.35 \\ 6.45 & 2.83 & 1.72 \end{bmatrix}, K_{ji} = \begin{bmatrix} 0.67 & 0.65 & 0.23 \\ 0.96 & 0.81 & 0.46 \\ 0.50 & 0.97 & 0.48 \end{bmatrix}, q_{ji} = \begin{bmatrix} 0.15 & 1.25 & 0.49 \\ 0.60 & 0.50 & 1.32 \\ 1.56 & 0.58 & 0.43 \end{bmatrix}$$

where row:resources and columns:species. In part B: $D = 0.5, r_i = 2.0, m_i = 0.5$, $S_1 = 23.33, S_2 = 35.97, S_3 = 25.17$,

$$v_{ji} = \begin{bmatrix} 3.15 & 3.86 & 2.41 \\ 4.16 & 5.15 & 5.81 \\ 3.81 & 2.44 & 3.46 \end{bmatrix}, K_{ji} = \begin{bmatrix} 0.76 & 0.68 & 0.27 \\ 0.12 & 0.71 & 1.00 \\ 0.58 & 0.36 & 0.30 \end{bmatrix}, q_{ji} = \begin{bmatrix} 4.05 & 5.00 & 3.39 \\ 6.05 & 6.83 & 7.02 \\ 4.96 & 3.35 & 4.90 \end{bmatrix}$$

4

LIMIT CYCLES IN THE DROOP MODEL OF MULTISPECIES COMPETITION

Tomás A. Revilla and Franz J. Weissing

The dynamics of three species competing for three resources based on Droop's equation and Liebig's law of the minimum is explored. Under continuous changes in model parameters the system shows transitions from competitive exclusion, oscillations and stable coexistence, associated to contrasting modes of consumption. The three-species community undergoes a sub-critical Hopf bifurcation, and depending on the parameter choices and initial conditions, oscillations converge to the community equilibrium, increase in amplitude to become stable limit cycles, or approach an heteroclinic cycle formed by the species monocultures. Certain scenarios of competitive exclusion that prevent rock-paper-scissor dynamics do also display oscillations, before ending up with a single winner that depends on the initial conditions.

Keywords: *resource competition, quota model, law of the minimum, consumption patterns, competitive oscillations, rock-paper-scissors dynamics, bifurcations*

4.1 INTRODUCTION

Competition among three or more populations displays a rich variety of outcomes (Buss and Jackson, 1979; Sinervo and Lively, 1996; Kerr et al., 2002) in comparison with the two species case. In the framework of Lotka-Volterra theory these outcomes correspond to a great extend to different configurations of the so called "community matrix" formed by the "competition coefficients" of the model. One would expect coexistence when intra-specific competition (coefficients) is (are) stronger than inter-specific (coefficients) competition, and competitive exclusion when intra-specific competition is weaker than inter-specific competition (but see Strobeck 1973); in both cases the system attains a stable equilibrium with high or low diversity respectively. On the other hand, non-equilibrium dynamics like oscillations can only occur between these extreme scenarios, due to nontransitive relationships of competitive hierarchy among the species, as shown by Gilpin (1975) and May and Leonard (1975).

Lotka-Volterra theory is phenomenological and non-mechanistic. Whether competition coefficients are big or small can only be known after competition took place since they cannot be obtained from first principles, an issue that undermines its utility for understanding the causes of diversity. In contrast, for certain systems resource competition theory (Grover, 1997) allows the necessary mechanistic interpretation through the explicitly consideration of resource dynamics along with those of consumers. The standard model of resource competition predicts the outcome of the interaction between two species competing for two resources in terms of their resource requirements, their consumption ratios and resource abundances in the environment (León and Tumpson, 1975; Tilman, 1977, 1980, 1982). Extending this model for multiple species and resources Huisman and Weissing (1999, 2001, 2002) found that the outcomes of competition are the result of trade-offs in consumption characteristics, summarized in the following "rules of thumb"

COEXISTENCE. If species have high consumption rates for resources for which their requirements are higher, we should expect stable coexistence. In ecological terms interspecific competition is very weak, a requisite for coexistence in classical competition models.

EXCLUSION. If species have low consumption rates for resources for which they have the highest requirements, competitive exclusion will occur, with a single winner that depends on the initial conditions. This is a scenario of very strong interspecific competition, making coexistence unattainable.

OSCILLATIONS. If species have high consumption rates for resources for which they have intermediate requirements, a non-transitive hierarchy emerges leading to competitive oscillations. The fate of the community depends on the nature of such oscillations. Oscillations can dampen out leading to coexistence at stable densities or they can become limit cycles, in both cases all species persist. But they can also have very large amplitudes where densities attain very low values for very long periods of time, ultimately leading to extinctions and non-invadable monocultures.

These trade-offs can be stated explicitly terms of the parameters of the "Monod type" of models frequently used in limnology and microbiology. Thus for example a high "half-saturation constant for growth" on a given resource corresponds to a high requirement for that resource and vice versa; and a high "resource content" of a given resource corresponds to a high consumption rate for that resource and vice versa. Indeed, the magnitudes of these parameters can be used to compare the species competitive performance (Grover, 1997)

The same "rules of thumb" work in the multispecies extension of the variable resource content model, the "quota model" (Revilla and Weissing, 2008). Quota models are interesting because they acknowledge the delay that exists between resource consumption and the processes of growth and reproduction, they are more suitable for describing competition under fluctuating resource conditions (Passarge et al., 2006), and they are important tools in the field of ecological stoichiometry (Klausmeier et al., 2004a). An attractive feature of them is that the consumption rate parameters, "maximum consumption rates" and "half-saturation constants for consumption" (not to be confused with half-saturation for growth), can be derived from first principles of chemistry and physiology (Aksnes and Egge, 1991).

In contrast with models based on the Monod equation, resource requirements and consumption rates in quota models are variable quantities that depend on many parameters. As a consequence, the same species display different consumption patterns under different equilibrium conditions, and so do the rules of competition. In the present contribution we explore the parametric dependence of competitive interactions in the multispecies quota model based on Droop's (1973) equation. The structure of this work is as follows, Section 2 is contains the model specification (2.1) and the conditions that allow the existence of biologically feasible equilibria (2.2). Section 3 presents our results in the form a bifurcation analysis of equilibria with respect to variation in a few parameters (3.1), an analysis of the causes of competitive oscillations (3.2), and the sensitivity of our results with respect to the simultaneous variation in many parameters (3.2).

4.2 COMPETITION MODEL

4.2.1 *System equations*

Our model describes the competition among 3 species with population densities N_i ($i = 1, \ldots, 3$) for 3 perfectly essential resources with densities R_j ($j = 1, \ldots, 3$). It also keeps track of the variable resource content of j per cell of i or quota Q_{ji}

$$\frac{dN_i}{dt} = N_i(\mu_i(Q_{1i}, Q_{2i}, Q_{3i}) - m_i) \tag{4.1a}$$

$$\frac{dQ_{ji}}{dt} = f_{ji}(R_j) - \mu_i(Q_{1i}, Q_{2i}, Q_{3i})Q_{ji} \tag{4.1b}$$

$$\frac{dR_j}{dt} = \phi_j(R_j) - \sum_{i=1}^{3} f_{ji}(R_j)N_i \tag{4.1c}$$

$$i, j = 1, 2, 3$$

Species i per capita growth rate is a function of quotas according to a combination of Droop's (1973) empirical formula and Liebig's law of the minimum

$$\begin{aligned} \mu_i(Q_{1i}, Q_{2i}, Q_{3i}) &= \min(\mu_{ji}(Q_{1i}), \mu_{2i}(Q_{3i}), \mu_{3i}(Q_{3i})) \\ \mu_{ji}(Q_{ji}) &= r_i \left(1 - \frac{q_{ji}}{Q_{ji}}\right) \end{aligned} \tag{4.2}$$

where below the quota threshold q_{ji} growth is defined as zero, and r_i is the growth rate under quota saturation. The per capita loss rate (e.g. mortality or flush rate in chemostats) m_i is constant. Cell division split quotas uniformly among the offspring, thus Q_{ji} decrease with the per capita growth rate, in a "dilution by growth" process (Grover, 1997). The quotas are renewed with specific resource consumption rates $f_{ji}(R_j)$

$$f_{ji}(R_j) = \frac{\nu_{ji} R_j}{K_{ji} + R_j} \tag{4.3}$$

The mechanistic justification of this equation is similar to Holling's type II functional response (Aksnes and Egge, 1991), being ν_{ji} and K_{ji} the maximum consumption rate and half-saturation constant respectively. The external resources are depleted in proportion of the abundance of the consumers times their uptake rates. In the absence of consumers, the dynamics of resource j is governed a linear turnover function

$$\phi_j(R_j) = D(S_j - R_j) \tag{4.4}$$

where the resource supply point $\mathbf{S} = (S_1, \ldots, S_3)$ is the steady steady state condition of the pristine resources.

4.2.2 *Equilibria*

According to equation (4.2) the instantaneous growth rate of species i is a function of one resource at a time, the "limiting resource". If j is the limiting resource there is a quota level that balances growth and losses $\mu_i = \mu_{1i}(Q^*_{1i}) = m_i$, this quota requirement is

$$Q^*_{ji} = \frac{r_i q_{ji}}{r_i - m_i} \tag{4.5}$$

In equilibrium there is an external resource level that corresponds to the quota requirement, which is found by setting $f_{ji}(R^*_{ji}) - m_i Q^*_{ji} = 0$ in (4.1b) and using (4.3) to solve for the external resource requirement of j for species i

$$R^*_{ji} = \frac{K_{ji} m_i Q^*_{ji}}{\nu_{ji} - m_i Q^*_{ji}} = \frac{K_{ji} m_i r_i q_{ji}}{\nu_{ji}(r_i - m_i) - m_i r_i q_{ji}} \tag{4.6}$$

The three planes $R_1 = R^*_{1i}, R_2 = R^*_{2i}, R_3 = R^*_{3i}$ with $R_j \geqslant R^*_{ji}$ on each of them, form the zero net growth isocline ZNGI (Tilman, 1982) of species i in the space of external resources $R_1 R_2 R_3$. In the region above the ZNGI ($R_j > R^*_{ji}$ for all j) species i increases; in the region below ($R_j < R^*_{ji}$ for at least one j) it decreases. The relation between the species ZNGI determines the feasibility of the different equilibria in the model, as follows.

The species equilibrium densities are the solutions of a linear system that results from the equilibrium condition $\dot{R}_j = 0$ of the resources in equation (4.1c)

$$\begin{aligned}\phi_1(R_1) &= f_{11}(R_1)N_1 + f_{12}(R_1)N_2 + f_{13}(R_1)N_3 \\ \phi_2(R_3) &= f_{21}(R_1)N_1 + f_{22}(R_1)N_2 + f_{23}(R_1)N_3 \\ \phi_3(R_3) &= f_{31}(R_1)N_1 + f_{32}(R_1)N_2 + f_{33}(R_1)N_3\end{aligned} \tag{4.7}$$

The trivial equilibrium (all consumers absent) always exist, for which $R_j = S_j$. The different monoculture (one species) and multispecies equilibria exist (with non-negative species densities) if and only if the following two conditions hold

I. The resource levels lie on the ZNGI of the species whose equilibrium is considered.

II. The resource turnover vector $\mathbf{\Phi} = (\phi_1, \phi_2, \phi_3)$ is parallel and opposite to the total consumption vector $\sum \mathbf{f}_i N_i$ at the ZNGI of the species whose equilibrium is considered, being $\mathbf{f}_i = (f_{1i}, f_{2i}, f_{3i})$ species *i* per capita consumption vector.

4.2.2.1 *Monocultures*

In species i monoculture equilibrium (denoted by ~) condition (I) means that the resource level point $\tilde{\mathbf{R}} = (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3)$ lies in one of the planar faces of i's ZNGI; thus $\tilde{R}_j = R^*_{ji}$ for the limiting resource, and $\tilde{R}_k > R^*_{ki}$ for the non-limiting resources $k \neq j$. The resource turnover vector $\mathbf{\Phi}$ always points toward the supply point **S**, and the consumption vector field flows towards the origin; thus, condition (II) holds if and only if the resource supply point **S** lies above the nullcline of *i*. There is only one point in the ZNGI of i where the turnover and consumption vectors are parallel and opposite, $\tilde{\mathbf{R}} = (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3)$. This is shown for the $R_1 R_2$ plane in Figure 4.1A. The equilibrium density of the monoculture $\tilde{N}_i$ satisfies all equations in (4.7) for $N_{\neq i} = 0$

$$\phi_j(\tilde{R}_j) = f_{ji}(\tilde{R}_j)\tilde{N}_i \tag{4.8}$$

but $\tilde{N}_i$ is obtained from the equation of the limiting resource j as $\tilde{N}_i = \phi_j(R^*_{ji})/f_{ji}(R^*_{ji})$. This of course requires us to know which one is the limiting resource in the first place. According to Legovic and Cruzado (1997) the limiting resource is that resource which results in the smallest value of $\tilde{N}_i$, thus in our three resource model

$$\tilde{N}_i = \min\left(\frac{\phi_1(R^*_{1i})}{f_{1i}(R^*_{1i})}, \frac{\phi_2(R^*_{2i})}{f_{2i}(R^*_{2i})}, \frac{\phi_3(R^*_{3i})}{f_{3i}(R^*_{3i})}\right) \tag{4.9}$$

Substituting $\tilde{N}_i$ in the equations corresponding to non-limiting resources of (4.8) we fully specify the resource level point $\tilde{\mathbf{R}} = (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3)$, and substituting the $\tilde{R}_j$ in equation (4.1b) with $\dot{Q}_{ji} = 0$ we get the quotas, with $\tilde{Q}_{ji} = Q^*_{ji}$ for the limiting resource and $\tilde{Q}_{ki} > Q^*_{ki}$ for the non-limiting ones.

The existence of the monoculture equilibrium implies that species i can grow when rare (since **S** is above the ZNGI) and that the trivial equilibrium is always unstable. Monocultures are internally stable (Legovic and Cruzado, 1997) against fluctuations in densities and resources (the equilibrium is approached monotonously or after transient oscillations, see Clodong and Blasius, 2004), but may be externally stable or unstable against invasion by other species.

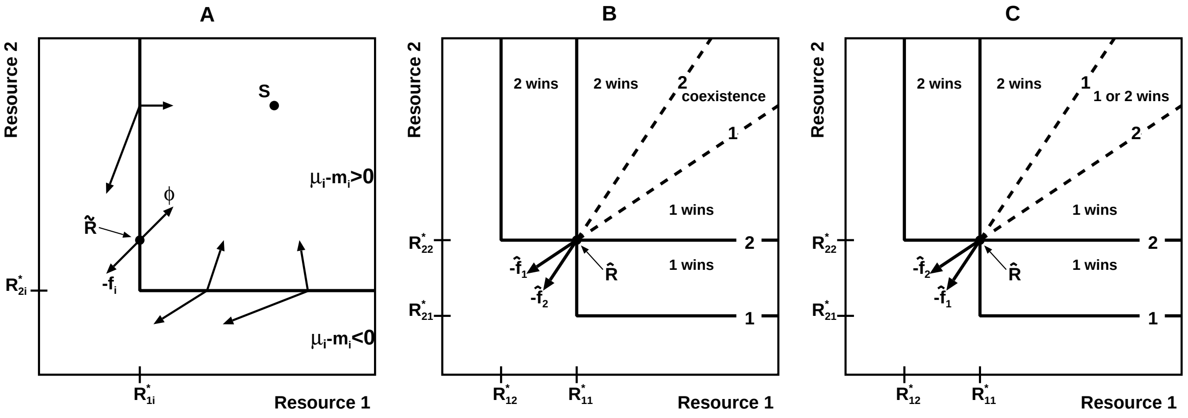


Figure 4.1: Zero net growth isoclines (ZNGI) and equilibrium conditions for two resources. (A). The ZNGI of species i is the L-shaped curve formed by the resource requirements R^*_{1i}, R^*_{2i}; above the ZNGI species i grows, below the ZNGI it decreases. Along the ZNGI the resource turnover $\mathbf{\Phi}$ vector points to the resource supply point $\mathbf{S}$; and the slope of the consumption vector $\mathbf{f}_i$ varies along the ZNGI, it aligns with the ZNGI as resources increase. The resource equilibrium level $\tilde{\mathbf{R}}$ of the monoculture of i is the point where both vectors are parallel and opposite. (B) A two-species equilibrium exists if both ZNGI cross and for supply points in the "wedge" formed by consumption vectors (dashed lines). The equilibrium is stable if each species consume comparatively more of the resource for which it has the highest requirement, in this case if the slope of $\mathbf{f}_2$ is higher than the slope of $\mathbf{f}_1$ (C). When each species consume comparatively less of the resource that limits its own growth the equilibrium is unstable, here when the slope of $\mathbf{f}_2$ is smaller than the slope of $\mathbf{f}_1$.

4.2.2.2 *Multispecies equilibria*

For two and more species equilibrium condition (I) requires the intersection of the species ZNGI's, thus they must have contrasting resource requirements. Out of many possible configurations, the one that follows

$$\begin{array}{l} R^*_{11} > R^*_{12} > R^*_{13} \\ R^*_{22} > R^*_{23} > R^*_{21} \\ R^*_{33} > R^*_{31} > R^*_{32} \end{array} \tag{4.10}$$

in which species i has the highest requirement for resource i and the smallest for resource $i \bmod 3 + 1$, allows the ZNGI to cross for all species combinations. For two species their ZNGI cross along L-shaped lines:

1. $(R_1 = R^*_{11}, R_2 = R^*_{22}, R_3 \geqslant R^*_{31}) \bigcup (R_1 \geqslant R^*_{11}, R_2 = R^*_{22}, R_3 = R^*_{31})$ for species 1 limited by resource 1 or 3, and species 2 limited by resource 2

2. $(R_1 = R^*_{11}, R_2 \geqslant R^*_{23}, R_3 = R^*_{33}) \bigcup (R_1 = R^*_{11}, R_2 = R^*_{23}, R_3 \geqslant R^*_{33})$ for species 1 limited by resource 1, and species 3 limited by resource 2 or 3

3. $(R_1 \geqslant R^*_{12}, R_2 = R^*_{22}, R_3 = R^*_{33}) \bigcup (R_1 = R^*_{12}, R_2 \geqslant R^*_{22}, R_3 = R^*_{33})$ for species 2 limited by resource 1 or 2, and species 3 limited by resource 3

And all three ZNGI met at the point $\hat{\mathbf{R}} = (R^*_{11}, R^*_{22}, R^*_{33})$, where each species is limited by the resource for which it has the highest requirement, i.e. species 1 by resource 1, species 2 by resource 2 and species 3 by resource 3.

The second equilibrium condition (II) requires that the resource supply point $\mathbf{S}$ falls in the cone formed by the consumption vectors $\mathbf{f}_i$ at the ZNGI intersection. In the well known example of two species competing for two resources this is the requirement saying that the supply point $\mathbf{S}$ lies in the wedge formed by the projections of the consumption vectors of species 1 and 2 at the intersection point (R^*_{11}, R^*_{22}) in the $R_1 R_2$ plane (the "wedge" or "cone" rule is nothing more than the application of the parallelogram rule of vector sum in two and higher dimensions). The stability of the equilibrium can be addressed by comparing the slopes of the consumption vectors: in Figure 4.1B the consumption vector of species 2 is steeper than the consumption vector of species 1, making the equilibrium locally stable; in Figure 4.1C the opposite configuration results in the instability of the equilibrium.

4.3 ANALYSIS AND RESULTS

The existence and local stability of equilibria depends on the species resource requirements R^*_{ji} and consumption vector $\mathbf{f}_i$ configurations. These in turn depend on multiple parameters, most importantly ν_{ji}, K_{ji}, q_{ji}, and varying them would allow to better describe the dynamical behaviour of the competitive system.

4.3.1 *Bifurcation of equilibria*

In line with the inequalities (4.10) let us assume that the species have resource requirements

$$\begin{aligned} R^*_{11} = R^*_{22} = R^*_{33} &= A \\ R^*_{12} = R^*_{23} = R^*_{31} &= B \\ R^*_{13} = R^*_{21} = R^*_{32} &= C \end{aligned} \tag{4.11}$$

$$A > B > C \tag{4.12}$$

such that species i has the highest requirement for resource *i*, and all three ZNGI intersect at the point (A, A, A) in resource space. Setting $S_1 = S_2 = S_3 > A$, all monocultures are feasible and the trivial equilibrium always unstable. Consumption rates at the intersection are given by equation (4.3) with $K_{ji} = K$ and

$$\begin{bmatrix} v_{11} & v_{12} & v_{13} \\ v_{21} & v_{22} & v_{23} \\ v_{31} & v_{32} & v_{33} \end{bmatrix} = \begin{bmatrix} u & v & w \\ w & u & v \\ v & w & u \end{bmatrix} \tag{4.13}$$

where

$$0 < u < 1,\ 0 < v < 1,\ w = 1 - u \tag{4.14}$$

are the maximum consumption rates on resources for which requirements are the highest (u), intermediate (v) or lowest (w). Cyclic parameter arrangements do not occur in nature, but they capture the essential features of competition dynamics (May and Leonard, 1975; Hofbauer and Sigmund, 1988; Li, 2001; Baer et al., 2006). We can investigate the effect of different consumption patterns through a reduced number of parameters. For example, if $u \to 1$ then $w \to 0$: consumption of resources with highest requirements is the highest and consumption of resources with lowest requirements is the lowest. In the other end of the spectrum, if $u \to 0$ then $w \to 1$: consumption is the highest for resources with the lowest requirements, and lowest for resources with the highest requirements. At intermediate values of u the discrepancy between consumption of resources with high and low requirements is small, and consumption upon resources for which requirements are intermediate is relatively high.

The system is fully specified using growth and supply rates given by (4.2) and (4.4) with $S_j = D = m_i = 1$, $A = 0.20$, $B = 0.15$, $C = 0.10$ and $K = 0.01$ (parametrization details are described in the Appendix). We proceed to study the bifurcation of equilibria as u varies between 0 and 1, for $v = 0.25$ and 0.75 using XPPAUT (Ermentrout, 2002). Figure (4.2) shows the corresponding bifurcation plots for species 1 (by symmetry species 2 and 3 show exactly the same graphs, with the appropriate labeling for i and j).

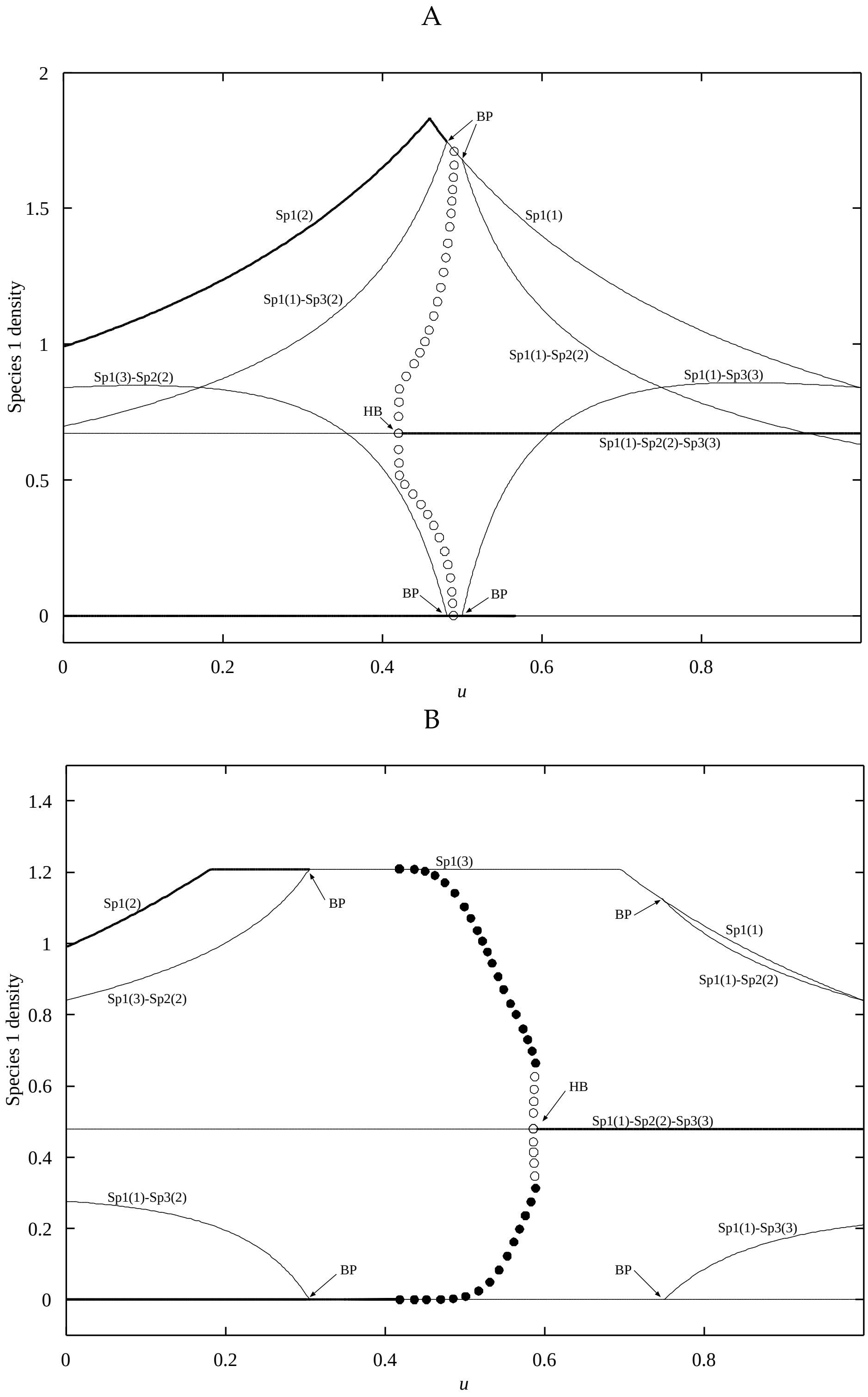


Figure 4.2: Bifurcation plots for species 1. (A) For $\nu = 0.25$ the three-species equilibrium displays a sub-critical Hopf bifurcation and unstable periodic orbits. (B) For $\nu = 0.75$ the periodic branch arising from the bifurcation changes from unstable to stable, see Fig. 4.4 for details. Sp$i(j)$: species i is limited by resource j, BP: branching point, HB: Hopf bifurcation, thick lines: stable equilibrium, thin lines: unstable equilibrium, full circles: stable limit cycle, open circles: unstable limit cycle.

Equilibrium densities change in different ways with the bifurcation parameter. As *u* changes monocultures experience limitation by different resources, as expected in equation (4.9). For species 1 for example

$$\tilde{N}_1 = \min\left(\frac{(1-C)}{wC/(K+C)}, \frac{(1-B)}{vB/(K+B)}, \frac{(1-A)}{uA/(K+A)}\right) \tag{4.15}$$

where the terms in parentheses correspond to limitation by resources 2, 3 and 1 respectively, as u goes from 0 to 1. The sharp corners of the monoculture curves (Sp1) in Figure 4.2 indicate the limitation switch.

The pairwise equilibria (1-2, 1-3) occur as discontinuous curves (Sp1-Sp2 or Sp1-Sp3) branching out from the monocultures or the extinct condition ($N_1 = 0$). The focal species or its competitor experiences different resource limitation in both branches, since the two ZNGI cross in a L-shaped line. For intermediate values of u, condition (II) fails, and pairwise equilibria are not feasible. As in the case of monocultures, the species are limited by their most needed resources when consumption is high on them, i.e. when u is big.

In contrast with monocultures and pairwise equilibria, the three species equilibrium is described by a continuous curve (Sp1-Sp2-Sp3) since each species is always limited by the resource for which it has the highest requirement. This equilibrium is characterized common resource concentrations $\hat{R}_1 = \hat{R}_2 = \hat{R}_3 = A$, and common species densities $\hat{N}_1 = \hat{N}_2 = \hat{N}_3 = \hat{N}$ which are independent of u (thus a flat line).

Stability also changes in different ways for the different equilibria. Low values of u result in stable monocultures and extinction equilibria, instability of the three species equilibrium, and pairwise equilibria being saddle points; thus, any positive initial condition leads to one the monocultures and the exclusion of the other two species. The opposite occurs for high values of u where monocultures and extinction equilibria are unstable, the three species equilibrium is stable, and pairwise equilibria being also saddle points; any positive initial condition leads to stable coexistence of all species.

At intermediate values of u competitive oscillations occur, as seen in Figure 4.3. The fate of such oscillations depends on the stability of the monocultures and the three-species equilibrium. The three-species equilibrium changes stability through a sub-critical Hopf bifurcation, i.e. where a branch of unstable periodic orbits overlaps the locally stable equilibrium. For $v = 0.25$ the unstable limit cycle is the boundary of the three-species equilibrium attraction basin. Depending on the initial conditions all species may end up coexisting at stable densities after oscillations damped out; or instead the oscillations increase in amplitude until one species exclude all the others (Fig. 4.3A). As u further increases and species consume comparatively more of the resources for which they have the highest requirements, the attraction basin of the three-species community grows until it becomes globally stable.

For $v = 0.75$ stable limit cycles occur for a wide range of the bifurcation parameter; all positive initial conditions result in non-equilibrium coexistence for all species (Fig. 4.3B). Unstable limit cycles do also exist but confined to a very small interval, where the branch of unstable cycles folds back into the much bigger branch of stable cycles, as pictured in Figure 4.4. In this interval, positive initial conditions end up either in a three-species

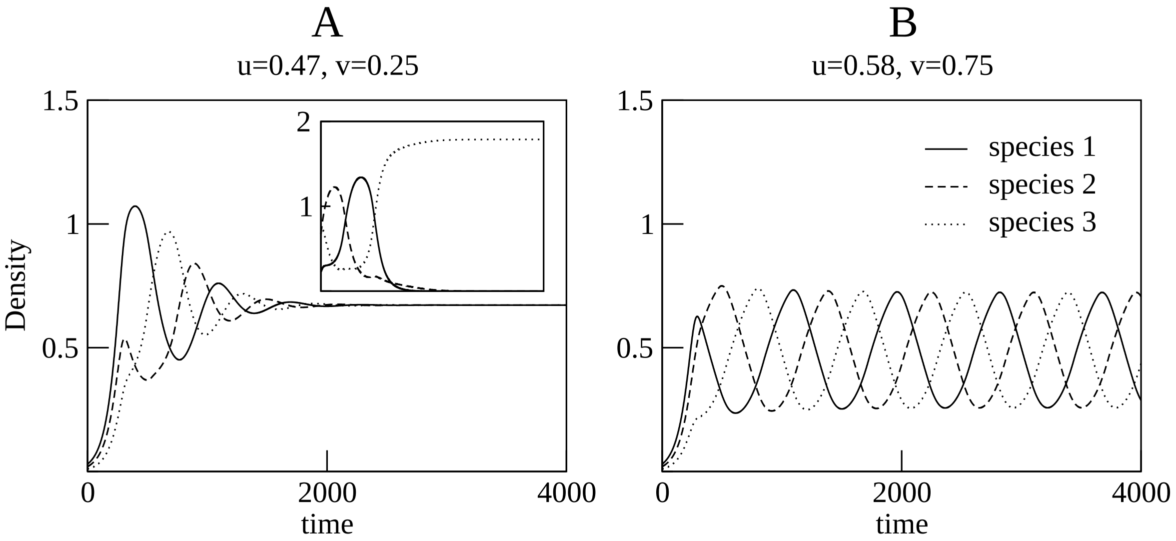


Figure 4.3: Competitive oscillations. (A) For $u = 0.47$ in Fig. 4.2A competition results in stable coexistence or competitive exclusion with the winner depending on the initial conditions (inset). (B). For $u = 0.58$ in Fig. 4.2B all species coexist through competitive oscillations.

equilibrium or non-equilibrium coexistence, depending on the initial conditions. Beyond the folding point competitive oscillations disappear and all positive initial conditions lead to equilibrium coexistence without transient oscillations.

4.3.2 *Competitive oscillations*

The causes of competitive oscillations can be understood by phase plane analysis in species space (Gilpin, 1975). Following Zhang (1991) we define species nullclines in the phase space $N_1N_2N_3$ as follows. Consider species 1 (alone or in company): it may be limited by resource 1 thus $R_1 = A$, or by resource 2 thus $R_2 = C$ or by resource 3 thus $R_3 = B$. Using equations (4.3), (4.13) and $K_{ji} = K$ the resource equilibrium conditions (4.7) for each case are

$$\begin{aligned} X_A &= uN_1 + vN_2 + wN_3 \\ X_C &= wN_1 + uN_2 + vN_3 \\ X_B &= vN_1 + wN_2 + uN_3 \end{aligned}$$

$$X_Y \equiv \frac{(K+Y)(S-Y)}{Y}, \; Y = A, B, C$$

Now consider the surface of the polyhedron enclosed by the three planes above and the $N_1 = N_2 = N_3 = 0$ planes: for densities above this surface consumption reduces

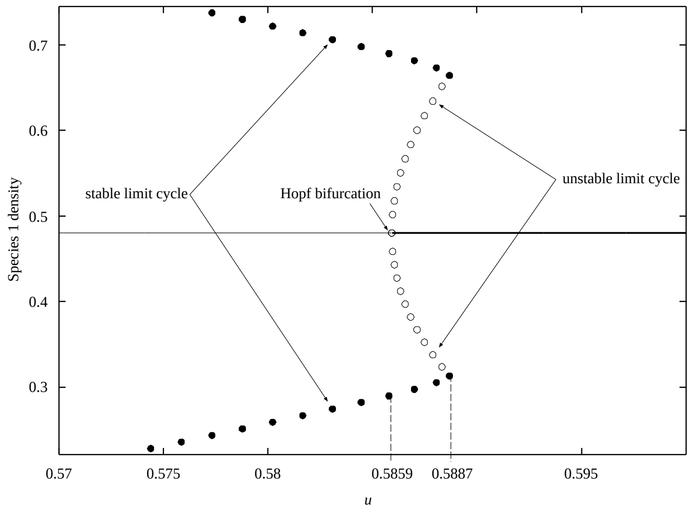


Figure 4.4: Enlarged portion of Figure 4.2B around the sub-critical Hopf bifurcation. The unstable periodic branch folds back and becomes stable. Between the bifurcation $u = 0,5859$ and and the folding point $u = 0,5887$ unstable limit cycles co-occur with stable limit cycles.

the limiting resource of species 1 below its requirement, so a decrease in N_1 follows; but for densities below this surface consumption is low and the limiting resource of species 1 increases above the requirement, so an increase in N_1 follows. Thus we can consider this polyhedral surface as the nullcline of species 1, and similarly for species 2 and 3, substituting $(X_A, X_C, X_B)^T$ by $(X_B, X_A, X_C)^T$ and $(X_C, X_B, X_A)^T$ respectively. The nullclines appear as polygonal curves when plotted on the phase planes N_1N_2, N_1N_3, N_2N_3, with each segment corresponding to limitation by one resource, their intersections corresponding to pairwise equilibria. We proceed to analyze the interaction between species pairs as we do with with Lotka-Volterra models.

Using the same u and v as in Figure 4.3A the intersection of the nullclines of species 1 and 2 in N_1N_2 seen in Figure 4.5 correspond to an unstable equilibrium (represented by the left branch of the Sp1-Sp2 curve in Figure 4.2A). The vector field indicates that species 1 or 2 are able to exclude each other depending on the initial conditions, and by symmetry the same result apply for the other two species pairs. Each monoculture is a stable node, and from this perspective the dynamics corresponds to competitive exclusion with the winner depending on the initial conditions. But as seen in the simulation, the approach to the monoculture equilibrium is accompanied by oscillations. This happens because of the following: species 3 can grow when rare in certain portions of species 1 and 2 attraction basins in the N_1N_2 plane, and that the attraction basin of species 1 is much bigger than the attraction basin of species 2. Thus for certain initial conditions, the exclusion of species 2 by species 1 allows a temporal increase of species 3, and in consequence a decrease in species 1 some time later. Considering the local dynamics in the N_1N_3 and N_2N_3 planes suggests a spiral flow in the $N_1N_2N_3$ phase space, in which the trajectories first approach and then move away from the monocultures in the sequence $1 \rightarrow 3 \rightarrow 2 \rightarrow 1$ before the final exclusion of all but one species.

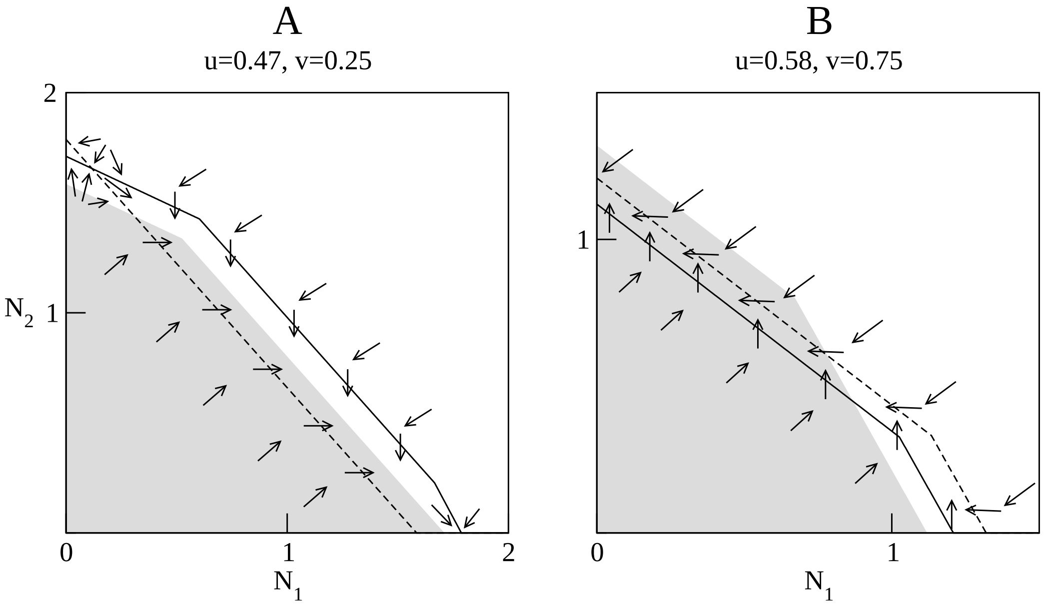


Figure 4.5: Graphical analysis in the N_1N_2 phase plane, with species 1 (solid), 2 (dashed) and 3 (gray-white boundary) nullclines. Species increase for points below their nullclines, and decrease for points above (for species 3 growth is positive in the gray region, and negative outside). (A) Nullclines corresponding to species in Fig. 4.3A. (B) Nullclines corresponding to species in Fig. 4.3B. See the text for further description.

For the u and v used in Figure 4.3B, notice that this time pairwise equilibria do not exist (the Sp1-Sp2 branch is absent for intermediate u in Fig. 4.2B). The vector field in Figure 4.5B shows that species 2 exclude species 1, and by symmetry species 3 excludes 3 and species 1 excludes 3. Each monoculture is a saddle point, stable against invasion by one species but unstable against invasion by the other; in other words the monocultures form a heteroclinic cycle. As species 2 excludes species 1 it allows species 3 to grow when rare, and considering species 1 vs species 3 and species 2 vs species 3 *mutatis mutandis*, we conclude that there is a spiral flow in the interior of $N_1N_2N_3$, with a sequence of competitive dominance $1 \rightarrow 2 \rightarrow 3 \rightarrow 1$. In this example any positive initial condition results in an oscillation that never settles down because all feasible equilibria are unstable. The type of oscillations however, have important consequences for diversity. The heteroclinic cycle may be an attractor, so species will spent increasingly longer times at very low densities, which in real world scenarios would imply their extinction, the destruction of the cycle and the emergence of a single winner; or as in our example, the heteroclinic may be unstable, such that oscillations move towards the interior and extinction is avoided.

4.3.3 *Sensitivity analysis*

Needless to say our parametrization greatly reduces the degrees of freedom in the dynamical system. We can remedy this to some extent and assess the robustness of our findings in a wider scope. Consider equation (4.3) for the consumption rate of resource j by species i when $R_j = A$

$$f_{ji}(A) \;=\; \frac{\nu_{ji}A}{K_{ji}+A} = \frac{xA}{K+A}$$

where $x = u, \nu, w$ according to the equation (4.13). Thus, for a given K_{ji} there is a

$$\nu_{ji} \begin{cases} = u\frac{K_{ji}+A}{K+A} & \text{for } \nu_{11}, \nu_{22}, \nu_{33} \\ = \nu\frac{K_{ji}+A}{K+A} & \text{for } \nu_{12}, \nu_{23}, \nu_{31} \\ = w\frac{K_{ji}+A}{K+A} & \text{for } \nu_{13}, \nu_{21}, \nu_{32} \end{cases} \tag{4.16}$$

satisfying the same consumption rate $f_{ji}(A)$. Indeed, there is an infinite number of ways to pick (ν_{ji}, K_{ji}) resulting in the same three-species equilibrium configuration for consumption patterns $f_{ji}(A)$, resources $\hat{R}_1 = \hat{R}_2 = \hat{R}_3 = A$ and densities $\hat{N}_1 = \hat{N}_2 = \hat{N}_3 = \hat{N}$ as before. Sampling K_{ji} from a uniform random distribution in the interval $[0, 2K]$, the corresponding ν_{ji} have means $\bar{\nu}_{11} = \bar{\nu}_{22} = \bar{\nu}_{33} = u$,$\bar{\nu}_{12} = \bar{\nu}_{31} = \bar{\nu}_{31} = \nu$ and $\bar{\nu}_{13} = \bar{\nu}_{21} = \bar{\nu}_{32} = w$ ($w = 1 - u$). We numerically integrated many systems with randomly assigned parameters (4th order Runge-Kutta, GNU Scientific Library Galassi et al. 2004, code available under request). All these systems share the same three-species equilibrium state as the examples in the cyclic parametrization, but their border equilibria are totally unrelated.

Figure 4.6A shows a simulation where ν_{ji} and K_{ji} belong to parameter distributions generated with the u and v used in Figure 4.3A. As in the cyclic case the competitive dynamics results in full species coexistence or competitive exclusion with the winner depending on the initial conditions. As predicted in the bifurcation analysis, the system displays oscillations, with species dominance sequence $1 \to 3 \to 2 \to 1$ as inferred from the phase plane analysis. As would be expected from random parametrization, the oscillations periods differ from case to case.

Figure 4.6B shows a simulation where ν_{ji} and K_{ji} belong to parameter distributions generated with the u and v used in Figure 4.3B. As in the cyclic case regular competitive oscillations occur, with species dominance sequence $1 \to 2 \to 3 \to 1$. Since $\nu_{ji}$and K_{ji} are variable, so are are the amplitudes and periods of the oscillations, although they all cycle around the exact same equilibrium point. In contrast with the cyclic case a significant number of cases end up in competitive exclusion, which results from the existence of two-species equilibria and locally stable monocultures (in other words, the species phase space for these scenarios look similar to Fig. 4.5A, but not like in Fig. 4.5B). A few oscillations are attracting heteroclinic cycles, with their periods and amplitudes increasing with time until maxima and minima become indistinguishable from extinction and monoculture equilibria.

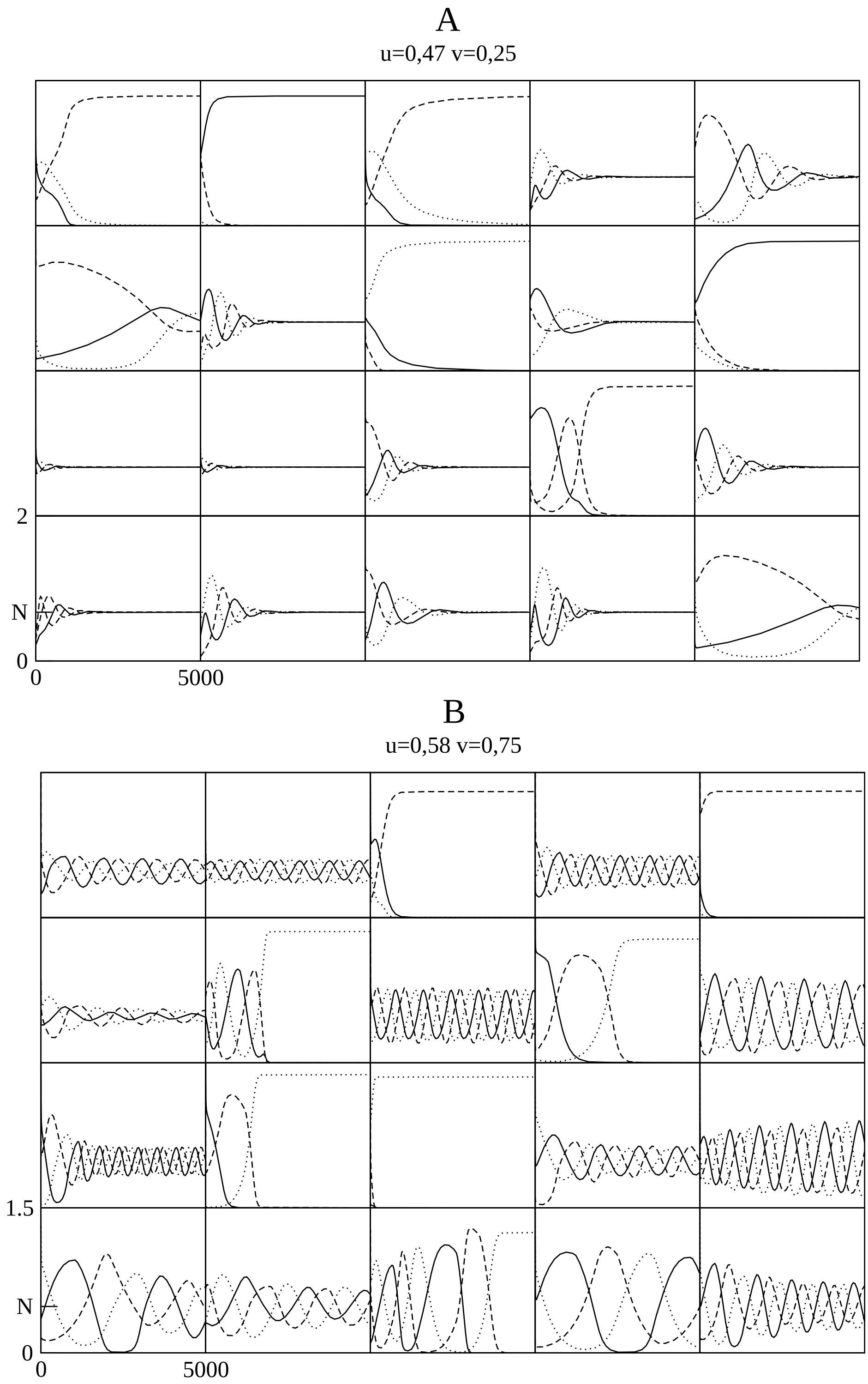


Figure 4.6: Simulations with K_{ji} sampled from the uniform distribution [0,0.01] and ν_{ji} computed with formula (4.16). Low-left panels show the density vs time scales and the common equilibrium density N; legend for species: 1(line), 2(dash), 3(points). (A) With ν_{ji} and K_{ji} generated with u and v from Figure 4.3A the system displays stable coexistence after oscillations dampen out, or competitive exclusion with the winner depending on the initial conditions. (B) With ν_{ji} and K_{ji} generated with u and v from Figure 4.3B the system displays regular competitive oscillations, heteroclinic oscillations and competitive exclusion.

We performed more simulations for larger samples (100 runs each), at different points in the $0 < u < 1$, with different distributions of K_{ji}. We found that

- Very high values of $\nu_{11}, \nu_{22}, \nu_{33}$ (corresponding to high u) result in stable coexistence and very low values (corresponding to high w) in competitive exclusion.
- The variance in the amplitude and periods of limit cycles decrease if the distribution of K_{ji} shifts from $[0, 2K]$ to $[K, 3K]$.
- The variance in the amplitude and periods of limit cycles increase if the distribution of K_{ji} get wider from $[0, 2K]$ to $[0, 4K]$. Competitive exclusion and heteroclinic cycles become more frequent.
- For low values of $\nu_{12}, \nu_{23}, \nu_{31}$ (corresponding to low v) the oscillation sequence is $1 \to 3 \to 2 \to 1$ and for high values it is $1 \to 2 \to 3 \to 1$.

The tendency to display competitive exclusion, stable coexistence, and oscillations according to specific consumption patterns, is robust with respect to the consumption parameters ν_{ji} and K_{ji}. Even the orientation of the cycles are consistently preserved. On the other hand, the final state of the community is very sensitive to parameters changes, they modify the amplitude and period of oscillations, whether cycles are regular or heteroclinic, and the geometry of the attraction basins of equilibria.

4.4 DISCUSSION

Besides a considerable number of parameters affecting resource consumption and growth, the dynamics of competition shows a consistent dependency on the species consumption characteristics. Strong consumption on resources for which requirements are high is expected to lead to coexistence and high diversity, and weak consumption upon them is expected to result in competitive exclusion and low diversity instead. When consumption is neither high or low on these highly needed resources, competitive oscillations are to be expected, and the sequence of oscillations is dictated by how strong are the consumption rates on resources for which requirements are intermediate.

But this consistency is not reliable for predicting the final state of the community. The interdependency of resource requirements and resource consumption lead to changes in the species consumption characteristics between the community and monoculture equilibria. The rules of the competitive game can be quite different between the community equilibrium and situations where some species are residents and others are invaders. The potential for displaying many equilibria and strong dependence on initial conditions, makes the accurate prediction of competitive outcomes a difficult task, even when the number of species is a low as in the present study.

Competitive oscillations could develop in different ways. In the simplest scheme the species form a strict non-transitive hierarchy of competitive dominance as in the game of Rock-Paper-Scissors, two-species equilibria are absent and the monocultures form a heteroclinic cycle. If this cycle and the three-species equilibrium are unstable, we see stable limit cycles. If the heteroclinic cycle is stable and the three-species equilibrium unstable, oscillations increase in amplitude and period and converge to the heteroclinic cycle. If the heteroclinic cycle is unstable and the three-species equilibrium stable, oscillation will dampen out and the system attains a stable coexistence equilibrium.

More complex dynamics result from the fact that the three-species equilibrium displays a sub-critical Hopf bifurcation. This originates an unstable limit cycle that may be encircled by a bigger stable one, as in the multispecies Monod model (Baer et al., 2006). Thus, some initial conditions result in damped oscillations around the equilibrium, and some other develop into cycles of increasing amplitude which end as stable limit cycles, heteroclinic oscillations or extinctions. The dependency of the dynamics on the initial conditions is not restricted to cases competitive exclusion, they are quite widespread.

Finally, it is important to notice that not all oscillatory dynamics are caused by non-transitivity in competition. Rock-Scissors-Paper dynamics can not develop when two-species equilibria exists, but the geometry of the attraction basins of the monocultures could induce the trajectories to spiral before a stable equilibrium, be it a monoculture or the three-species community, is attained. This configuration do also exists in Lotka-Volterra models ("case 32" in Zeeman, 1993). Although transitory, we must consider that compared with Lotka-Volterra and Monod models, it may take a long time and several up and downs before the system settles down, due to the delay associated with the quota dynamics; a time scale in which invasions or evolution may occur (Fussmann et al., 2003).

APPENDIX: PARAMETRIZATION FOR BIFURCATION ANALYSIS

Let $r_i = r, m_i = m, K_{ji} = K, S_j = S$ and define the non-dimensional variables

$$t' = Dt,\ R'_j = R_j/S,\ Q'_{ji} = Q_{ji}/q,\ N'_i = qN_i/S$$

where *q* is a positive quantity with the same units as Q_{ji} (e.g. one of the original q_{ji}). The scaled version of our model is

$$\begin{aligned}\frac{dN'_i}{dt} &= N'_i(\mu'_i - m') \\ \frac{dQ'_{ji}}{dt} &= \nu'_{ji} g(R'_j) - \mu'_i Q'_{ji} \\ \frac{dR'_j}{dt} &= (1 - R'_j) - \sum_{i=1}^{n} \nu'_{ji} g(R_j) N'_i\end{aligned}$$

$$\mu'_i = r' \min_j \left(1 - \frac{q'_{ji}}{Q'_{ji}}\right),\ g(R'_j) = \frac{R'_j}{K' + R'_j}$$

with parameters

$$r' = r/D, m' = m/D, q'_{ji} = q_{ji}/q, \nu'_{ji} = \nu_{ji}/Dq, K' = K/S$$

We will omit the primes to avoid confusion. As motivated in the main text, suppose circulant symmetry for the resource requirements R^*_{ji} and the matrix of maximum uptake rates ν_{ji}

$$\{R^*_{ji}\} = \begin{bmatrix} A & B & C \\ C & A & B \\ B & C & A \end{bmatrix}, \{v_{ji}\} = \begin{bmatrix} u & v & w \\ w & u & v \\ v & w & u \end{bmatrix}$$

with $A = 0.20$, $B = 0.15$, $C = 0.10$, and u, v, w given by (4.14). Combining (4.6) and (4.5) we construct a q_{ji} matrix which is also circulant

$$\{q_{ji}\} = \begin{bmatrix} q_A & q_B & q_C \\ q_C & q_A & q_B \\ q_B & q_B & q_A \end{bmatrix} = \left(\frac{r-m}{rm}\right) \begin{bmatrix} ug(A) & vg(B) & wg(C) \\ wg(C) & ug(A) & vg(B) \\ vg(B) & wg(C) & ug(A) \end{bmatrix}$$

with $r = 1.5$, $m = 1$, $K = 0.01$.

Our setup results in a three-species equilibrium where $\hat{R} = (A, A, A) = (0.20, 0.20, 0.20)$ and common species densities

$$\hat{N}_i = \frac{(1-A)}{g(A)} \times \frac{(u^2 + v^2 + w^2 - uv - uw - vw)}{(u^3 + v^3 + w^3 - 3uvw)}$$

but with u, v, w varying according to (4.14) the second quotient in the right hand side is simply $1/(1+v)$, thus $\hat{N}_i = (1-A)/(g(A)(1+v)) = 0.84/(1+v)$. $\hat{R}_j$ and $\hat{N}_i$ are invariant regarding our bifurcation parameter *u*. The following is the corresponding XPPAUT (Ermentrout (2002)) file for this system

```
--- Begin circulant.ode ---
# Parameters
par u=0.47,  v=0.25
name s=1, k=0.01, r=1.5
name A=0.2, B=0.15, C=0.1
# Quota thresholds
qa=(r-1)*u*A/(r*(k+A))
qb=(r-1)*v*B/(r*(k+B))
qc=(r-1)*(1-u)*C/(r*(k+C))
# Growth rate
mu(x,y,z) = max(r*(1 - max( max( qa/x, qc/y ), qb/z) ),0)

# ODE System
# Consumers
dn1/dt = n1*(mu(q11,q21,q31)-1)
dn2/dt = n2*(mu(q22,q32,q12)-1)
dn3/dt = n3*(mu(q33,q13,q23)-1)
# Resources
dr1/dt = s -r1 -u*r1/(k+r1)*n1     -v*r1/(k+r1)*n2     -(1-u)*r1/(k+r1)*n3
dr2/dt = s -r2 -(1-u)*r2/(k+r2)*n1 -u*r2/(k+r2)*n2     -v*r2/(k+r2)*n3
dr3/dt = s -r3 -v*r3/(k+r3)*n1     -(1-u)*r3/(k+r3)*n2 -u*r3/(k+r3)*n3
# Quotas
  # Sp1
```

```
dq11/dt = u*r1/(k+r1)     - mu(q11,q21,q31)*q11
dq21/dt = (1-u)*r2/(k+r2) - mu(q11,q21,q31)*q21
dq31/dt = v*r3/(k+r3)     - mu(q11,q21,q31)*q31
  # Sp2
dq12/dt = v*r1/(k+r1)     - mu(q22,q32,q12)*q12
dq22/dt = u*r2/(k+r2)     - mu(q22,q32,q12)*q22
dq32/dt = (1-u)*r3/(k+r3) - mu(q22,q32,q12)*q32
  # Sp3
dq13/dt = (1-u)*r1/(k+r1) - mu(q33,q13,q23)*q13
dq23/dt = v*r2/(k+r2)     - mu(q33,q13,q23)*q23
dq33/dt = u*r3/(k+r3)     - mu(q33,q13,q23)*q33

# Initial values
init r1=1, r2=1, r3=1
init q11=1, q12=1, q13=1
init q21=1, q22=1, q23=1
init q31=1, q32=1, q33=1
init n1=1, n2=0.5, n3=0.9

# Settings
@ dt=0.01 bound=10000 total=4000 yp1=n1 yp2=n2 yp3=n3 \
ylo=0 yhi=2 xhi=4000 nout=200 nplot=3
--- End circulant.ode ---
```

5

COMMONALITIES AND DISCREPANCIES AMONG MULTISPECIES COMPETITION MODELS

Tomás A. Revilla and Franz J. Weissing

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

$$\frac{dN_i}{dt} = N_i \left\{ r_i - \sum_{k=1}^{n} a_{ik} N_k \right\} \tag{5.1}$$

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 priory 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

$$\frac{dN_i}{dt} = N_i \{\mu_i(R_1, \ldots, R_m) - m_i\} \tag{5.2a}$$

$$\frac{dR_j}{dt} = \phi_j(R_j) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, \ldots, R_m) N_i \tag{5.2b}$$

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 μ_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 ϕ_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, 1987; 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 μ_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 μ_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 ϕ_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 μ_{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 μ_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 μ_{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 μ_{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)

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

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

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

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

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

where ν_{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

$$\phi_j = D(S_j - R_j) \tag{5.9}$$

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

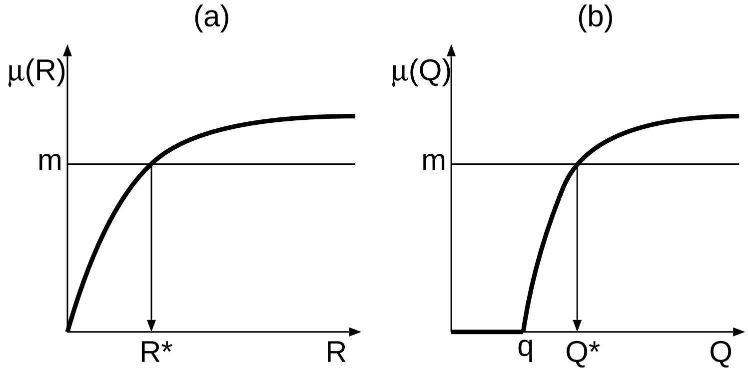


Figure 5.1: (a) In the Tilman model the per capita growth rate μ is typically a saturating function of the resource concentration R. There is a concentration $R = R^*$ for which the per capita growth and mortality rates are exactly balanced $\mu(R^*) = m$. (b) In the Quota model the per capita growth rate μ is a saturating function of the nutrient quota Q, and is often assumed to be zero for quota levels below a threshold value q. There is a quota level $Q = Q^*$ for which the per capita growth and mortality rates are exactly balanced $\mu(Q^*) = m$.

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

$$\begin{aligned} \frac{dN_1}{dt} &= N_1\{r_1 - a_{11}N_1 - a_{12}N_2\} \\ \frac{dN_2}{dt} &= N_2\{r_2 - a_{21}N_1 - a_{22}N_2\} \end{aligned}$$

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_i/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

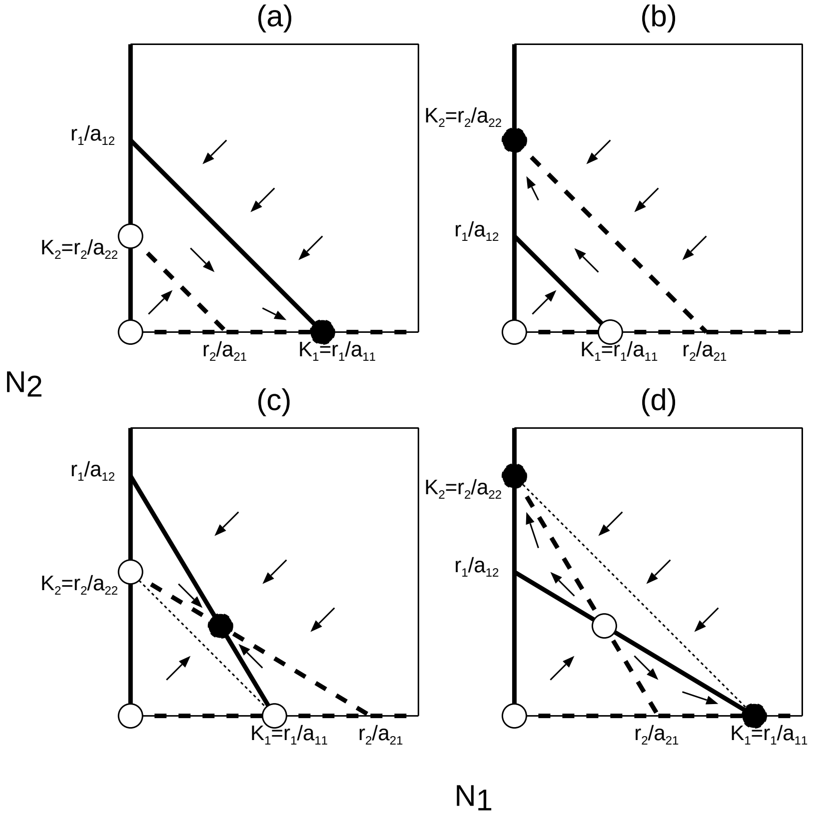


Figure 5.2: The outcome of the Lotka-Volterra model depends on the geometry of the nullclines of species 1 (solid lines) and 2 (dashed lines). Species 1 increases (arrows point right) in the region left to its "zero" nullcline (vertical axis) and right to its "non-zero" nullcline (solid line), and decreases 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

$$a_{11}a_{22} > a_{12}a_{21} \tag{5.10}$$

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_i. Each species i has a minimal resource requirement R^*_{1i} at which its growth rate is balanced by its loss rate $\mu_i(R^*_{ji}) = m_i$ (Fig. 5.1a). 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,

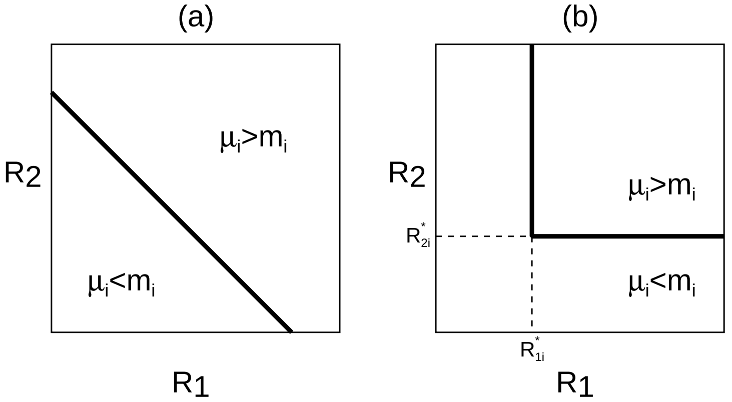


Figure 5.3: For two resources the nullcline of a species correspond to those resource combinations where net growth is zero. For resource concentrations above the nullcline a species increases, and for concentrations below it decreases. (a) In case of perfectly substitutable resources, the nullcline 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).

1997). 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_1R_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 μ_{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 essential 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 had 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 $(\hat{N}_1, \hat{N}_2)$. If resources are supplied linearly as in (5.9) we have

$$D(S_j - \hat{R}_j) - c_{j1}\mu_1(\hat{R}_1, \hat{R}_2)\hat{N}_1 - c_{j2}\mu_2(\hat{R}_1, \hat{R}_2)\hat{N}_2 = 0$$

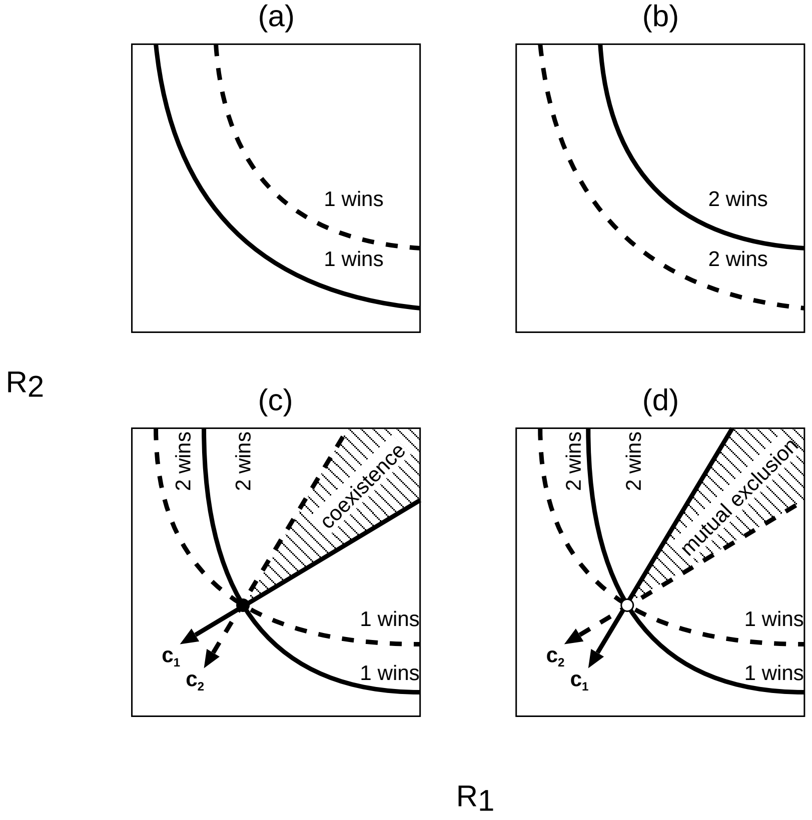


Figure 5.4: The outcomes of competition between two species for two resources in the Tilman model. The nullclines of the two species are plotted in resource space, solid for species 1, dashed for 2. (a) The nullcline of species 1 lies below that of species 2. In this case , species 1 outcompetes species 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, $\mathbf{c}_2 = (c_{12}, c_{22})$, is steeper than the consumption vector of species 1, $\mathbf{c}_1 = (c_{11}, c_{21})$. 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 $\mathbf{S} = (S_1, S_2)$ 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 $\mathbf{S}$ does not belong to the wedge, then, depending on the resource ratios, species 1 or 2 wins. (d) When $\mathbf{c}_1$ is steeper than $\mathbf{c}_2$ 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_1, S_2) lies in the region bounded by two lines, the slope of which are given by the species consumption vectors $\mathbf{c}_1 = (c_{11}, c_{21}), \mathbf{c}_2 = (c_{12}, c_{22})$ 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

$$c_{11}c_{22} > c_{12}c_{21} \tag{5.11}$$

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 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 $f_{ji}(R^*_{ji}) = m_i Q^*_{ji}$, 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. 5.1b). In consequence, coexistence between two species requires more than one resource.

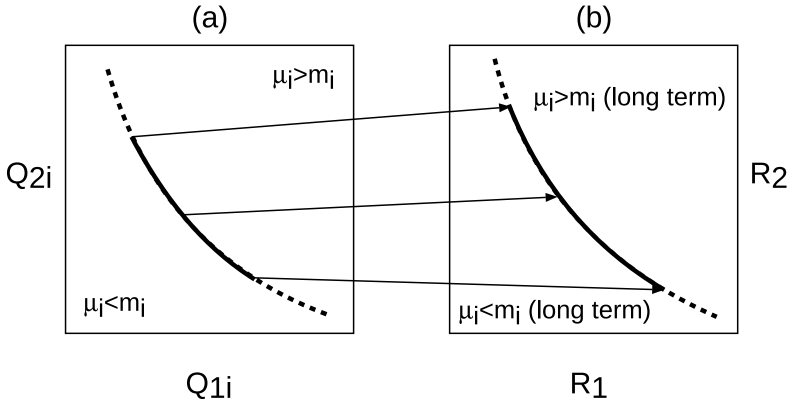


Figure 5.5: (a) In the storage based model the nullcline of species i divides the quota space of species i in zones of net positive and net negative growth. (b) The nullcline in quota space can be mapped into a "quasi-nullcline" in resource space. If resources are kept above the quasi-nullcline, species 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 $R_1 R_2$-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 $\mathbf{c}_i = (c_{1i}, c_{2i})$ 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 $\mathbf{f}_i = (f_{1i}(R_1), f_{2i}(R_2))$. At the community equilibrium, when $dQ_{ji}/dt = 0$, 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

$$\underbrace{\begin{bmatrix} f_{1i}(\hat{R}_1) \\ f_{2i}(\hat{R}_2) \end{bmatrix}}_{\mathbf{f}_i} = m_i \begin{bmatrix} \hat{Q}_{1i} \\ \hat{Q}_{2i} \end{bmatrix} \doteq m_i \underbrace{\begin{bmatrix} c_{1i} \\ c_{2i} \end{bmatrix}}_{\mathbf{c}_i}$$

turns out that both $\mathbf{f}_i$ and $\mathbf{c}_i$ 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 $\mathbf{f}_i(R_1, R_2)$ is resource dependent, whereas $\mathbf{c}_i$ 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 5.4a, 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 5.4c, 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

$$f_{11}(\hat{R}_1) f_{22}(\hat{R}_2) > f_{12}(\hat{R}_1) f_{21}(\hat{R}_2) \tag{5.12}$$

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. 5.4d).

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 $Q_{1i} = Q^*_{1i}$ and $Q_{2i} = Q^*_{2i}$ for which $\mu_i = m_i$. Given equation (5.3b) at equilibrium, $f_{ji}(R^*_{ji}) = m_i Q^*_{ji}$, 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 5.3a. 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):

$$R_j = S_j - c_{j1}N_1 - c_{j2}N_2 \tag{5.14}$$

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):

$$\begin{aligned}\frac{1}{N_i}\frac{dN_i}{dt} &= b_{1i}(S_1 - c_{1i}N_i - c_{1k}N_k) + b_{2i}(S_2 - c_{2i}N_i - c_{2k}N_k) - D \\ &= \underbrace{b_{1i}S_1 + b_{2i}S_2 - D}_{r_i} - \underbrace{(b_{1i}c_{1i} + b_{2i}c_{2i})}_{a_{ii}} N_i - \underbrace{(b_{1i}c_{1k} + b_{2i}c_{2k})}_{a_{ik}} N_k \end{aligned} \tag{5.15}$$

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 (5.10) 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

$$\frac{1}{N_i}\frac{dN_i}{dt} = \mu_i - D = \min[b_{1i}R_1, b_{2i}R_2] - D \tag{5.16}$$

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

$$\begin{aligned} \frac{1}{N_i}\frac{dN_i}{dt} &= \min[b_{1i}(S_1 - c_{1i}N_i - c_{1k}N_k), b_{2i}(S_2 - c_{2i}N_i - c_{2k}N_k)] - D \\ &= \min[\underbrace{(\underbrace{b_{1i}S_1 - D}_{r_{i1}} - \underbrace{b_{1i}c_{1i}}_{a_{ii1}}N_i - \underbrace{b_{1i}c_{1k}}_{a_{ik1}}N_k),}_{\text{resource 1 is limiting}} \underbrace{(\underbrace{b_{2i}S_2 - D}_{r_{i2}} - \underbrace{b_{2i}c_{2i}}_{a_{ii2}}N_i - \underbrace{b_{2i}c_{2k}}_{a_{ik2}}N_k)]}_{\text{resource 2 islimiting}} \end{aligned} \tag{5.17}$$

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 $r_1 = b_{11}c_{11}N_1 + b_{11}c_{12}N_2$, but if its it limited by resource 2, its nullcline will be $r_1 = b_{21}c_{21}N_1 + b_{21}c_{22}N_2$. 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 true (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

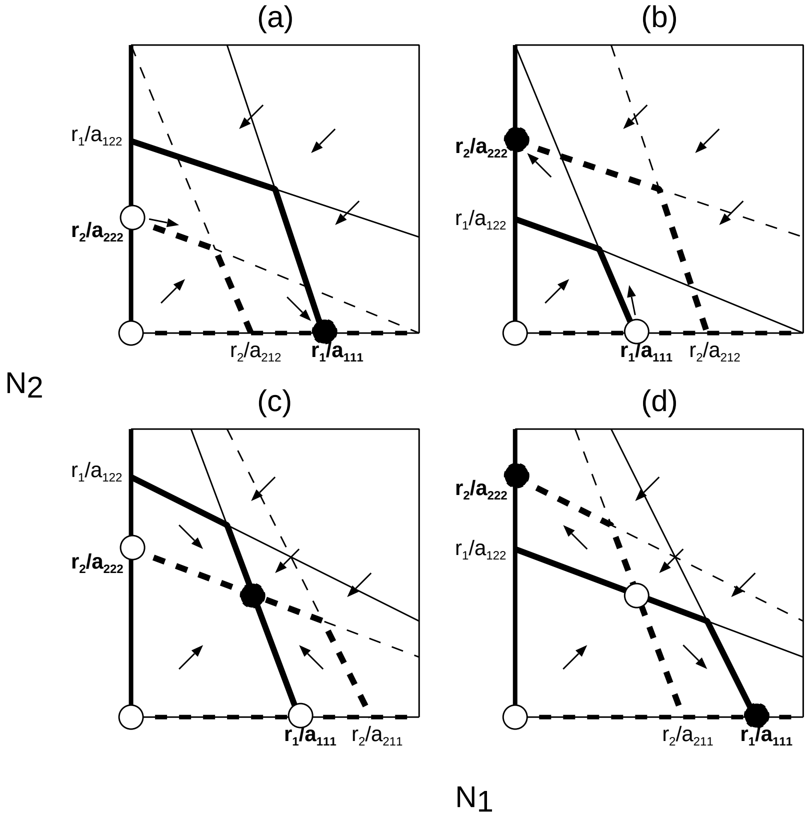


Figure 5.6: Nullclines of two species competing for two perfectly essential resources, performed in the species space (solid for species 1, dashed for species 2). If the resource supply concentrations are such that each species can be limited by two resources, Liebig's law dictates that the nonzero nullclines 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.

5.4.1 *Lotka-Volterra model*

Consider community equilibrium in the Lotka-Volterra model, i.e. an equilibrium where $N_i > 0$ for all species. From (5.1) with $dN_i/dt = 0$, such an equilibrium is characterized by a set of linear equations:

$$\sum_{k=1}^{n} a_{ik} N_k = r_i \tag{5.18}$$

Each equation represents a nullcline in a multidimensional species space. Figure 5.7a 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.

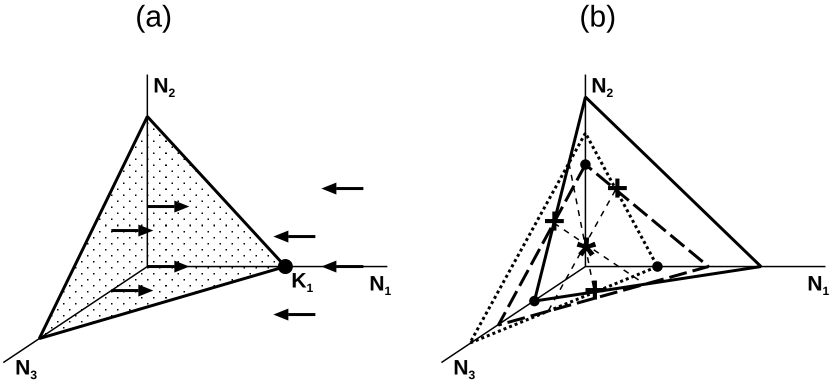


Figure 5.7: Equilibrium analysis for the three species Lotka-Volterra model. (a) The nullcline of species 1: N_1 increases in the region below the plane and decreases above it. The round dot is the carrying capacity $K_1 = r_1/a_{11}$, or monoculture equilibrium. (b) The nullclines of three species intersecting 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.

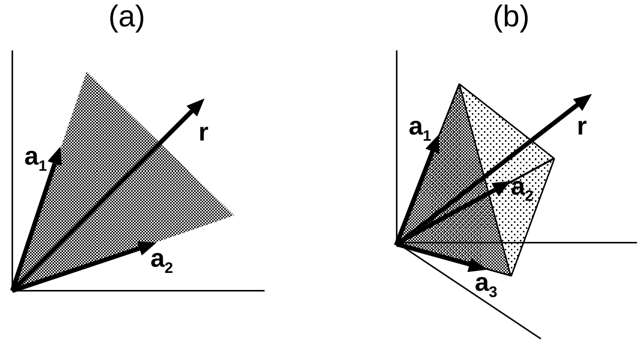


Figure 5.8: A n-species Lotka-Volterra system has a positive solution (all $\hat{N}_i > 0$) if the vector of intrinsic growth rates $\mathbf{r} = (r_1, \ldots, r_n)^T$ is contained in the cone formed by the columns of the matrix of competition coefficients, $\mathbf{a}_i = (a_{i1}, \ldots, a_{in})^T$.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

5.4.2 *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 shorty after). In the n dimensional resource space $R_1 \cdots R_n$, 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 $\hat{\mathbf{R}} = (\hat{R}_1, \dots, \hat{R}_n)$ or multiple discrete points $\hat{\mathbf{R}}, \hat{\mathbf{R}}', \hat{\mathbf{R}}'', \dots$ etc. In the special case of Liebig's law (5.5) the growth rates are given by $\mu_i = \min_j[\mu_{ji}(R_j)]$, and the multiple resource requirements R^*_{ji}, 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 $R^*_{1i}, R^*_{2i}, R^*_{3i}$. When two nullclines like these intersect, they form a line, and the intersection of this line with the third nullcline results in a point $\hat{\mathbf{R}} = (\hat{R}_1, \dots, \hat{R}_n)$. 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 $(R^*_{ii} > R^*_{ik}, k \neq i)$, the intersection of the nullclines occurs exactly at one point:

$$\hat{\mathbf{R}} = (\hat{R}_1, \hat{R}_2, \dots, \hat{R}_n) = (R^*_{11}, R^*_{22} \dots, R^*_{nn}) \tag{5.19}$$

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 n-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 $\hat{\mathbf{R}}$ 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

$$\sum_{i=1}^{n} c_{ji} m_i N_i = \phi_j(R_j) \tag{5.20}$$

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 ϕ_i is given by (5.9) and $m_i = D$, equation (5.20) can be written as $\frac{\boldsymbol{\phi}}{D} = \mathbf{CN}$, where $\boldsymbol{\phi} = (\phi_1, \dots, \phi_n)$ is the resource supply vector, $\mathbf{N}$ is the vector of species densities, and $\mathbf{C} = \{c_{ji}\}$ is the consumption matrix, i.e. a matrix whose columns correspond to the species consumption vectors $\mathbf{c}_i = (c_{1i}, \dots, c_{ni})^T$. If the determinant of $\mathbf{C}$ is not zero, we can compute the equilibrium densities as $\hat{\mathbf{N}} = D^{-1}\mathbf{C}^{-1}\hat{\boldsymbol{\phi}}$, in which $\hat{\boldsymbol{\phi}}$ corresponds to the supply vector evaluated at the intersection of the nullclines in resource space, i.e. $\hat{\boldsymbol{\phi}} = \boldsymbol{\phi}(\hat{\mathbf{R}})$. As in the case of the Lotka-Volterra model, the cone rule also applies: $\hat{\mathbf{N}}$ is a community equilibrium if the supply vector $\boldsymbol{\phi}$ falls in the cone formed by the columns of the consumption matrix, the $\mathbf{c}_i$. In case of linear resource renewal as in (5.9), the cone rule can be stated more explicitly as follows: the supply point $\mathbf{S} = (S_1, \ldots, S_n)$ falls in the cone spanned by lines originating at the nullcline crossing $\hat{\mathbf{R}}$, with the orientation (slope) of these lines given by the species consumption vectors $\mathbf{c}_i$. In the R_1R_2 space this cone is the hatched "wedge" in Figures 5.4c,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 $(\hat{\mathbf{R}}, \hat{\mathbf{R}}', \hat{\mathbf{R}}'', \ldots)$ if are they 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 $\mathcal{R}$. 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 $(m \geqslant n)$, 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):

$$\sum_{i=1}^{n} f_{ji}(R_j)N_i = \phi_j(R_j) \tag{5.21}$$

These equations can be written in matrix form as $\boldsymbol{\phi} = \mathbf{F}\mathbf{N}$, where $\mathbf{F} = \{f_{ji}(R_j)\}$ 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 $\hat{\mathbf{N}} = \hat{\mathbf{F}}^{-1}\hat{\boldsymbol{\phi}}$ (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 $\mathbf{f}_i(\mathbf{R})$ are functions in resource space.

5.4.4 *Comparison*

In the three models it is possible to relate the species densities in equilibrium, $\hat{N}_i$, 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):

$$\mathbf{M}\hat{\mathbf{N}} = \boldsymbol{\rho} \tag{5.22}$$

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 $\mathbf{C} = \{c_{ji}\}$, and in the Quota model it is the matrix of consumption rates at equilibrium $\hat{\mathbf{F}} = \{f_{ji}(\hat{R}_j)\}$. The vector $\boldsymbol{\rho}$ 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 $\boldsymbol{\rho}$ 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, $\boldsymbol{\rho}$ 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 $\hat{\mathbf{N}} = \mathbf{M}^{-1}\boldsymbol{\rho}$, as long as $\mathbf{M}$ can be inverted. If $\mathbf{M}$ can not 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 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 $\hat{\mathbf{N}}$ by the method of matrix inversion like in the Lotka-Volterra model, provided that $\mathbf{M} = \mathbf{C}$ (Tilman model) or $\mathbf{M} = \hat{\mathbf{F}}$ (Quota model) is invertible. Likewise, the community equilibrium may not exist because some rows or columns of $\mathbf{M}$ 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) $\hat{\mathbf{N}}$ may be feasible, but we cannot use the method of matrix inversion to find them (the number of rows and columns of $\mathbf{M}$ 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 counterbalanced 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):

$$\boldsymbol{\rho} - \sum \mathbf{v}_i \hat{N}_i = \mathbf{0} \tag{5.23}$$

where $\mathbf{0}$ is a vector of zeros, and the vector $\mathbf{v}_i$ is the i-th column of $\mathbf{M}$. In equation (5.23) $\boldsymbol{\rho}$ can be interpreted as the force exercised by a stretched spring, $\mathbf{v}_i$ 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 $\mathbf{M}$ is positive (e.g. gravity points downwards, never upwards) and $\boldsymbol{\rho}$ is positive (e.g. springs pull when stretched, they do not push), $\hat{\mathbf{N}}$ will be positive (masses are positive) if and only if the vector $\boldsymbol{\rho}$ belongs to the cone formed by the columns of $\mathbf{M}$.

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

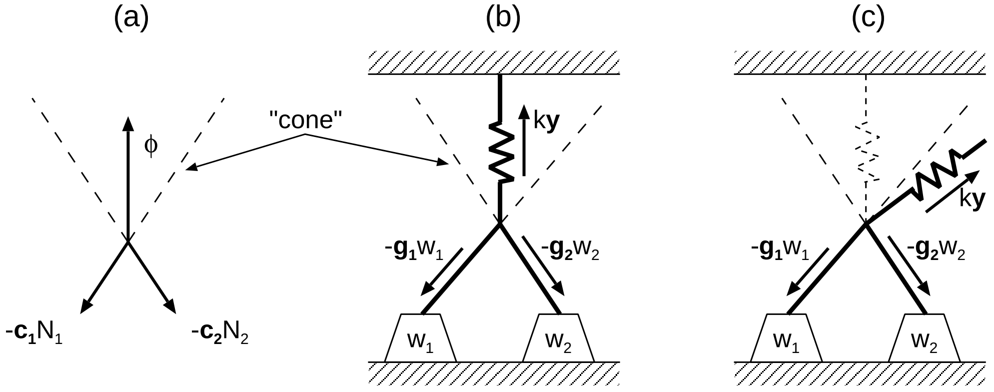


Figure 5.9: Interpretation of the "cone rule", using Tilman's model in (a) and a mechanical example in (b). In Tilman's model, the magnitude of the supply vector $\boldsymbol{\phi}$ is proportional to the distance between the supply point and the resource concentrations (i.e. $\phi_j = D(S_j - R_j)$ 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. $k\mathbf{y} = k|\Delta y|$ according to Hooke's law). In Tilman's model the consumption vector of a species is given by its resource contents as $\mathbf{c}_i = (c_{1i}, \ldots, c_{mi})^T$, 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 $\mathbf{g}_i$ is the component gravity's acceleration $(\mathbf{g})$ along the wire of object i. The force of the pull is proportional to the object's mass $(\mathbf{g}_i w_i)$. In both examples, the vector pointing upwards ($\boldsymbol{\phi}$ or $k\mathbf{y}$) belongs to the cone defined by dashed lines, the slope of which are given by the vectors pointing downwards ($\mathbf{c}_i$ or $\mathbf{g}_i$). 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 $(\mathbf{g})$ 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 5.9a 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 $n-1, n-2, \dots, 1$ species, i.e. border equilibria. In a border equilibria, we have two sets of species: the set $\mathcal{K}$ of *residents* for which $N_k > 0$, and the set $\mathcal{L}$ of potential *invaders* for which $N_l = 0$. 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 $\mathcal{K}$. External stability refers to stability against invasion by small numbers of invaders from $\mathcal{L}$.

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:

$$\frac{1}{N_l}\frac{dN_l}{dt} = r_l - \sum_{k\in\mathcal{K}} a_{lk}\tilde{N}_k \tag{5.24a}$$

$$\frac{1}{N_l}\frac{dN_l}{dt} = \mu_l(\tilde{R}_1,\ldots,\tilde{R}_m) - m_l \tag{5.24b}$$

$$\frac{1}{N_l}\frac{dN_l}{dt} = \mu_l(\tilde{Q}_{1l},\ldots,\tilde{Q}_{ml}) - m_l \tag{5.24c}$$

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 $N_i = 0$ 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, $N_3^{-1} dN_3/dt > 0$. 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 $(k \in \mathcal{K})$, we just have to ignore the part of the system associated with the invaders $(l \in \mathcal{L})$. 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):

$$\mathbf{J} = -\mathbf{D}\mathbf{A} \tag{5.25}$$

In this equation $\mathbf{D}$ 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 $\mathbf{A}$ 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 (5.2a) adopts the form:

$$\mathbf{J} = -\mathbf{D}\mathbf{C} \tag{5.26}$$

where $\mathbf{D}$ is a diagonal matrix whose elements are $(\partial\mu_i/\partial R_i)N_i$ evaluated at the equilibrium, and $\mathbf{C} = \{c_{ji}\}$ 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 $\mathbf{C}$ 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.

5.5.3.3 *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 8×8 matrix jacobian, and for 3 species and 3 resources we must deal with a 15×15 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 $(dQ_{ji}/dt \approx 0)$. This allows us obtain the jacobian matrix of a much simpler system, that involves only the equations of the species densities (Appendix B):

$$\mathbf{J} = -\mathbf{D}\hat{\mathbf{F}} \tag{5.27}$$

where $\mathbf{D}$ is a diagonal matrix with elements $\hat{N}_i \partial\mu_i/\partial R_i$ and $\hat{\mathbf{F}} = \{f_{ji}(\hat{R}_j)\}$ 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 $\partial\mu_i/dR_i$ makes sense only because of the quasi-steady-state assumption for the quotas, such that $\frac{\partial\mu_i}{\partial R_i} = \frac{\partial\mu_i}{\partial Q_{ii}}\frac{\partial Q_{ii}}{\partial R_i}$. 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 $\hat{\mathbf{F}}$ 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 (5.20) in the resident community $\mathcal{K}$, can substituted as $\tilde{R}_j = \phi_j^{-1}(\sum_{k \in \mathcal{K}} c_{jk}\tilde{N}_k)$ 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

Model (equation)	Equilibrium	jacobian matrix	Assumption
Lotka-Volterra (5.1)	$\mathbf{A}\hat{\mathbf{N}} = \mathbf{r}$	$\mathbf{J} = -\mathrm{diag}(\mathbf{r} \circ \hat{\mathbf{N}})\mathbf{A}$	none
Tilman model (5.2)	$\mathbf{C}\hat{\mathbf{N}} = \frac{1}{D}\hat{\boldsymbol{\phi}}$	$\mathbf{J} = -\mathrm{diag}(\frac{\partial \mu}{\partial \mathbf{R}} \circ \hat{\mathbf{N}})\mathbf{C}$	MBC
Quota model (5.3)	$\hat{\mathbf{F}}\hat{\mathbf{N}} = \hat{\boldsymbol{\phi}}$	$\mathbf{J} = -\mathrm{diag}(\frac{\partial \mu}{\partial \mathbf{R}} \circ \hat{\mathbf{N}})\hat{\mathbf{F}}$	MBC+QSS

Table 5.1: Equilibrium equations and jacobian matrices. An equilibrium is internally stable if all the eigenvalues of the jacobian matrix have negative real parts. The hat (^) indicates evaluation at the equilibrium. The symbol ∘ denotes an element wise product of vectors. MBC: mass balance constraint, QSS: quota at steady state.

and Quota) to the same number of equations of a n-species Lotka-Volterra model. The corresponding jacobian matrix becomes:

$$\mathbf{J} = -\mathbf{DM} \tag{5.28}$$

where $\mathbf{D}$ is a diagonal matrix that contains the species densities at equilibrium multiplied by rate terms, and $\mathbf{M}$ is the same matrix that determines the feasibility of the equilibrium (see section 5.4): the community matrix $\mathbf{A}$ (Lotka-Volterra), the matrix of resource contents $\mathbf{C}$ (Tilman model) or the consumption matrix $\hat{\mathbf{F}}$ at the equilibrium (Quota model). We will call $\mathbf{M}$ 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 $\mathbf{M}$ instead of the full jacobian. For example consider the 3×3 matrix $\mathbf{M}$ 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 $\mathbf{M}$ 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

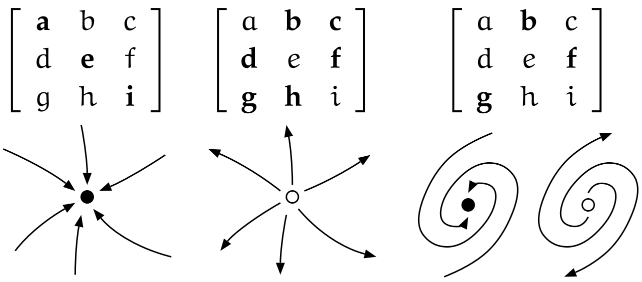


Figure 5.10: The structure of the interaction matrix $\mathbf{M}$ ($\mathbf{A}, \mathbf{C}$ or $\hat{\mathbf{F}}$). The elements in **bold** are greater than the elements in normal typeface in the same row or column. The diagrams below illustrate the local dynamics in the proximity of the community equilibrium. A closed circle denotes a stable equilibrium, an open circle an unstable one.

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 comparisson to intra-specific competition. If the matrix $\mathbf{M}$ 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 tens 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 $\mathbf{M}$ is positive, the equilibrium may be stable or unstable, but if negative, it will be unstable.

5.6 global dynamics

In this section, we try to relate the local stability of equilibria with the global dynamics. We focus first on the scenarios that lead to competitive oscillations, and later on the less studied but equally important cases in which the communities have alternative states.

5.6.1 *Competitive oscillations*

The pioneer works of May and Leonard (1975) and Gilpin (1975) with the Lotka-Volterra model revealed that a oscillations are possible for the 3-, 4- and 5-species scenario. Smale (1976) showed that given a high enough number of species ($n \geqslant 5$) 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 $\mathbf{C}$ (Tilman model) or $\hat{\mathbf{F}}$ (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 $\mathbf{M}$ ($\mathbf{A}$, $\mathbf{C}$ or $\hat{\mathbf{F}}$), 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.

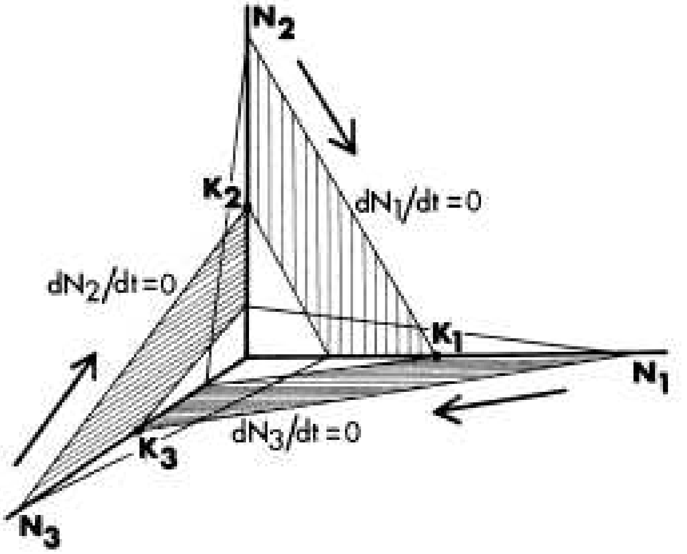


Figure 5.11: Competitive oscillations in the Lotka-Volterra model. In this arrangement of nullclines, 2-species equilibria do not exist. If we consider species pairs: species 1 excludes species 2, species 3 excludes species 1 and species 2 excludes species 3. This results in a sequence of species replacement $1 \rightarrow 3 \rightarrow 2 \rightarrow 1$ 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).

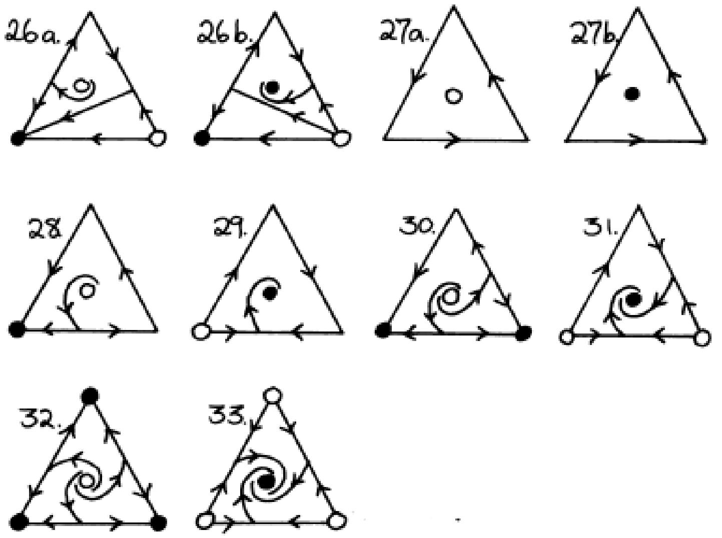


Figure 5.12: The dynamics of the three-species Lotka-Volterra model can be represented in a triangular phase plane or "simplex". The vertex of the triangles represent monoculture equilibria, the intersection of a trajectory and an edge represents a border equilibrium, and the community equilibrium lies 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 $(\mathbf{A})$ or the consumption matrix $(\mathbf{C}, \hat{\mathbf{F}})$ 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. 5.2d). 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. 5.4d). In these simples 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

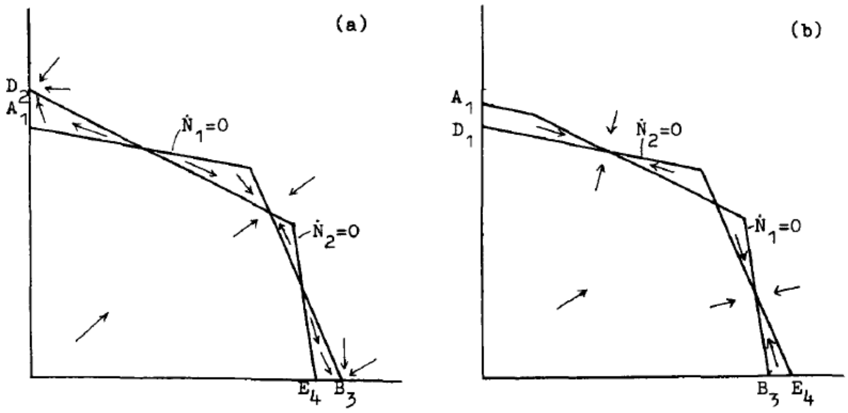


Figure 5.13: A possible configuration of nullclines in species space (the $\dot{N}_i = 0$), for two species competing for four perfectly essential resources. (a) The system has three alternative stable states, the monocultures and the community equilibrium. Coexistence depends on the initial conditions. (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 extense 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, 1975; 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 (5.2) 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:

$$\frac{dN_i}{dt} = N_i G_i(N_1, \ldots, N_n) \tag{5.29}$$

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 $(\partial G_i/\partial N_k < 0)$. 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 θ-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:

$$T_j(t) = R_j(t) + \sum_i c_{ji} N_i(t) \tag{5.30}$$

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:

$$\begin{aligned}
\frac{dT_j}{dt} &= D(S_j - R_j) - \sum_i c_{ji}\mu_i N_i + \sum_i c_{ji}(\mu_i - D)N_i \\
\frac{dT_j}{dt} &= D[S_j - (R_j + \sum_i c_{ji} N_i)] \\
\frac{dT_j}{dt} &= D[S_j - T_j]
\end{aligned}$$

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:

$$R_j = S_j - \sum_i c_{ji} N_i \tag{5.31}$$

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:

$$T_k(t) = R_k(t) + \sum_i Q_{ki}(t) N_i(t) \tag{5.32}$$

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 $dR_j/dt, dQ_{ji}/dt$ and dN_i/dt from (5.3) we obtain:

$$\begin{aligned}
\frac{dT_j}{dt} &= D(S_j - R_j) - \sum_i f_{ji} N_i + \sum_i Q_{ji}(\mu_i - D) N_i + \sum_i N_i (f_{ji} - \mu_i Q_{ji}) \\
\frac{dT_j}{dt} &= D[S_j - (R_j + \sum_i Q_{ji} N_i)] \\
\frac{dT_j}{dt} &= D[S_j - T_j]
\end{aligned}$$

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:

$$R_j = S_j - \sum_i Q_{ji} N_i \tag{5.33}$$

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 $dQ_{ji}/dt \approx 0$, even if the system is far from the equilibrium. In consequence, the differential equations of the quotas can be substituted by:

$$f_{ji}(R_j) \approx \mu_i \tilde{Q}_{ji} \tag{5.34}$$

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

These assumptions result in a reduced system formed by the n differential equations (5.3a). The jacobian matrix of this subsystem has elements

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

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

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

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

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

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

$$\frac{\partial \dot{N}_i}{\partial N_k} = -\frac{\hat{N}_i}{D} \widehat{\frac{\partial \mu_i}{\partial Q_{ii}}} \widehat{\frac{\partial Q_{ii}}{\partial R_i}} f_{ik}(\hat{R}_i) \tag{5.35}$$

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

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

$\mathbf{J} = \left\{ \frac{\partial \dot{N}_i}{\partial N_k} \right\}$ is the jacobian matrix of the reduced system. $\mathbf{D} = \mathrm{diag}\left\{ \frac{\hat{N}_i}{D} \widehat{\frac{\partial \mu_i}{\partial Q_{ii}}} \widehat{\frac{\partial Q_{ii}}{\partial R_i}} \right\}$ is a diagonal matrix with positive elements in the diagonal. And $\hat{\mathbf{F}} = \{f_{ik}(\hat{R}_i)\} = \{f_{ji}(\hat{R}_j)\}$ is the consumption matrix.

6

EFFECTS OF PLANT-SOIL FEEDBACKS ON THE DYNAMICS OF COMPETITIVE PLANT COMMUNITIES

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Plant-soil feedback effects can have important consequences for interactions between plants. However, quantification of these effects is difficult due to the vast belowground diversity and technical problems inherent to measuring and manipulating soil communities. Therefore, there is a need for mathematical models to improve our understanding of plant-soil interactions. Pioneering mathematical models on plant-soil feedback effects have been developed by Bever and colleagues (Bever et al., 1997; Bever, 1999, 2003). In their most recent version of the model ("Bever model") a few particular cases where plant-soil feedback affected plant coexistence and dynamics were described, but an exploration of all possible plant-soil feedback effects was not presented. The aim of our paper is to provide a full analysis of the Bever model, which contributes to our general understanding of plant-soil interactions and the consequences for plant community dynamics and diversity. We analyzed the model by means of a new type of graphical analysis, which provides a rather complete analysis of equilibria and their stability, and is still relatively easy to perform and understand. We found that plant coexistence could be explained by an interaction between net soil feedback effect and competition strength between the plants. Net positive feedback generally leads to species exclusion, but when competition coefficients are small enough plant species can coexist. Net negative feedback enhanced the range of plant coexistence by means of competitive oscillations. This result highlights that plant-soil feedbacks may enhance plant community diversity.

Keywords: *Graphical analysis, plant-soil feedback, coexistence, oscillations, diversity*

6.1 INTRODUCTION

Ecologists have long recognized that interactions between plants are mediated by many abiotic (e.g. soil texture, nutrient availability, topography) and biotic factors (e.g. grazing, plant competition and facilitation) (e.g. Harper, 1977; Tilman, 1988). More recent research has stressed the influence, of below-ground biota (the soil community) on interactions between plants (Klironomos, 2003; Callaway et al., 2004), by exerting positive or negative effects on the growth of specific plants (van der Putten et al., 1993; van der Putten and Van der Stoel, 1998; van der Heijden et al., 1998; Olff et al., 2000; De Deyn et al., 2003; Klironomos, 2003; van der Heijden et al., 2003). These effects have been shown to influence species at higher trophic levels (e.g. plant herbivores and their predators) as well (Soler et al., 2005). Therefore, interactions between soil communities and plants can potentially have a significant influence on species composition and diversity in many different parts of an ecosystem (van der Putten et al., 2001; Wardle et al., 2004).

The interaction between plant growth and soil communities, referred to as plant-soil feedback, is a two-step process: the presence of a specific plant changes the composition of the soil community, which in turn alters the growth rate of that specific plant (Bever, 2003; Reynolds et al., 2003). Quantifying the effect of soil organisms on plant growth, however, is difficult due to the vast below-ground diversity, and the technical problems inherent to measuring and manipulating soil communities (Bever, 2003; van der Putten et al., 2009). Therefore, a coupling of empirical results to mathematical models may improve our understanding of the role of plant-soil interactions in community assembly and diversity (van der Putten et al., 2009).

Pioneering work on coupling empirical soil feedback results to mathematical models has been performed by Bever and colleagues (Bever et al., 1997; Bever, 1999, 2003). These models are appealing to many empirical plant-soil ecologists because they do not require specific knowledge on the diversity of soil communities, or the effects of individual soil-borne species on plant growth. As a result, model predictions can be tested with relatively straightforward experiments (Bever, 1994; Bever et al., 1997). Bever (2003) proposed a framework that introduces plant-soil feedback into the classical Lotka-Volterra competition model, which has motivated several subsequent model studies on similar topics Bonanomi et al. (2005); Umbanhowar and McCann (2005); Eppinga et al. (2006); Eppstein et al. (2006); Eppstein and Molofsky (2007).

Using the model framework, Bever (2003) highlighted two particular cases where plant-soil feedback affected coexistence of 2 competitive plant species: 1) negative plant-soil feedback facilitating coexistence between plants and 2) negative plant-soil feedback driving oscillations in plant abundances (Bever, 2003). However, there may be more ways in which plant-soil feedbacks can affect coexistence and dynamics of plant competitors which can be revealed by a full analysis of the model, i.e., an exploration of all possible parameter combinations. Such an analysis contributes to our general understanding of plant-soil feedback effects (van der Putten et al., 2009). The aim of our study is provide a complete analysis of the model by Bever (2003), referred here as the 'Bever model'. In section 2 we will introduce the Bever model. In section 3 we will analyze the Bever model using a new graphical technique, which provides a rather complete analysis of equilibria and their stability, and is still

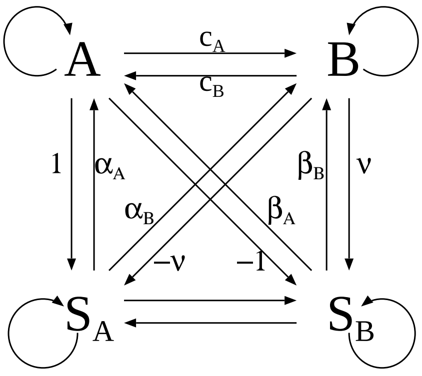


Figure 6.1: Schematic representation of potential interactions between two plants A and B and their associated soil communities S_A and S_B in the Bever model.

relatively easy to perform and understand. We will decompose the analysis into different components. We start with the simplest scenario where 1 plant species (a monoculture) is affected by a static soil community. The second component examines how a static soil community can influence the outcome of competition between 2 plant species. Then, we explain in which ways the soil community can influence the plant community, i.e. by exerting positive or negative feedback. Finally, we combine plant and soil dynamics to show the full analysis of the Bever model. In section 4 we will present insights provided by the model to a few important aspects regarding plant-soil interactions: 1) we justify the definition of feedback in a mathematical model, 2) we study under which conditions plant-soil interactions drive oscillations in plant abundances, 3) we discuss the consequences of oscillations for plant species coexistence and plant community diversity and 4) we examine the generality of our results obtained by invasion analysis and our new graphical technique.

6.2 THE BEVER MODEL

The "Bever model" (Bever 2003, Fig 6.1) studies the effects of two soil communities S_A and S_B on two plant species A and B. Each soil community in the model is specifically associated with one of the plant species (Yeates, 1999; Wardle et al., 2004) that positively affects the growth rate of that specific soil community. On their turn, specific soil communities can have both positive and negative effects on growth of the plant they are associated with, and on the competing plant species (e.g. van der Putten and Van der Stoel, 1998; De Deyn et al., 2003; Klironomos, 2003), referred to as feedback effects. The dynamics of the plant populations A and B and the soil communities S_A and S_B are described by the following equations:

$$\frac{dN_A}{dt} = r_A N_A \left\{ 1 + \alpha_A S_A + \beta_A S_B - \frac{N_A + c_B N_B}{K_A} \right\} \tag{6.1a}$$

$$\frac{dN_B}{dt} = r_B N_B \left\{ 1 + \alpha_B S_A + \beta_B S_B - \frac{N_B + c_A N_A}{K_B} \right\} \tag{6.1b}$$

$$\frac{dS_A}{dt} = S_A S_B \frac{N_A - \nu N_B}{N_A + N_B} \tag{6.1c}$$

$$\frac{dS_B}{dt} = S_A S_B \frac{\nu N_B - N_A}{N_A + N_B} \tag{6.1d}$$

Here N_i is the density of plant species *i*, r_i is the intrinsic per capita growth rate of species *i*, K_i is the carrying capacity of species *i* when growing in isolation, and c_i is the per capita effect of species *i* on the growth rate of the competitor species, relative to the per capita effect of *i* on the growth rate of its own population. In the presence of soil effects, each soil community is associated with one of the two plant species, where S_i is the density of the biota associated with plant species *i*.

N_A and N_B are the densities of the two plant populations, r_A and r_B are the intrinsic per capita growth rates of the plant species, K_A and K_B are the carrying capacities of the plant species when growing in isolation, and c_A and c_B are the competition coefficients which are expressed as the per capita effects of each species on the growth rate of the competitor species (interspecific competition), relative to the per capita effect on the growth rate of its own population (intraspecific competition). S_A and S_B are the densities of the two soil communities, where S_A is specifically associated with plant species A and S_B with plant species B. In the absence of soil effects, the dynamics of the two competing plants species are described by the Lotka-Volterra competition dynamics (6.1a,6.1b, for $S_A = S_B = 0$).

The species specific effects of the soil communities on their plants, α_A and β_B, for plant A and B respectively, will be called "within" association effects, and the non-specific effects, α_B and β_A , will be called "cross" association effects. The net feedback effect of soil community composition on plant community dynamics will depend on both within and cross association feedback effects. These feedback effects can take any sign, in correspondence with mutualistic or pathogenic relationships. In mutualistic relationships plant growth may be favored by the presence of their symbionts, e.g. arbuscular mychorrhizal fungi (AMF), which enhance plant access to limiting resources. On the other hand, soil pathogens and root herbivores, e.g. root feeding nematodes, can negatively affect plant growth by direct removal of nutrients from root tissue and by reduction of soil nutrient uptake (Bever et al., 1997).

The effect of the plants on their respective soil communities is measured in relative terms, where ν is the ratio of the effect of plant B on its soil community against the effect of A on its soil community.

The model of Bever has been based on the dynamics of old-field communities (Bever, 1994). For these communities, it is reasonable to assume that both plant and soil communities have reached a relatively constant biomass density, but that the abundance of plant species still varies between years (Bever, 1994). Hence, it is assumed that $dS_A/dt + dS_B/dt = 0$ implying that the sum $S_A + S_B$ is constant. Bever models the soil communities as fractions of the total soil community. Hence, $S_A + S_B = 1$ and equations (6.1c,6.1d) can be substituted by

$$\frac{dS_A}{dt} = S_A(1 - S_A)\frac{N_A - \nu N_B}{N_A + N_B} \tag{6.2}$$

6.3 GRAPHICAL ANALYSIS

Our analysis will focus on equilibria and their stability. In order to do this it will be useful to split the analysis in several components. First, we discuss the effects of the soil dynamics on plants growing in isolation, which lead us to the concept of *soil stability*. Second, we consider the effects of a fixed soil composition on plant competition, which help us define the concept of *competitive stability*. Third, we take into account the net effects of the plant-soil *feedbacks*, and how to distinguish when they are positive or negative. Fourth, we integrate our criteria for soil stability, competitive stability, and feedbacks in a graphical methodology for the analysis of the complete system of equations (6.1a,6.1b) and (6.2).

6.3.1 *Plant monocultures*

Let us start by considering the absence of plant B, i.e. $N_B = 0$. This means that plant A is a monoculture, and its dynamical equation (6.1a) becomes

$$\frac{dN_A}{dt} = r_A N_A \left\{ 1 + \alpha_A S_A + \beta_A S_B - \frac{N_A}{K_A} \right\}$$

which has the structure of a logistic equation and where (after rearrangement) the carrying capacity takes the form of

$$\kappa_A = K_A(1 + \alpha_A S_A + \beta_A S_B) \tag{6.3a}$$

In the absence of plant B the soil dynamics (6.2) follows $dS_A/dt = S_A(1 - S_A)$, which is positive for $0 < S_A < 1$. Because of the constraint $S_A + S_B = 1$, in a monoculture of A the soil community associated with plant A completely eliminates the soil community associated with plant B. As a consequence, in the long term plant A attains a stable monoculture equilibrium $\mathbf{A_A} : K_A(1 + \alpha_A)$ corresponding to the state where its soil biota is dominant $(S_A = 1)$. There is another monoculture equilibrium $\mathbf{A_B} : K_A(1 + \beta_A)$, corresponding to dominance by B's soil biota $(S_A = 0)$ which is unstable.

If we reverse the roles and consider plant B the monoculture, i.e. $N_A = 0$, the soil dependent carrying capacity of plant B will be

$$\kappa_B = K_B(1 + \alpha_B S_A + \beta_B S_B) \tag{6.3b}$$

Mutatis mutandis, in the monoculture of B the soil community associated with plant B completely replaces the soil community associated with plant A. Thus the monoculture of B has two equilibria, $\mathbf{B_A} : N_B = K_B(1 + \alpha_B)$ corresponding to dominance of A's soil community $(S_A = 1)$ which is unstable; and $\mathbf{B_B} : N_B = K_B(1 + \beta_B)$ corresponding to dominance of B's soil community $(S_A = 0)$ which is stable.

Recapitulating, we have that $\mathbf{A_B}$ is unstable regarding fluctuations in soil composition (to increases above $S_A = 0$), whereas $\mathbf{A_A}$ is stable (to decreases below $S_A = 1$) in this respect. For this reason, we say that $\mathbf{A_B}$ is soil-unstable and $\mathbf{A_A}$ is soil-stable. On the other hand $\mathbf{B_B}$ is soil-stable (to increases above $S_A = 0$) and $\mathbf{B_A}$ is soil-unstable (to decreases below $S_A = 1$). The concept of *soil stability* is important not only for judging the stability of monoculture equilibria but also for community equilibria that happen to be characterized by S_A being 0 or 1.

It is important to remind that the monoculture equilibria $\mathbf{A_A}, \mathbf{A_B}, \mathbf{B_A}, \mathbf{B_B}$ can only exist if $\alpha_A, \beta_A, \alpha_B, \beta_B > -1$ respectively. This is an assumption that we will maintain for the rest of this article.

6.3.2 *Effect of a static soil community on plant competition*

Consider a static soil composition, i.e. $dS_A/dt = dS_B/dt = 0$. In that case the Lotka-Volterra equations alone (6.1a,6.1b) suffice to describe the plant competition. The conditions for coexistence or exclusion can be found by means of the graphical analysis of the system nullclines (Case, 2000), which are

$$\kappa_A = N_A + c_B N_B \quad (6.4a)$$

$$\kappa_B = N_B + c_A N_A \quad (6.4b)$$

for plants species A and B respectively, at a given fixed composition of the soil community. It is a standard result from Lotka-Volterra competition theory that a community equilibrium where both A and B coexist does exist when one of the following two conditions are met

- $c_A < \kappa_B/\kappa_A$ and $c_B < \kappa_A/\kappa_B$. In this case both monocultures can be invaded by the other species, and the coexistence equilibrium is globally stable.
- $c_A > \kappa_B/\kappa_A$ and $c_B > \kappa_A/\kappa_B$. In this case both monocultures are stable, and the community equilibrium is unstable. The outcome of competition depends on the initial conditions.

Hence a community or "interior" equilibrium does exist whenever

$$\left(\frac{\kappa_B}{\kappa_A} - c_A\right)\left(\frac{\kappa_A}{\kappa_B} - c_B\right) > 0 \quad (6.5)$$

and such equilibrium is stable whenever $c_A c_B < 1$ (i.e. interspecific competition is on average weaker than intraspecific competition).

It is useful to illustrate the conditions for equilibrium and stability using a plot like in Figure 6.2. Let define the ratios of (soil dependent) carrying capacities $x \equiv \kappa_B/\kappa_A$ and $y \equiv \kappa_A/\kappa_B$, thus the relation between x and c_A determines whether B can invade the monoculture of A, while the relation between y and c_B determines whether A can invade the monoculture of B. For given c_A and c_B all feasible plant competitive systems belong to the hyperbola $xy = 1$ in the xy plane. If $c_A c_B < 1$ (Fig. 6.2a), this hyperbola intersects the coexistence region (doubly hatched area), which means that stable coexistence is possible

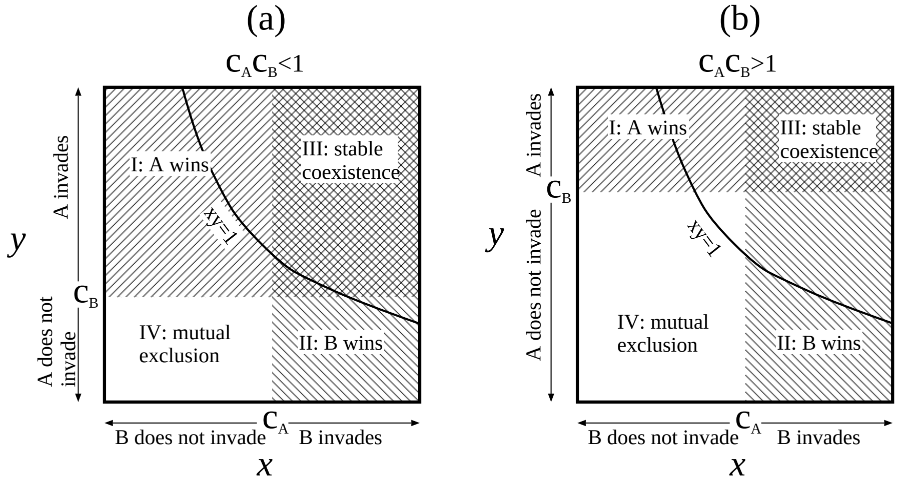


Figure 6.2: Outcomes of the Lotka-Volterra system (6.1a,6.1b). The plane is divided into four invasibility zones I, II, III, IV, such that B invades if $x > c_A$ and A invades if $x > c_B$, where $x \equiv \kappa_B/\kappa_A, y \equiv \kappa_A/\kappa_B$ are the carrying capacity ratios in (6.5). (a) If $c_A c_B < 1$ stable equilibria exist at the intersection of the hyperbola $xy = 1$ with zone III, in which A and B invade. (b) If $c_A c_B > 1$ unstable equilibria exist at the intersection of $xy = 1$ with zone IV, where neither A or B can invade, and depending on the initial conditions A or B wins the competition. Intersection at I or II do not result in equilibrium, instead A or B always wins, respectively.

for certain ratios κ_B/κ_A. But in case of $c_A c_B > 1$ (Fig. 6.2b), the hyperbola intersects the mutual exclusion region and stable coexistence is not possible at all.

Summarizing, for a given soil composition, monocultures and community equilibria (if they exist) are classified as stable or unstable regarding fluctuations in population densities. As we did before with respect to soil fluctuations, it is proper to define *competitive stability*: a monoculture is competitively stable if it cannot be invaded, or competitively unstable if it is invadable; a community equilibrium is competitively stable if $c_A c_B < 1$, or competitively unstable if $c_A c_B > 1$.

6.3.3 *Positive versus negative feedbacks*

According to (6.3), in the total absence soil feedback effects ($\alpha_A = \alpha_B = \beta_A = \beta_B = 0$) $\kappa_A = K_A$ and $\kappa_B = K_B$ for any value of S_A. As a consequence $x = K_B/K_A$ and $y = K_A/K_B$, i.e. all feasible competitive systems are represented by a single point of the hyperbola $xy = 1$ in Figure 6.2 no mater the soil composition. In the presence of soil feedbacks we have instead that x and y vary with S_A, which can take any value between 0 and 1. This means that all feasible competitive systems belong to a continuous portion or of the $xy = 1$ hyperbola, which we will refer to as the *feasibility arc* or simply the "arc". Figure 6.3 indicates that the coordinates of the end points of this arc are

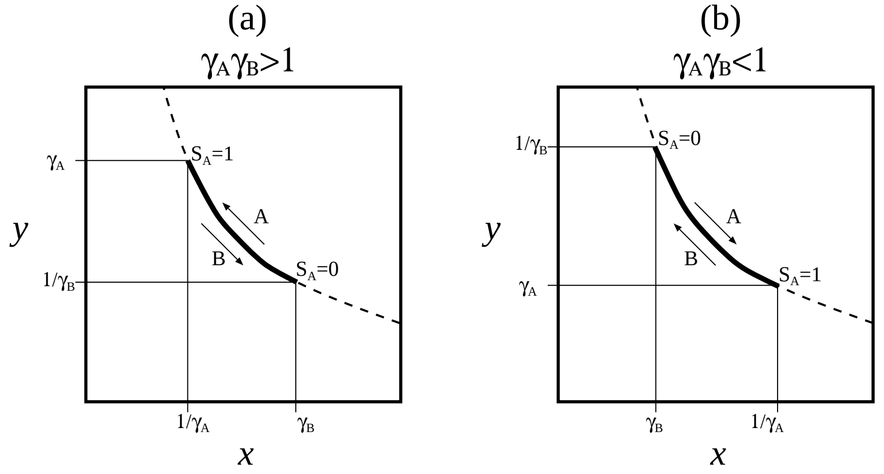


Figure 6.3: Effects of soil feedbacks on the feasibility of equilibria. Since soil composition S_A is bounded by [0,1] the set of feasible Lotka-Volterra systems belong to a *feasibility arc* of the unit hyperbola $xy = 1$, the end points of which are determined by the *feedback ratios* γ_A, γ_B. (a) If $\gamma_A \gamma_B > 1$ the net feedback is positive, plants attain maximum relative densities when their associate soil biotas are dominant, i.e. κ_A/κ_B is maximum at $S_A = 1$, and κ_B/κ_A is maximum at $S_A = 0$. (b) If $\gamma_A \gamma_B < 1$ the net feedback is negative, and plants attain minimum relative densities when their associated soil biotas are dominant.

$$\begin{aligned}
\text{at } S_A = 0: &\quad x = \gamma_B, \quad y = \gamma_B^{-1} \\
\text{at } S_A = 1: &\quad x = \gamma_A^{-1}, \quad y = \gamma_A
\end{aligned}$$

where the quantities γ_A and γ_B are

$$\gamma_A = \frac{K_A(1+\alpha_A)}{K_B(1+\alpha_B)}, \gamma_B = \frac{K_B(1+\beta_B)}{K_A(1+\beta_A)} \tag{6.6}$$

According to the model's description (equations 6.1 and Fig. 6.1) we can interpret γ_A and γ_B in the following way. If we consider plant species A, the numerator of γ_A turns out to be the maximum monoculture density that A attains with its associated soil community, i.e. due to "within" association feedback; on the other hand the denominator of γ_A is the maximum monoculture density that B attains due to "cross" feedbacks. Thus γ_A measures the net contribution of the feedback for plant A after accounting the non-specific effects of its soil community, i.e. losses, towards plant B. For this reason we call γ_A the *feedback ratio* for plant A, and similarly γ_B will be the *feedback ratio* for plant B. The product $\gamma_A \gamma_B$ of the feedback ratios will tell us the size and orientation of the hyperbolic arc

- $\gamma_A \gamma_B > 1$: species specific (within) feedback benefits are stronger than non-specific (cross) feedback benefits. As shown in Figure 6.1a κ_B/κ_A is maximum if $S_A = 0$ and κ_A/κ_B is maximum if $S_A = 1$ (S_A increases along $xy = 1$ from lower-right to upper-left). A consequence of this is that a plant species is less vulnerable to invasion when its associated soil biota is dominant (i.e. the difference $x - c_A$ decreases as $S_A \rightarrow 1$ and $y - c_B$ decreases as $S_A \rightarrow 0$). In other words the (geometric) average or **net feedback is positive**, i.e. $\log(\gamma_A\gamma_B) > 0$.

- $\gamma_A\gamma_B < 1$: non-specific (cross) feedback benefits are stronger than specific (within) feedback benefits. This time 6.1b shows that κ_B/κ_A minimum $S_A = 0$ and κ_A/κ_B is minimum at $S_A = 1$ (S_A increases along $xy = 1$ from upper-left to lower-right). In this case, plants become more prone to be invaded when its associated soil biota is dominant (i.e. the difference $x - c_A$ increases as $S_A \rightarrow 1$ and $y - c_B$ increases as $S_A \rightarrow 0$). In this case the (geometric) average or **net feedback is negative**, i.e. $\log(\gamma_A\gamma_B) < 0$.

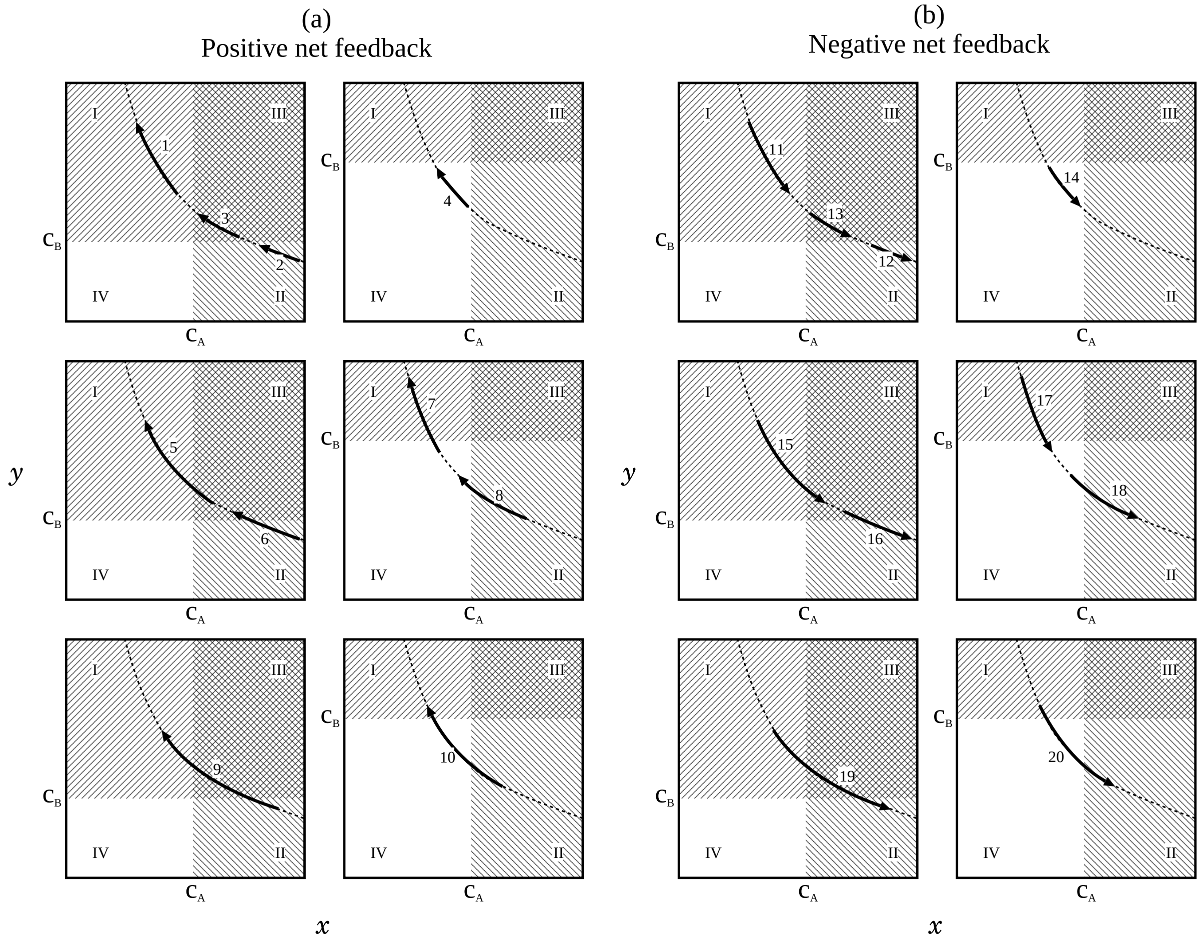
We can envision the plant competitive system as "moving" along the feasibility arc of the hyperbola $xy = 1$ as we vary the soil community composition. If the net feedback is positive the system moves "up" if we raise S_A, or "down" if we raise S_B. If the net feedback is instead negative, these directions are reversed. Such changes in S_A and S_B are driven by the abundance of the plants, meaning that there is a feedback that drives the system up or down these arcs in the combined plant-soil system.

The size of the feasibility arc increases with the absolute magnitude of the net feedback, $|\log(\gamma_A\gamma_B)|$. Thus, in the absence of net feedback effects ($\alpha_A = \alpha_B = \beta_A = \beta_B \rightarrow \gamma_A\gamma_B = 1$) the arc degenerates into a point of the unit hyperbola, and the plant community becomes a soil-independent Lotka-Volterra system, as if feedbacks were zero as discussed at the beginning.

6.3.4 *Combining plant and soil dynamics*

Combining the plots in Figures 6.3 and 6.2 provides us with a graphical method that is often sufficient for a rather complete characterization of the dynamics of the coupled plant-soil community described by equations (6.1a), (6.1b) and (6.2). As Figure 6.4 shows, there are 20 different ways or "cases" in which the feasibility arc can intersect the invasion zones. We will highlight two particular cases to illustrate the derivation of coexistence and invasion conditions in terms of competition coefficients and feedback ratios, and in the next section we treat more complex but interesting cases. See the Appendix A for a complete overview of the cases. Our graphical method is in the same spirit as the "recovery plane" analysis of Eppinga et al. (2006), in which the factors on the left-hand-side of inequality (6.5) are plotted against each other.

Figure 6.5a depicts case 12, where all feasible systems fit entirely in the region where only species B invades (II). As there are no other equilibria to consider (since the arc does not intersect III or IV), we conclude that independently of the state of the soil, only species B can grow in this system. Thus, species B and the system converges to the monoculture equilibrium $\mathbf{B_B}$ in which $S_A = 0$. In fact, in all cases where the feasibility arc lies within zones I or II (cases 1, 2, 11 and 12), one of the plants always wins, independently of the initial conditions. When the arc lies in zone III (cases 3 and 13) both can invade and coexist. And when it lies in zone IV (cases 4 and 14) neither can invade when rare, and the winner depends on the initial conditions, an outcome that is called *founder control* (Bolker et al.,


(a)
Positive net feedback

(b)
Negative net feedback

Figure 6.4: Intersection of the feasibility arc of Fig. 6.3 with the invasion zones of Fig. 6.2. The arc is represented as an arrow, thus indicating its orientation: the "head" ($x = \gamma_A^{-1}, y = \gamma_A$) corresponds to $S_A = 1$ and the "tail" ($x = \gamma_B, y = \gamma_B^{-1}$) to $S_A = 0$. A monoculture of species A will follow the orientation of the arc (S_A increases), whereas a monoculture of plant B will move in the opposite sense (S_B increases). There are 20 intersection "cases", differing in the relative position and arc orientation with respect to the invasion zones. The location of the end points (head & tail) with respect to the invasion zones determines if a species can invade or not.

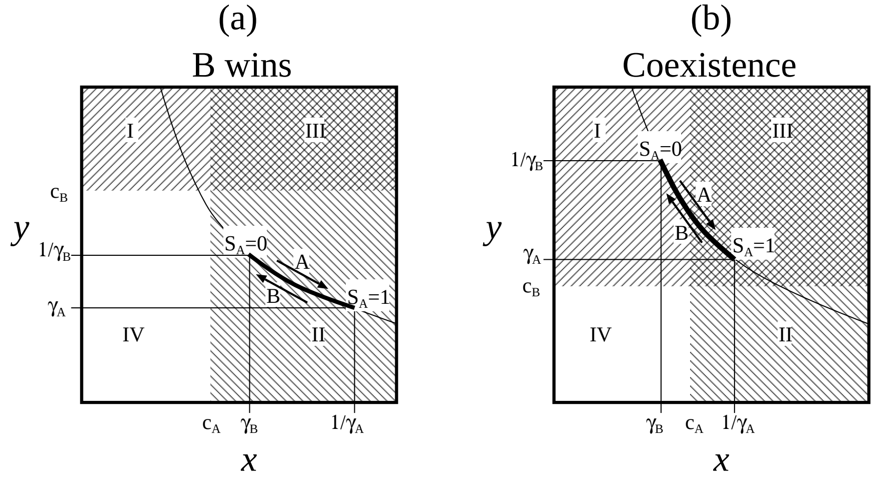


Figure 6.5: Graphical analysis of two cases depicted in Fig. 6.4. (a) In case 12 the feasibility arc occurs in a zone where only species B can invade (II) and a coexistence equilibrium is not possible, thus species B always wins. (b) In case 15 the monoculture of species A would evolve towards the $S_A = 1$ end of the arc, which lies in a zone where species B can invade (III). The monoculture of B will instead evolve towards the $S_A = 0$, located in the zone where species A can invade (I). As a consequence both can grow when rare and coexist.

2003). Thus, whenever the feasibility arc lies completely inside an invasion zone, the qualitative outcomes of plant competition do not depend on the net direction of the feedback, positive or negative.

In Figure 6.5b we show case 15, which is a bit more complex because the feasibility arc spans two invasion zones. In a monoculture of plant A, the soil composition will change towards the $S_A = 1$ end of the arc, which lies in the invasion zone of species A and B (III). In contrast, in the monoculture of species B, the soil composition change towards the $S_A = 0$ end of the arc, which lies in the invasion zone of species A (I). We conclude that in this case, soil community effects enable coexistence of the two plant species.

As indicated by Figure 6.5, the position of the arc's end points with respect to the invasion zones tell us whether a plant can invade or not. Whenever plant A is a monoculture, it will attain the equilibrium state $\mathbf{A_A}$ which corresponds to the $S_A = 1$ end of the arc. Thus $\mathbf{A_A}$ can be invaded plant B if only only if

$$c_A < \gamma_A^{-1} \tag{6.7}$$

and by symmetry, the monoculture of plant B attains the equilibrium state $\mathbf{B_B}$ corresponding to the $S_A = 0$ end of the arc, which can be invaded by plant A if and only if

$$c_B < \gamma_B^{-1} \tag{6.8}$$

Combining both inequalities, we obtain a necessary condition for mutual invasion

$$(c_A c_B)(\gamma_A \gamma_B) < 1 \tag{6.9}$$

which coincides with the requirement for stable coexistence in Lotka-Volterra models ($c_A c_B < 1$) in the absence of net feedback ($\alpha_A = \alpha_B = \beta_A = \beta_B$). This lead to the prediction that the more negative the feedbacks (low $\gamma_A \gamma_B$) the higher the chances of coexistence via mutual invasion. On the other hand if feedbacks are strongly positive (high $\gamma_A \gamma_B$), coexistence via mutual invasion demands lower competition strength (low $c_A c_B$). Back to the graphs in Figure 6.4: when the feedback is negative, further decrease of the product $\gamma_A \gamma_B$ widens the feasibility arc, until the end points fall in the zones where monocultures can be invaded. When feedback is positive, further increase of the product $\gamma_A \gamma_B$ also widens the feasibility arc, but this time the arc has the reverse orientation and in consequence the end points will end up in zones where monocultures cannot be invaded; to make coexistence possible again, c_A or c_B must be lowered such that the arc is forced to lie inside the mutual invasion zone III.

Although quite similar with standard Lotka-Volterra theory, conditions (6.7,6.8) and (6.9) only tells us about invasion. As we will show, neither conditions (6.7,6.8) are sufficient, nor condition (6.9) necessary, for plant coexistence in general.

6.4 RESULTS AND DISCUSSION

In this section, we employ the graphical method presented in section 3 to address some important aspects of the plant-soil interaction. First of all, we justify our definition of net positive and net negative feedbacks. Second, we study the mechanism by which competitive oscillations emerge in Bever's model. Third, we discuss the consequences of competitive oscillations for the maintenance of plant diversity. And lastly, we critically examine the generality of results obtained by means of invasion analysis and our graphical methodology.

6.4.1 *Positive and negative feedbacks*

As seen in Figure 6.3 we use the product $\gamma_A \gamma_B$ to unequivocally discriminate between scenarios in which the net plant-soil feedback is positive or negative. If $\gamma_A \gamma_B > 1$ the net feedback is positive, i.e. self-enhancing, because each plant attains its highest relative abundance –as measured by ratios of soil dependent carrying capacities κ_A/κ_B– when its associated soil biota is dominant. On the other hand, if $\gamma_A \gamma_B < 1$ the net feedback is negative, i.e. detrimental, because the pattern is the absolute opposite.

In contrast with us, Bever employs the soil feedback interaction coefficient $I_S = \alpha_A - \alpha_B - \beta_A + \beta_B$ to distinguish between net positive $I_S > 0$, and net negative $I_S < 0$, plant-soil effects. In previous works I_S was originally meant to be used in models without density dependence (Bever et al., 1997; Bever, 1999), and its extrapolation for the present system requires to consider equivalent competitors (Bever, 2003), e.g. parameter symmetry.

In most cases our criterion and Bever's coincide, but it is very easy to find examples where it does not. Let for example have $\alpha_A = -0,06, \beta_B = 0,52, \alpha_B = -0,41, \beta_A = 0,95$, this results in $I_S = -0,08$ indicating negative feedback according to Bever and $\gamma_A \gamma_B = 1,242$ indicating positive feedback according to us. Discrepancies in the opposite direction are possible too, e.g. $\alpha_A = 0,76, \beta_B = -0,95, \alpha_B = 0,18, \beta_A = -0,62$ results in $I_S = 0,25$ (Bever positive) and $\gamma_A \gamma_B = 0.196$ (us negative). Since I_S cannot tell apart net positive or negative feedback in all cases as $\gamma_A\gamma_B$ does, we consider our choice the most appropriate in the present context.

We can reconcile both approaches, by deriving a net interaction coefficient that relaxes the assumption of parameter symmetry:

$$I_S = \log(\gamma_A\gamma_B) = \log(1+\alpha_A) - \log(1+\alpha_B) - \log(1+\beta_A) + \log(1+\beta_B) \tag{6.10}$$

Equation (6.10) only converges to $I_S \approx \alpha_A - \alpha_B - \beta_A + \beta_B$ for small values of the feedback coefficients. This suggests that when relatively strong plant-soil community effects are measured in empirical home vs. away experiments, it is necessary to use equation (6.10) to predict the consequences of plant-soil feedbacks for the plant community.

6.4.2 *When do oscillations occur?*

Perhaps one of the most interesting results in Bever (2003) is a numerical example showing that species that cannot coexist in the absence of feedback, can do so by means of competitive oscillations under net negative feedbacks. When trying to run the same example, we found instead that a coexistence equilibrium is rapidly achieved. We concluded that the example provided is a numerical artifact due to the use of inappropriate integration methods. As a consequence we tried to figure out how and under which conditions are oscillations possible.

Population cycles are frequently associated with predator-prey dynamics. Competitive oscillations however, are a common feature in Lotka-Volterra equations (Gilpin, 1975; May and Leonard, 1975) and resource competition models (Huisman and Weissing, 2001; Revilla and Weissing, 2008). In these models, oscillations require at least three competitors such that species **P** outcompetes species **R**, **S** outcompetes **P** and **R** outcompetes **S**, as in the **R**ock-**P**aper-**S**cissors game. Mathematically, the monocultures of **R**, **P** and **S** are connected by means of heteroclinic orbits, i.e. a sequence of paths $\mathbf{R} \to \mathbf{P} \to \mathbf{S} \to \mathbf{R}$ forms a cycle. Although the Bever model involves only two plant competitors, it has in fact four monocultures: $\mathbf{A_A}, \mathbf{A_B}, \mathbf{B_B}, \mathbf{B_A}$, and this allows us to construct an heteroclinic cycle as follows.

First, let us assume that conditions (6.7) and (6.8) hold. This means that both plants monocultures can be invaded when their associated soil biotas are dominant, in other words $\mathbf{A_A}$ and $\mathbf{B_B}$ are unstable against invasion. Second, let us assume each monoculture cannot be invaded when the invader's soil biota is dominant, in other words $\mathbf{A_B}$ and $\mathbf{B_A}$ are stable against invasion. The conditions that allow this to happen can be easily found. Consider the monoculture $\mathbf{A_B}$ of plant A where $N_A = K_A(1+\beta_A), N_B = 0, S_A = 0$; substituting it in equation (6.1b) shows that plant B cannot invade this equilibrium ($dN_B/dt|_{\mathbf{A_B}} < 0$) if

$$c_A > \gamma_B \tag{6.11}$$

on the other hand in the monoculture $\mathbf{B_A}$ of plant B we have $N_B = K_B(1+\alpha_B), N_A = 0, S_A = 1$; and its substitution in equation (6.1a) shows that plant A cannot invade this equilibrium ($dN_A/dt|_{\mathbf{B_A}} < 0$) if

$$c_B > \gamma_A \tag{6.12}$$

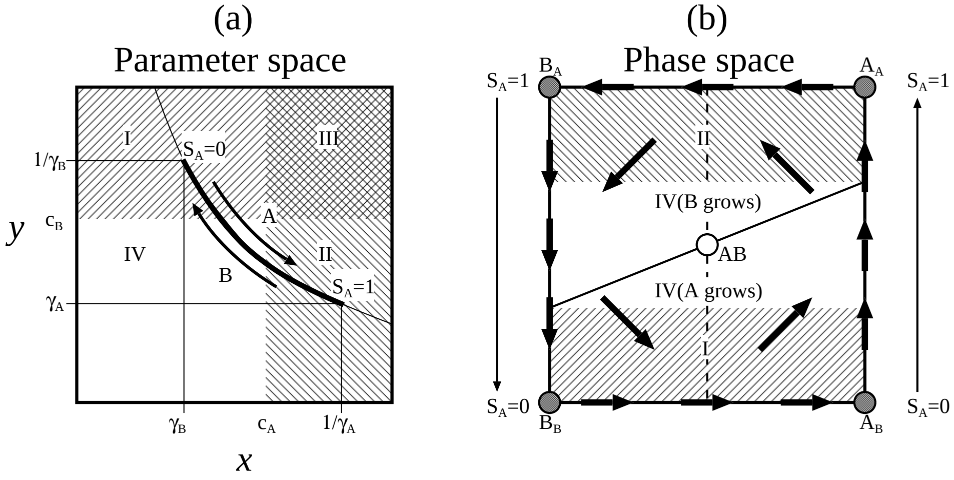


Figure 6.6: Competitive oscillations. (a) The monoculture of species A evolves from a non-invadable (I) to an invadable (II) condition, and the monoculture of B from non-invadable (II) to invadable (I); in both directions, the system passes through the zone of unstable community equilibria (IV). (b) The parameter space is mapped into a phase space where circles represent equilibria (white: unstable, gray:saddle) at the corresponding invasion zones (this mapping is explained in Appendix A). The diagonal line represents the A-B nullcline (species A grows towards the right B grows towards the left), and the dashed line is the soil nullcline (S_A increases in the right, and decreases in the left); their intersection corresponds to the internal equilibrium predicted in (a). Monocultures are competitively or soil stable, but not both: they are saddle points forming a heteroclinic cycle around the internal equilibrium **AB** which is competitively unstable. The system oscillates permanently.

In a the graphical representation of Figure 6.4, conditions (6.7,6.8) and (6.11,6.12) can simultaneously occur if and only if: the $S_A = 1$ end point of the feasibility arc lies in the zone where only plant B invades (II), and if the $S_A = 0$ end point of the arc lies in the zone where only plant A invades (I); in other words only for cases 19 and 20. Let see what happens in case 20, shown in detail in Figure 6.6a:

1. at $S_A = 1$ plant B invades $\mathbf{A_A}$: the system moves towards $\mathbf{B_A}$ $(\mathbf{A_A} \rightarrow \mathbf{B_A})$
2. $\mathbf{B_A}$ is soil unstable: the system moves towards $\mathbf{B_B}$ $(\mathbf{B_A} \rightarrow \mathbf{B_B})$ and $S_A \rightarrow 0$
3. at $S_A = 0$ plant A invades $\mathbf{B_B}$: the system moves towards $\mathbf{A_B}$ $(\mathbf{B_B} \rightarrow \mathbf{A_B})$
4. $\mathbf{A_B}$ is soil unstable: the system moves towards $\mathbf{A_A}$ $(\mathbf{A_B} \rightarrow \mathbf{A_A})$ and $S_A \rightarrow 1$

Thus the four monoculture equilibria are saddle points connected through heteroclinic orbits in the sequence $\mathbf{A_A} \rightarrow \mathbf{B_A} \rightarrow \mathbf{B_B} \rightarrow \mathbf{A_B} \rightarrow \mathbf{A_A}$. That is how oscillations originate, and Figure 6.6b shows a representation of the corresponding dynamics, where plants A and B take turns trying to outcompete each other.

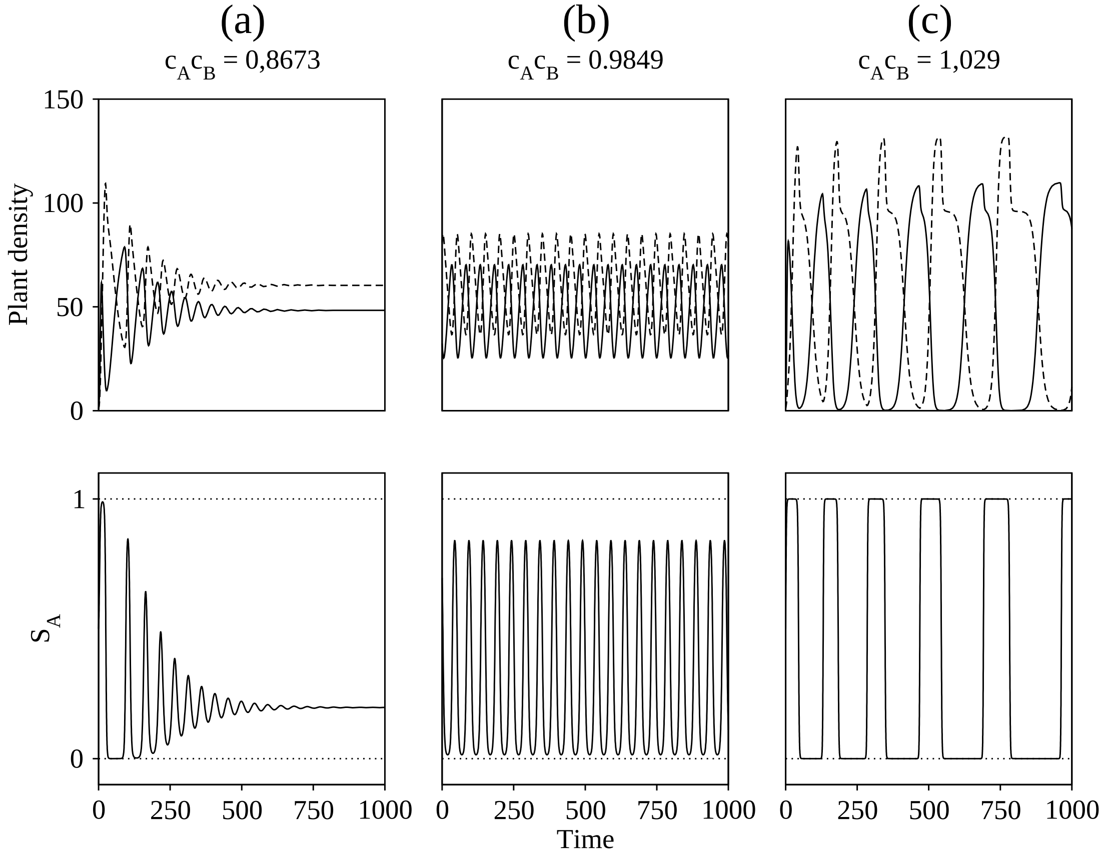


Figure 6.7: Competitive oscillations for increasing competition strength $c_A c_B$. Top row shows plants A (solid line) and B (dashed line) densities, bottom row indicates the soil composition. In (a) $c_A = 0,885$ and $c_B = 0,98$, oscillations damped out. In (b) $c_A = 1,005$ and $c_B = 0,98$, oscillations persist as limit cycle. In (c) $c_A = 1,05$ and $c_B = 0,98$, oscillations are heteroclinic. The other parameters are as in Bever (2003): $r_A = 0,7$; $K_A = 100$; $r_B = 0,5$; $K_B = 120$; $\alpha_A = -0,03$; $\beta_A = 0,1$; $\alpha_B = 0,1$; $\beta_B = -0,2$ and $\nu = 0,8$.

Figure 6.7 shows the temporal evolution of such oscillations. Using Bever's parametrization the system always converges to a coexistence equilibrium (Fig. 6.7a). By increasing the strength of competition, $c_A c_B$, this equilibrium becomes unstable and give rise to limit cycles (Fig.6.7b). With further increases in competition strength the cycles become heteroclinic, i.e. oscillations attain very low minima for increasingly longer times (Fig. 6.7c). Heteroclinic oscillations are considered mathematical artifacts: sooner or later one plant species will get extinct in real life scenarios. If c_A or c_B become too large, one of the conditions, (6.7) or (6.8), is no longer fulfilled. At this point, the heteroclinic cycle driving the oscillations no longer exists.

As indicated by this numerical example, the local stability of the community equilibrium changes from stable to unstable when the product $c_A c_B$ is smaller than 1 ($c_A c_B \approx 0,975$), which is in contrast with the standard Lotka-Volterra stability threshold $c_A c_B = 1$. This is a consistent result and it can be explained by our graphical method as follows. Competitive oscillations require that the arc end points $S_A = 0$ and $S_A = 1$ lie in zones I and II respectively; consequently, the arc joining them must pass trough zones III or IV which explains the existence of an "internal" coexistence equilibrium $\mathbf{AB}: \hat{N}_A > 0, \hat{N}_B > 0, 0 < \hat{S}_A < 1$ (and the non-existence of "border" equilibria, i.e. with $\hat{S}_A = 0$ or 1). If the arc intersects zone IV (Fig. 6.6a), the internal equilibrium is competitively unstable ($c_A c_B > 1$); thus oscillations will persist. On the other hand, if the arc intersects zone III instead, the internal equilibrium is competitively stable ($c_A c_B < 1$), which is necessary but not sufficient to guarantee stability; thus oscillations can persist or vanish. Summarizing: the equilibrium **AB** is always unstable if $c_A c_B > 1$, but cannot guaranteed to be stable if $c_A c_B < 1$. Conclusion: the $c_A c_B$ stability threshold of an internal equilibrium is lower than 1 (Appendix B), i.e.

$$c_A c_B = 1 - \epsilon \tag{6.13}$$

where ϵ is a positive quantity. If the soil equilibrium composition $\hat{S}_A$ happens to be very close to 0 or 1, or if there is parameter symmetry for $r_A = r_B, K_A = K_B, \nu = 1$ and $c_A = c_B = c$ (but not for $\alpha_A, \alpha_B, \beta_A, \beta_B$), we recover the standard Lotka-Volterra stability threshold.

Since it is geometrically impossible to place $\mathbf{A_A}$ in the exclusive invasion zone of B (II) and $\mathbf{B_B}$ in the exclusive invasion zone of A (I) when $\gamma_A \gamma_B > 1$, oscillations cannot develop under net positive feedback. We conclude that persistent competitive oscillations, that means limit cycles, require: 1) net negative feedback $\gamma_A \gamma_B < 1$, 2) mutual invasion, and 3) unstable community equilibria.

6.4.3 *Does negative soil feedback enhances coexistence?*

An important conclusion of Bever (2003) is that net negative feedbacks enhance coexistence and promote high diversity, while net positive feedbacks leads to exclusion and low diversity. This can be understood graphically: it is easier to conceive soil-stable monocultures $\mathbf{A_A}(S_A = 1)$ and $\mathbf{B_B}(S_A = 0)$ inside the invasion zones of plants B (II) and A (I) respectively if the feasibility arc in Figure 6.2 is oriented according to the pattern of net negative feedbacks as in Figure 6.3a, compared with the opposite orientation under net positive feedbacks as in Figure 6.3b.

But since negative feedbacks can in theory lead to competitive oscillations, we have to evaluate their consequences for the long term dynamics of the community. On the one hand, coexistence through oscillations is coexistence after all: no species can be excluded (in a mathematical sense). On the other hand, coexistence through oscillations is a relatively uncertain mode of coexistence: populations can be driven close to very low densities in which case extinction may occur due to demographic stochasticity (as in the enrichment paradox of Rosenzweig, 1971). Thus, successful invasion (6.7,6.8) does not imply the realization of long term coexistence.

To get an idea why this is an important issue, let us compare the occurrence of limit versus heteroclinic cycles using the pattern seen in Figure 6.6 as an example. There, oscillations develop above $c_A c_B = 0,975$ (i.e. between Figs. 6.6a,b) and must end somewhere below $c_A c_B = 1,559$ the point where the requirement for mutual invasion (6.9) does not hold anymore. If we consider $c_A c_B = 1,029$ (Fig. 6.6c) as the switching point between limit cycles and heteroclinic cycles, then limit cycles occur for a rather small region

($\frac{1{,}029-0{,}975}{1{,}559-0{,}975} \times 100 \approx 9{,}2\%$) in parameter space in comparison with heteroclinic cycles. In other words, a small increase in the strength of competition results in a very large increase in the amplitude of oscillations, and thus the risk of extinction.

In addition, equation (6.13) predicts that oscillations may occur in a system for which the plants would otherwise coexist at stable densities in the absence of net feedback (i.e. when $1-\epsilon < c_A c_B < 1$ and $\alpha_A = \alpha_B = \beta_A = \beta_B$). Unfortunately, the extend of destabilization brought by negative feedbacks cannot be evaluated in the present model, since we do not have an explicit algebraic expression for the quantity ϵ in appearing in (6.13).

If competitive oscillations turn out to be a common feature, Bever's conclusion regarding the role of negative feedbacks in the maintenance of diversity could be considered premature, because of the destabilizing effects on stable communities. On the other hand, in a spatial context the risks associated with large amplitude oscillations can be compensated by migration; and heteroclinic cycles could also mean local opportunities for invasion, and regional persistence.

6.4.4 *Invasion requirements and coexistence requirements*

Invasion analysis is a powerful technique for the analysis of dynamical systems in ecology and evolution (Case, 2000). When properly used, invasion criteria are very useful to predict the range of dynamics that a dynamical system can possibly display. In the present context, by considering (6.7) and (6.8), and the direction of the net feedback, we can list all possible dynamics of Bever's model as in Table 6.1.

However, there can be some limitations using invasion analysis which can be illustrated by the following example. Consider a scenario of net positive feedback ($\gamma_A \gamma_B > 1$) as in Figure 6.8a (case 5), where the feasibility arc of the competitive system is such that $c_A > \gamma_A^{-1}$ and $c_B < \gamma_B^{-1}$, and mutual invasion criterion (6.9) does not hold: plant species A is able to grow when rare since (6.8) holds, but plant species B cannot since (6.7) does not hold.

However, coexistence may still be possible. As indicated in Figure 6.8a, the $S_A = 0$ end point of the arc lies in zone III, which means that there is a competitively stable plant community equilibrium when $S_A = 0$. Following our previous notation, let call this equilibrium $\mathbf{AB_B}$ since the soil is dominated by B's soil biota. If the ratio of plant equilibrium densities is $N_A/N_B < \nu$ then according to (6.2) $dS_A/dt < 0$, thus for small fluctuations vanish and $\mathbf{AB_B}$ is soil stable. Thus, $\mathbf{AB_B}$ is a local attractor because is competitively stable and soil stable. The other end point of the arc $S_A = 1$ lies in zone I, where a coexistence equilibrium is not possible and plant A attains a competitively stable and soil stable monoculture $\mathbf{A_A}$, i.e. another local attractor. As a consequence, the system has two alternative stable states: the coexistence equilibrium $\mathbf{AB_B}$ dominated by B's soil community and the soil-stable monoculture $\mathbf{A_A}$ dominated by A's soil community, as shown in Figure 6.8b.

In contrast if at $\mathbf{AB_B}$ the density ratios are $N_A/N_B > \nu$ then $dS_A/dt > 0$ and small fluctuations of S_A increase, making $\mathbf{AB_B}$ soil unstable, while $\mathbf{A_A}$ remains stable in both senses (soil and competitively). In this case A always wins, as predicted by the invasion criterion.

This example illustrates two things. The first is a limitation in our graphical analysis, which cannot address soil stability in all the cases, like it does with respect to competitive

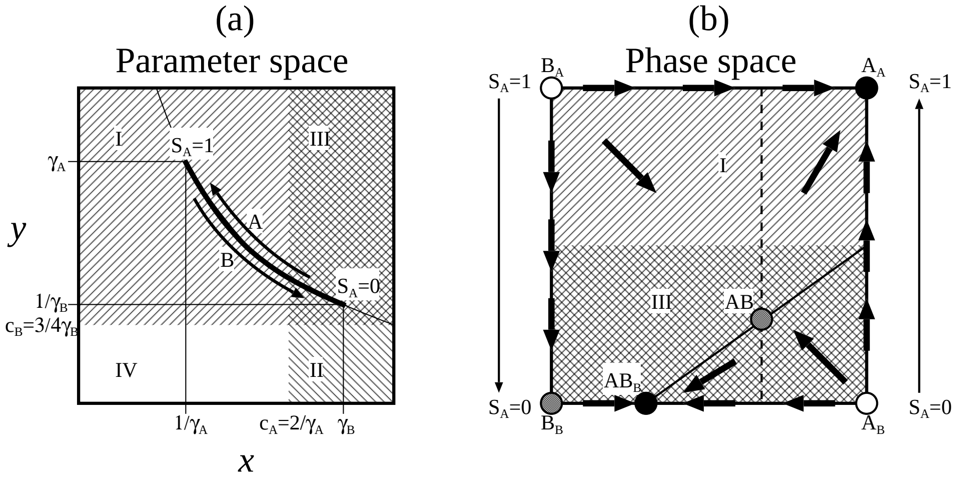


Figure 6.8: Alternative stable states. (a) In this configuration a monoculture of species A evolves from an invadable (III) to a non-invadable zone (I), whereas a monoculture of B can be invaded always: coexistence by means of mutual invasion is ruled out. However, there are coexistence equilibria because the feasibility arc intersects the zone of mutual invasion (III). (b) The phase space shows the equilibria (white: unstable, black: stable, gray: saddle) and the invasion zones. The diagonal line representing the A-B nullcline (both species grow towards it) intersects $S_A = 0$ giving rise to the coexistence equilibrium $\mathbf{AB_B}$ predicted in part (a). If the vertical dashed line representing the soil-nullcline (S_A increases to the right, and decreases to the left) intersects the A-B nullcline there will be an internal equilibrium **AB** that is a saddle point; and depending on the initial conditions the system moves towards the monoculture of $\mathbf{A_A}$ dominated by A's soil biota, or towards the coexistence equilibrium $\mathbf{AB_B}$ dominated by B's soil biota.

	Positive net feedback $\gamma_A \gamma_B > 1$	Negative net feedback $\gamma_A \gamma_B < 1$
Both invade $c_A \gamma_A < 1$ $c_B \gamma_B < 1$	1. Stable coexistence ($S_A = 1$) 2. Stable coexistence ($S_A = 0$) 3. Stable coexistence ($S_A = 0$ or $S_A = 1$, depends on initial conditions)	1. Stable coexistence ($0 < S_A < 1$) 2. Competitive oscillations
A invades $c_B \gamma_B < 1$ B does not $c_A \gamma_A > 1$	1. A wins 2. A wins or stable coexistence (depends on initial conditions)	A wins
B invades $c_A \gamma_A < 1$ A does not $c_B \gamma_B > 1$	1. B wins 2. B wins or stable coexistence (depends on initial conditions)	B wins
None invade $c_A \gamma_A > 1$ $c_B \gamma_B > 1$	A or B wins (depends on initial conditions)	A or B wins (depends on initial conditions)

Table 6.1: The sign of the net feedback and the invasion criteria determine the outcomes of the model. In case of stable coexistence the soil composition is indicated. In case of exclusion, the soil composition consists entirely to the one associated with the winner ($S_A = 1$ if A wins, $S_A = 0$ if B wins).

stability (in other words we cannot infer the magnitude of ν in the graphs). Second, it shows the limitations of invasion analysis. Invasion analysis is a powerful technique for the analysis of dynamical systems in ecology and evolution (Case, 2000), perhaps the best example is the classical Lotka-Volterra model where mutual invasion and stable coexistence are synonymous. But if the model being considered displays multiple equilibria and alternative stable states, as is the present case, it is erroneous to state that mutual invasion is a requisite for coexistence.

Nevertheless, when properly used, invasion criteria remain very useful for predicting the range of dynamics that a dynamical system can possibly display. In the present context, invasion conditions (6.7) and (6.8), and the direction of the net feedback, allow us to list all the possible dynamics of Bever's model as shown in Table 6.1.

6.5 GENERAL CONCLUSIONS

In this paper we performed a more complete analysis of the Bever (2003) model to get more insight in plant species coexistence and dynamics and the potential role of plant-soil feedback affecting those. We found that plant species coexistence could be explained by an interaction between net soil feedback (γ_i) and competition strength (c_i) between the plants, i.e. when feedback becomes more positive competition coefficients have to be lower in order to allow plant coexistence. This means that more negative plant soil feedback result in higher chances for coexistence. Negative soil feedback has been suggested previously as one of the mechanisms to explain plant species coexistence and consequently to maintain plant diversity (Bever et al., 1997; van der Heijden et al., 2008). Results of different recent empirical studies, as well as a meta-analysis of more than 300 plant-soil feedback experiments, indeed provide evidence for this hypothesis (Bever, 1994; Mills and Bever, 1998; De Deyn et al., 2003; Kulmatiski et al., 2008; Bradley et al., 2008).

We addressed four important issues concerning plant-soil feedback effects. First, we discussed the definition of feedback in a mathematical model. We showed that the assumption of parameter symmetry that is needed to calculate Bever's interaction coefficient (I_S) can be relaxed when introducing the relative feedback coefficient, $\log(\gamma_A, \gamma_B)$. Our results show that especially in experiments where large soil community effects are measured, it may be important to use the relative feedback coefficient to assess plant community consequences.

Second, we found that negative soil feedback can drive oscillations in plant abundances, but only under different conditions than presented by Bever. Stability of soil-driven plant dynamics was dependent on the competition strengths between the plants, i.e., the more competitive the plants were, the less stable coexistence was. We do not know how realistic it is that oscillations in plant abundances in nature are driven by soil feedback, because the range in which we found oscillations was very narrow and cycles quickly resulted in heteroclinic cycles, which in real life scenarios will probably result in extinction of one of the two plant species. We are not aware of any empirical study directly testing the effect of negative soil feedback on plant oscillations. However, there are suggestions that soil-borne pathogens may play an important role determining plant community dynamics (Olff et al., 2000). Moreover, different studies showed that soil feedback can enhance succession (van der Putten et al., 1993; De Deyn et al., 2003) and thus, can drive plant community dynamics. However, these dynamics are not necessarily oscillations of the same plant species, but may be different plant species succeeding each other.

Third, we discussed the consequences of oscillations for plant community diversity. We found that in the presence of negative soil feedback plant coexistence was possible under conditions that would otherwise lead to competitive exclusion of one of the two plant species. This was coexistence by means of oscillations of plant abundances, i.e., soil feedback increased the range in which oscillations occurred. Thus, in the presence of soil feedback oscillations would occur in situations that would otherwise allow stable coexistence between the plant species. Therefore, we can conclude that net negative plant-soil feedback can either promote or limit plant community diversity, depending on the role of oscillations on plant diversity. On the one hand, negative feedback enlarged the range in which plants could coexist, thus in that sense coexistence and consequently diversity was enhanced by soil feedback. On the other hand, soil feedback can be viewed as a factor destabilizing plant species coexistence, because it causes oscillations in situations that otherwise would allow stable coexistence between the plant species. In real life scenarios the oscillations, especially the heteroclinic cycles may enhance chances for exclusion of one of the plant species, thereby reducing plant diversity.

Fourth, we presented an overview of the dynamics of the model analyzed with our new graphical method. The Bever model, relatively simple at first sight, already showed quite complex dynamics, however, this new graphical technique provided a rather complete analysis of equilibria and their stability and is still relatively easy to perform and understand. Results obtained by the graphical analysis agree with results from the mathematical analysis. Although our new technique was very useful in providing a full model analysis and overview of all scenarios, we have to conclude that there were some limitations because it could not address soil stability in all cases.

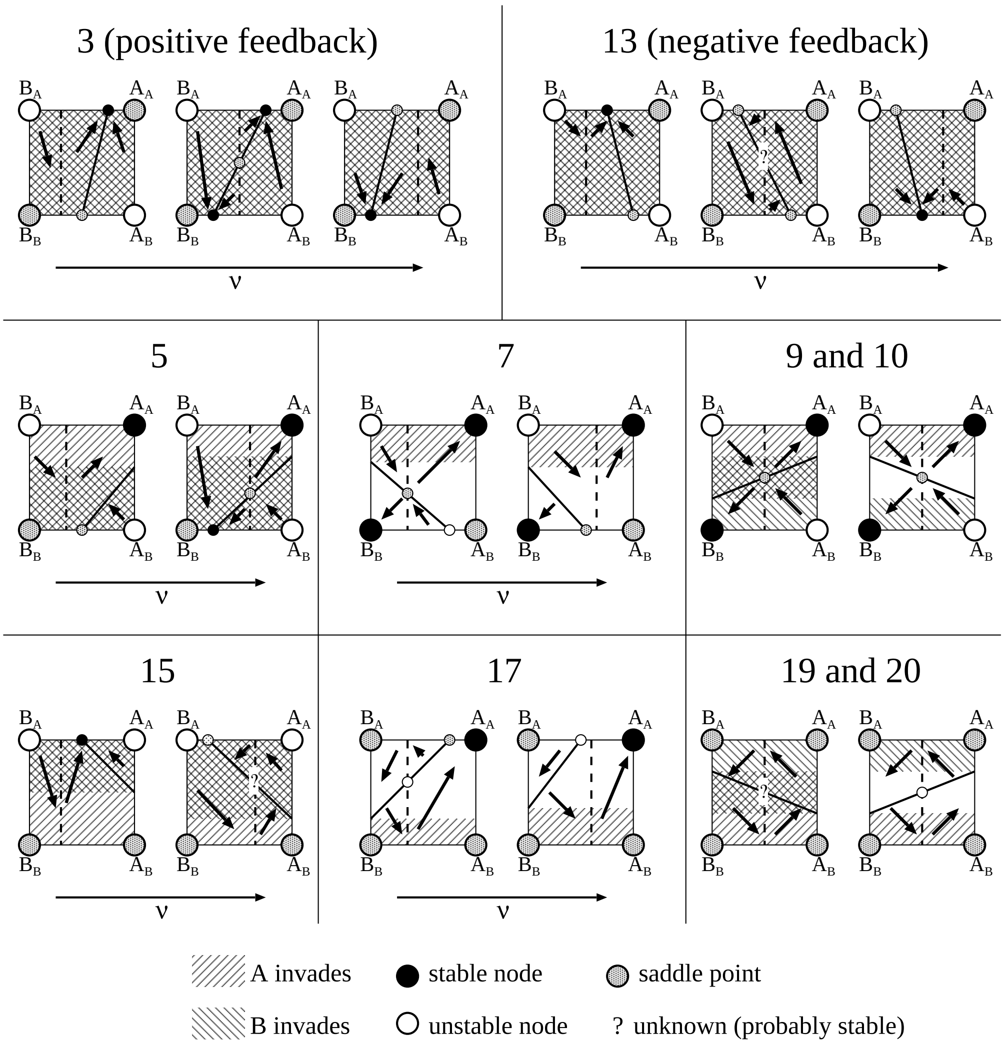
Most of our general conclusions agree with Bever, i.e., that plant species coexistence is dependent on an interplay between net plant-soil feedback and competition strength and that negative soil feedback can drive plant community dynamics. However, some of our results disagreed with Bever's findings. First, we found that it was better to express net soil feedback as the relative feedback coefficient $\log(\gamma_A \gamma_B)$, instead of the interaction coefficient (I_S). Second, we found that even under positive feedbacks, in general associated with species exclusion and loss of plant diversity, plant species are able to coexist if competition coefficients are low enough. Therefore, we conclude that mutual invasion is not a necessary requirement for coexistence, yet it does increase chances a lot. Third, soil feedback driven oscillations as presented by Bever were probably caused by the use of inappropriate integration methods, since redoing the simulations with similar parameter settings resulted in stable coexistence between the two plant species. However, we were able to find a range of parameters under which plant-soil interactions led to sustained oscillations.

Although most of the insights gained from the Bever model and our new analysis coincide, we still think we have to be careful translating these findings to the real world. On the one hand because the model is relatively simple. For example, one assumption of the model is that the soil community is always saturated, i.e. $S_A + S_B = 1$. In old-field ecosystems this assumption may hold (Bever, 1994), but extrapolation to other systems may be difficult. To get better insight in plant-soil interactions and their consequences for community dynamics and diversity, it would be useful to develop a more mechanistic model. On the other hand, oscillations in plant abundances occurred in a very narrow range and may result in exclusion of one of the plant species easily. Therefore, we cannot be sure whether it is likely to discover a phenomenon like the oscillations in nature. Finally, the oscillations extended the range where plant coexistence was possible, which led to the important conclusion that soil feedback may enhance plant diversity. However, this form of non-equilibrium coexistence may lead to stochastically driven extinction of plant species in real ecosystems. An outstanding challenge is to examine whether plant oscillations occur in nature under the conditions predicted by the model, and their role in maintaining plant diversity.

APPENDIX A: GRAPHICAL ANALYSIS

Figure 6.4 is useful for classifying and describing the main features of the dynamics in terms of the invasion conditions. For example in cases 1, 2, 11 and 12 it is easy to see that only one species A or B always wins, because only one of them is able to grow for any soil composition. In cases 4 and 14 we have that any resident species will be protected against invasion, and any equilibrium that may exist will be competitively unstable, for any soil composition.

However, cases 3, 5-10, 13, 15-20 are more complicated. In these situations, it is sometimes useful to have a graphical representation in the familiar form of a phase space and nullclines. Although this is possible for three-dimensional system like the Bever mode, the following two-dimensional representation is more convenient:



The phase space is constructed according to the following rules:

- The horizontal axis indicates the plant composition: plant A is dominant on the right, plant B on the left. The vertical axis indicates soil composition: A's soil biota is dominates on the top, B's soil biota dominates on the bottom.

- The corners represent the plant monocultures, with $\mathbf{A_B}, \mathbf{B_B}$ corresponding to $S_A = 0$, and $\mathbf{A_A}, \mathbf{B_A}$ corresponding to $S_A = 1$. Depending on the competitive stability conditions (6.7, 6.8, 6.11, 6.12) and their soil stability, the corners are classified as stable, unstable or saddle points.

- The invasion zones intersected by the feasibility arc become the domains of attraction in the phase plot, placed in the same order as they are encountered by traversing the arc from $S_A = 0$ to 1 (and using the same fill patterns).

- If the arc intersects zones III or IV the corresponding domain of attraction in the phase plot is divided by a diagonal line. This line, representing coexistence equilibria, is the *plant nullcline*, i.e. a nullcline for the plant composition, not the plant densities. In case of intersecting zone III, the plant composition moves towards the line (communities are competitively stable). In case of intersection with zone IV, the plant composition moves away from the line (communities are competitively unstable).

- The plane is divided by vertical that represents the *non trivial soil nullcline*: S_A increases at the right of the line ($N_A > \nu N_B$ in eq. 6.2), and decreases at the left ($N_A < \nu N_B$ in eq. 6.2). The smaller the ν the bigger the portion of the plane where S_A increases, and viceversa. The top ($S_A = 1$) and the bottom ($S_A = 0$) sides of the plane are *trivial soil nullclines*.

- A coexistence equilibrium corresponds to the intersection of the plant nullcline with a soil nullcline, trivial or not. For this reason, there can be border equilibria where $S_A = 0, S_A = 1$ or an internal equilibrium where S_A is intermediate. Depending on its location with respect to the attraction domains and the non trivial plant nullcline, an equilibrium is declared stable, unstable or a saddle point.

Because of symmetry, we do not show cases 6, 8, 16 and 18 because they are qualitatively equivalent to cases 5, 7, 17 and 18 (by swapping the "A" and "B" labels). Cases 3 and 13 are very similar in the stability of their monocultures, and because of having border equilibria. However, they display qualitatively different dynamics. Under net positive feedbacks (case 3) the system can display alternative stable states: coexistence with dominance of plant A and its soil community or coexistence with dominance by plant B and its soil community. On the other hand, under net negative feedbacks (case 13) there can not be alternative stable states, and oscillations may develop (though we suspect they dampen out given the geometry of the nullclines).

The majority of cases under net positive feedback result in competitive exclusion. However, some can display alternative stable states, and coexistence depending on the initial conditions (5 and 6). On the other hand, the majority of scenarios under net negative feedback promote mutual invasion and coexistence (17 and 18 are the exceptions), including non-equilibrium coexistence through oscillations (19 and 20).

APPENDIX B: STABILITY OF THE INTERNAL EQUILIBRIUM

Consider an internal equilibrium **AB**, where $N_A > 0, N_B > 0$ and $0 < S_A > 1$. We already know that if the net feedback is positive ($\gamma_A\gamma_B > 1$) **AB** lies in the zone of competitive instability (zone IV in 6.6a). Thus, under net negative feedback the community equilibrium will be always unstable, and the oscillations will persist.

Thus, from here onwards we will consider that the net feedback is negative ($\gamma_A\gamma_B < 1$). In this case **AB** is locally stable if and only if all eigenvalues λ of the jacobian matrix of the dynamical system (6.1a,6.1b,6.2) evaluated at **AB**

$$\mathbf{J} = \begin{bmatrix} -\frac{r_A N_A}{K_A} & -\frac{c_B r_A N_A}{K_A} & r_A N_A(\alpha_A - \beta_A) \\ -\frac{c_A r_B N_B}{K_B} & -\frac{r_B N_B}{K_B} & r_B N_B(\alpha_B - \beta_B) \\ \frac{S_A(1-S_A)}{N_A+N_B} & -\nu\frac{S_A(1-S_A)}{N_A+N_B} & 0 \end{bmatrix} \tag{6.14}$$

have negative real parts. The eigenvalues of **J** are the solutions of the characteristic equation

$$\lambda^3 - T(\mathbf{J})\lambda^2 + M(\mathbf{J})\lambda - D(\mathbf{J}) = 0 \tag{6.15}$$

where $T(\mathbf{J}) = \frac{\partial F}{\partial N_A} + \frac{\partial G}{\partial N_B}$, $M(\mathbf{J}) = \frac{\partial F}{\partial N_A}\frac{\partial G}{\partial N_B} - \frac{\partial F}{\partial N_B}\frac{\partial G}{\partial N_A} - \frac{\partial F}{\partial S_A}\frac{\partial H}{\partial N_A} - \frac{\partial G}{\partial S_A}\frac{\partial H}{\partial N_B}$ and $D(\mathbf{J}) = \frac{\partial G}{\partial N_A}\frac{\partial H}{\partial N_B}\frac{\partial F}{\partial S_A} + \frac{\partial H}{\partial N_A}\frac{\partial F}{\partial N_B}\frac{\partial G}{\partial S_A} - \frac{\partial F}{\partial S_A}\frac{\partial H}{\partial N_A}\frac{\partial G}{\partial N_A} - \frac{\partial G}{\partial S_A}\frac{\partial H}{\partial N_B}\frac{\partial F}{\partial N_A}$ are respectively the trace, the sum of the principal minors and the determinant of the jacobian matrix. According to the Routh-Hurwitz criterion all eigenvalues have negative real parts if and only if:

1. $T(\mathbf{J}) < 0$
2. $D(\mathbf{J}) < 0$
3. $M(\mathbf{J}) > 0$
4. $-T(\mathbf{J})M(\mathbf{J}) + D(\mathbf{J}) > 0$

where

$$D = -\frac{S_A(1-S_A)r_A r_B N_A N_B}{N_A+N_B}\left\{\frac{(\beta_A-\alpha_A)(1+c_A\nu)}{K_B} + \frac{(\alpha_B-\beta_B)(c_B+\nu)}{K_A}\right\} \tag{6.16}$$

$$M = \frac{r_A r_B N_A N_B(1-c_A c_B)}{K_A K_B} + \nu\frac{S_A(1-S_A)[r_B(\alpha_B-\beta_B)+r_A(\beta_A-\alpha_A)]}{1+\nu} \tag{6.17}$$

$$\begin{aligned} -TM+D &= \left\{\frac{r_A N_A}{K_A}+\frac{r_B N_B}{K_B}\right\}\left\{\frac{r_A r_B N_A N_B(1-c_A c_B)}{K_A K_B} + \nu\frac{S_A(1-S_A)[r_A\delta_A + r_B\delta_B]}{1+\nu}\right\} \\ &\quad -\frac{S_A(1-S_A)r_A r_B N_A N_B}{N_A+N_B}\left\{\frac{\delta_A(1+c_A\nu)}{K_B} + \frac{\delta_B(c_B+\nu)}{K_A}\right\} \end{aligned} \tag{6.18}$$

Simple inspection of (6.14) shows that the first condition always holds. Before continuing with 2, 3 and 4, let assume *Asumption 1*: that the net feedback is negative because $\alpha_B, \beta_A >$

α_A, β_B and define $\delta_A = \beta_A - \alpha_A > 0$ and $\delta_B = \alpha_B - \beta_B > 0$. Thus condition 2 holds since *D* is negative. Condition 3 holds if and only if

$$c_A c_B < 1 + \frac{K_A K_B S_A(1 - S_A)[r_A\delta_A + r_B\delta_B]}{r_A r_B(N_A + N_B)} \tag{6.19}$$

and for condition 4 we will employ two more assumptions in order to check its valitidy. *Assumption 2*: consider an equilibrium in which S_A is very close to 0 or 1, such that the product $S_A(1 - S_A)$ is very small. These circumstances allows to approximate equation (6.18) by

$$-TM + D \approx \left\{\frac{r_A N_A}{K_A} + \frac{r_B N_B}{K_B}\right\}\left\{\frac{r_A r_B N_A N_B(1 - c_A c_B)}{K_A K_B}\right\} \tag{6.20}$$

and condition 4 holds if and only if $c_A c_B < 1$, which already validates condition 3.

Assumption 3: let consider the symmetry $r_A = r_B = r$, $K_A = K_B = K$, $\nu = 1$ and $c_A = c_B = c$ (but not for $\alpha_A, \alpha_B, \beta_A, \beta_B$). As a result, plant equilibrium densities must be $\hat{N}_A = \hat{N}_B = N$ and $-TM + D$ can be easily factored as follows

$$\begin{aligned}
-TM + D &= \frac{2rN}{K}\left\{\frac{r^2N^2(1-c^2)}{K^2} + \frac{S_A(1-S_A)r(\delta_A+\delta_B)}{2}\right\} \\
&\quad - \frac{S_A(1-S_A)r^2N(1+c)(\delta_A+\delta_B)}{2K} \\
&= \frac{rN}{K}\left\{\frac{2r^2N^2(1-c^2)}{K^2} + S_A(1-S_A)r(\delta_A+\delta_B) - \frac{rS_A(1-S_A)(1+c)(\delta_A+\delta_B)}{2}\right\} \\
&= \frac{rN}{K}\left\{\frac{2r^2N^2(1-c^2)}{K^2} + S_A(1-S_A)r(\delta_A+\delta_B)\left[1 - \frac{1+c}{2}\right]\right\} \\
&= \frac{rN}{K}\left\{\frac{2r^2N^2(1-c)(1+c)}{K^2} + S_A(1-S_A)r(\delta_A+\delta_B)\frac{1-c}{2}\right\} \\
&= \frac{rN(1-c)}{K}\left\{\frac{2r^2N^2(1+c)}{K^2} + \frac{S_A(1-S_A)r(\delta_A+\delta_B)}{2}\right\} \qquad (6.21)
\end{aligned}$$

The quantity in curly braces is positive, so the sign of $TM - D$ is that of $1 - c$. Thus for $c < 1$ both condition 4, and also condition 3, holds and the internal equilibrium is locally stable.

Only under after making three assumptions we obtain the result that the stability of **AB** changes exactly at $c_A c_B = 1$. Thus in general, the stability threshold cannot be $c_A c_B = 1$. Since we already know that any equilibrium is competitively unstable if $c_A c_B > 1$ (6.2b), we must conclude that under net negative feedbacks the internal equilibrium remains stable as long as

$$c_A c_B < 1 - \epsilon$$

where ϵ is a positive quantity smaller than 1.

7

AFTERTHOUGHTS

The major part of my thesis focused on the dynamics of multispecies resource competition. In this final chapter I want to put my results in a broader context, looking ahead to get an idea how they are affected if additional features are taken into account.

Ecological communities are highly complex, yet they also display consistent spatial and temporal patterns that seem to be quite robust, independent of many details. An example is Damuth's (1981) rule that population density N tends to be inversely proportional to body mass w to the power of $-3/4$: $N \propto w^{-3/4}$. Another example is the empirical law that the number S of species found in an area of size A tends to obey a power law $S \propto A^z$ where z is a scaling exponent (MacArthur and Wilson, 1967). It is a major challenge to understand these empirical laws in terms of ecological mechanisms.

Physics provide us with examples on how such understanding can be achieved. My favorite example is the ideal gas theory. Empirical observation reveals under low pressures the pressure P, volume V and temperature T of a gas are related by the ideal gas law $PV = nRT$, in which n is the number of moles of gas and R is the universal gas constant. One mole is 6.02×10^{23} molecules, a quantity that dwarfs the number of individuals in ecological communities. How does the dance of a virtually infinite number of molecules results in the gas law? In physical theory, an answer is given by a surprisingly simple model that considers a gas as a huge collection of point particles that encounter randomly and exchange energy in elastic collisions (Halliday and Resnick, 1974). Real interactions between these particles are not taken into consideration. Such a gas does not exist in the real world, but the model is nevertheless useful since it demonstrates how macroscopic state variables like P and T are related with particle properties like masses and velocities. At a later stage, particle interactions were included in the model (Moore, 1972), yielding the Van der Waals equation, which considerably improves the ideal gas law, though not being perfect. Even in this more sophisticated model, some of the main conclusions of the simpler theory hold (for example, that temperature is directly proportional to the mean kinetic energy of molecules). Despite its many oversimplifications, the kinetic theory of gases allows physicists to connect the classical mechanics of individual particles with the phenomenological laws of thermodynamics. Had Galileo, Newton and their followers included all intricacies of the real world from the start in their models, today's physics would still be a descriptive science (Nabi, 1981).

Can we apply similar approaches in ecology? A promising example is the *Metabolic Theory of Ecology* (MTE) (Brown et al., 2004). This theory starts with the simple assumption that all physiological rates are limited by metabolism. Moreover, MTE maintains that metabolism scales with body mass according to Kleiber's law and with respect to temperature according to the Arrhenius equation (Moore, 1972). Since ecological rates (e.g. growth, mortality, predation) are dependent on metabolic rates, MTE is able to predict a multitude of ecological relationships (Brown et al., 2004). For example, the $-3/4$ exponent in Damuth's rule is viewed as a direct consequence of the $3/4$ exponent in Kleiber's law.

These predictions of are based on extremely simplified assumptions concerning the upscaling from biochemical principles to individual metabolism and from individual organisms to the population, food web and even ecosystem level. Until now, such upscaling has not reached the level of sophistication found in physics, since it is not really rooted in lower-level principles. Moreover, interactions among individuals and populations are

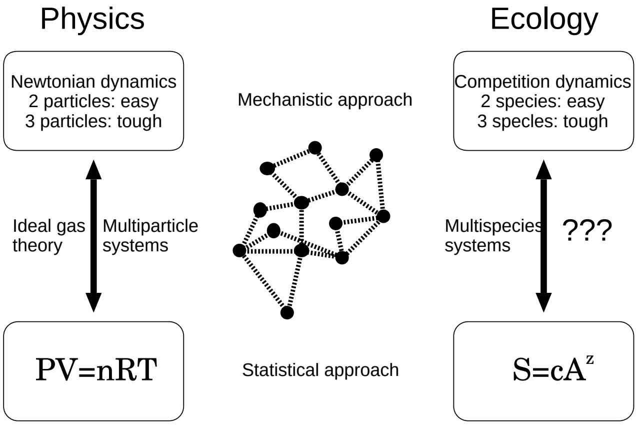


Figure 7.1: In physics, it is a general insight that it is relatively easy to study the mechanics of two particles, but very difficult to do so for three or more particles. Thanks to statistical mechanics it is nevertheless possible to describe large systems consisting of many particles, as it happens with the ideal gas law. In ecology, we face a similar challenge. There are large scale patterns, like species-area relationships, yet there is no firm theory that explains how these patterns arise as a consequence of ecological interactions among the many components of an ecosystem.

typically neglected or trivialized. One of my original goals was to see whether, and to what extent, such interactions matter for understanding higher-level patterns and processes.

The interactions of only two species are generally quite easy to understand. For example, the competition among two species has a simple dynamics: the system will always converge to an equilibrium that is easy to characterize. The interaction of three or more species can, however, be highly complex. For example, the competition among three or more species can lead to oscillations (Gilpin, 1975; May and Leonard, 1975; Zeeman, 1993), and deterministic chaos is possible in case of more than three species (Smale, 1976; Arneodo et al., 1982). This is reminiscent to the situation in classical mechanics where two-particle dynamics is simple, but three-particle dynamics is highly complex and often chaotic (Fig. 7.1). In analogy with the transition from a mechanistic to a statistical description in physics, one might wonder whether a mechanistic view of the interaction of multiple populations will also give rise to simple statistical rules.

To address this, I considered the most basal type of ecological interaction, namely the competition of autotrophic organisms for abiotic resources such as mineral nutrients or light. The goal was to uncover the rules governing such competition, on the way to answering question like: is a mechanistic view of multispecies competition consistent with the statistical patterns predicted by a theory like MTE? The mechanistic analysis of multispecies competition turned out to be a difficult enterprise, and in fact it became the main focus of my thesis. The main insights obtained are summarized in section 1 of this chapter. Section 2 is more speculative, since I try to extrapolate my findings on competition to more complex ecological scenarios like food webs. In section 3, I get back to the original aim at linking MTE and species interactions.

7.1 COMPETITION

In simple models of competition for essential resources Huisman and Weissing (2001) formulated a few "rules of thumb" concerning the predicted outcome of competition for several relationships between resource requirements and resource consumption patterns:

1. If each species tends to consume most of the resources for which it has the highest requirements, the system will tend to equilibrium where as many species will coexist as there are limiting resources.
2. If each species tends to consume most of the resources for which it has the lowest requirements, competitive exclusion is to be expected. It depends on the initial conditions which species will outcompete all its competitors.
3. If each species tends to consume most of the resources for which it has intermediate requirements, competitive oscillations and chaotic dynamics are to be expected. Even in a homogeneous environment, more species can stably coexist than there are limiting resources.

At equilibrium, not more species can stably coexist than there are limiting resources (the Principle of Competitive Exclusion, Gause, 1934; Hardin, 1960; Grover, 1997). However, under non-equilibrium conditions, many more species can persist than the number of resources. It has been argued (Huisman and Weissing, 1999) that this might offer a solution for the paradox of the plankton, the observation that hundreds of competing algal species do coexist on a handful of mineral resources in an homogeneous medium (Hutchinson, 1961).

This is, however, still an open question. The mathematical model that produces the aforementioned results (e.g. the "Monod model" described by equations (7.17) ignores an important characteristic of algae that is crucial in competition under fluctuating resource conditions, namely the ability to store resources (Ducobu et al., 1998). It is therefore natural to ask: are the above rules of thumb robust? how likely are competitive oscillations in the presence of the buffering effects of storage? how is the dynamics of competition affected by the delay between resource uptake and resource-limited growth?

In order to explore these questions I considered the following resource storage model of multispecies competition

$$\begin{aligned}
\frac{dN_i}{dt} &= N_i\{\mu_i(Q_{1i},\dots,Q_{mi}) - m_i\} \\
\frac{dQ_{ji}}{dt} &= f_{ji}(R_j) - \mu_i(Q_{1i},\dots,Q_{mi})Q_{ji} \\
\frac{dR_j}{dt} &= \phi_j(R_j) - \sum_{i=1}^{n} f_{ji}(R_j)N_i
\end{aligned} \tag{7.1}$$

Here N_i is the density of species i, R_j is the concentration of resource j and Q_{ji} is the content of resource j stored per species i also called the quota. The net dynamics of species i results from the balance between its growth rate μ_i and its mortality m_i rate. The dynamics of the quotas result from the balance between consumption f_{ji} and their metabolization at a rate that is proportional to growth $\mu_i Q_{ji}$ (dilution by growth, Grover, 1997). The resource balance depends on the net supply rate ϕ_j and its consumption by all species. In numerical simulations μ_i, f_{ji} and ϕ_j are given by

$$\begin{aligned} \mu_i(Q_{1i},\dots,Q_{mi}) &= r_i \min_j \left[1 - \frac{q_{ji}}{Q_{ji}}\right] && (7.2) \\ f_{ji}(R_j) &= \frac{\nu_{ji} R_j}{K_{ji} + R_j} && (7.3) \\ \phi_j(R_j) &= D(S_j - R_j) && (7.4) \end{aligned}$$

where μ_i follows the Droop (1973) formula and Liebig's (1840) law of the minimum for perfectly essential resources; r_i is the maximum growth rate, and q_{ji} is the threshold growth quota, such that $\mu_i = 0$ if $Q_{ji} \leqslant q_{ji}$. Resource consumption attains its maximum ν_{ji} under saturating resource concentrations, and K_{ji} is the half-saturation constant (Aksnes and Egge, 1991). Resources follow the dynamics of a chemostat where D is the resource turnover rate and S_j the resource input concentration (Grover, 1997).

Simulations

In Chapter 2, I performed an extensive computer simulation study of the storage model, in order to find out whether, and to what extent, the "rules of thumb" formulated by Huisman and Weissing (2001) extend to this more complex class of competition models. The general conclusion was that the rules of thumb hold fairly well in the multispecies storage model. Equilibrium coexistence occurs in virtually all cases where species tended to consume most of the resources for which they had the highest requirements; and competitive exclusion was observed in all cases where consumption was highest for the least needed resources When species tend to consume most of those resources for which they have intermediate requirements, competitive oscillations do indeed occur regularly. However, in a substantial proportion of the simulations (about 75%) these oscillations were transitory, collapsing into competitive exclusion or stable coexistence at equilibrium.

The storage model is inherently more complex than the model without storage. To illustrate this, let us consider a specific scenario where five species compete for five resources. In models without storage, such a scenario can be characterized by 50 parameters, namely 5×5 consumption rate parameters c_{ji} and 5×5 half-saturation constants H_{ji}, which directly translate into the 25 resource requirement parameters R^*_{ji}. In our case, I chose the following parameter configuration (where rows correspond to resources and columns correspond to species):

$$[R^*_{ji}] = \begin{bmatrix} \mathbf{1{,}9} & 1{,}8 & 1{,}6 & 1{,}6 & 1{,}4 \\ 1{,}3 & \mathbf{1{,}9} & 1{,}8 & 1{,}8 & 1{,}6 \\ 1{,}7 & 1{,}3 & \mathbf{2{,}0} & 1.8 & 1{,}7 \\ 1{,}7 & 1{,}6 & 1{,}3 & \mathbf{1{,}8} & 1{,}7 \\ 1{,}9 & 1{,}8 & 1{,}7 & 1{,}5 & \mathbf{1{,}9} \end{bmatrix}, [c_{ji}] = \begin{bmatrix} 1.2 & 1.0 & \mathbf{3.4} & 3.0 & 1.8 \\ 2.0 & 1.8 & 0.8 & \mathbf{3.4} & 2.8 \\ 2.6 & 2.2 & 1.2 & 0.8 & \mathbf{3.2} \\ \mathbf{3.4} & 2.4 & 2.2 & 1.8 & 1.2 \\ 1.6 & \mathbf{3.6} & 2.2 & 2.0 & 1.0 \end{bmatrix} \qquad (7.5)$$

In this configuration species 1 has the highest requirement for resource 1, species 2 for resource 2 and so on (bold R^*_{ji}), and each species consume most of the resources for which it has intermediate requirements (bold c_{ji}). According to the rules of thumb, this pattern should generate oscillations or chaos, and it does, as seen in Figure 7.2a.

In the storage model, resource requirements and consumption rates depend on the 75 model parameters ν_{ji}, K_{ji} and q_{ji} in an intricate and non-linear way. Starting with a set of consumption and growth parameters, it is extremely difficult (or infinitely frustrating) to tell if the resource requirements and consumption rates will match a given pattern. The opposite however, is straightforward: given R^*_{ji} and c_{ji} (and knowing that at equilibrium the f_{ji} of the storage model is equal to $m_i c_{ji}$ of the model without storage), an infinite set of parameter combinations ν_{ji}, K_{ji}, q_{ji} can be generated, which all lead to the same resource requirements and consumption patterns at equilibrium (Chapter 2, Appendix). In other words, for each specific model without storage, there are infinitely many realizations of the storage model sharing the same characteristics of resource limitation and resource uptake at the community equilibrium. The question is whether all of these realizations exhibit at least qualitatively the same dynamics as the model without storage.

Figure 7.2b exemplifies that the answer to this question is negative. The figure shows 20 realizations of the storage model. The parameters of these realizations are chosen at random but with one restriction: they reproduce the same resource requirements and consumption pattern at equilibrium (7.5) as the model without storage in Figure 7.2a. Like in the simpler model used as template, all realizations of the storage model have a tendency to exhibit oscillations. Indeed, many display a the similar chaotic dynamics (the cycle of species 1-2-4 is interrupted at irregular intervals by the rise and decline of species 3 and 5). However, a small but significant number of realizations display regular oscillations, and in few of them some actually species went extinct (see also chapters 3 and 4). These simulations show another distinctive feature of the storage model, which is that the time scale of the dynamics is much longer than in models without storage.

Stability and dynamics

The analytical study of the multispecies storage model is not an easy task. Given n species and m resources, the storage model consists of $n + m + n \times m$ time dependent variables (species + resources + quotas). For example 2 species and 2 resources results in an 8-dimensional system, 3 species and 3 resources in a 15-dimensional system, and our previous numerical example is 35-dimensional. The jacobian matrices associated with these systems have $(n + m + n \times m)$ rows and columns, making it quite unlikely to ever obtain general and 'nice' criteria for the stability of equilibria. At present only the case of two species has been studied in some detail by Li and Smith (2007).

In Chapter 3, I derived some partial results on stability, which are more broadly applicable to higher-dimensional storage models. I showed that – like models without storage – the local dynamics around each equilibria is strongly dependent on the consumption pattern of the competing species, i.e., on the structure of the consumption matrix $[f_{ji}]$ evaluated at equilibrium. Compared with the jacobian matrix the consumption matrix has only n rows and m columns, simplifying the analysis considerably. More importantly, the stability

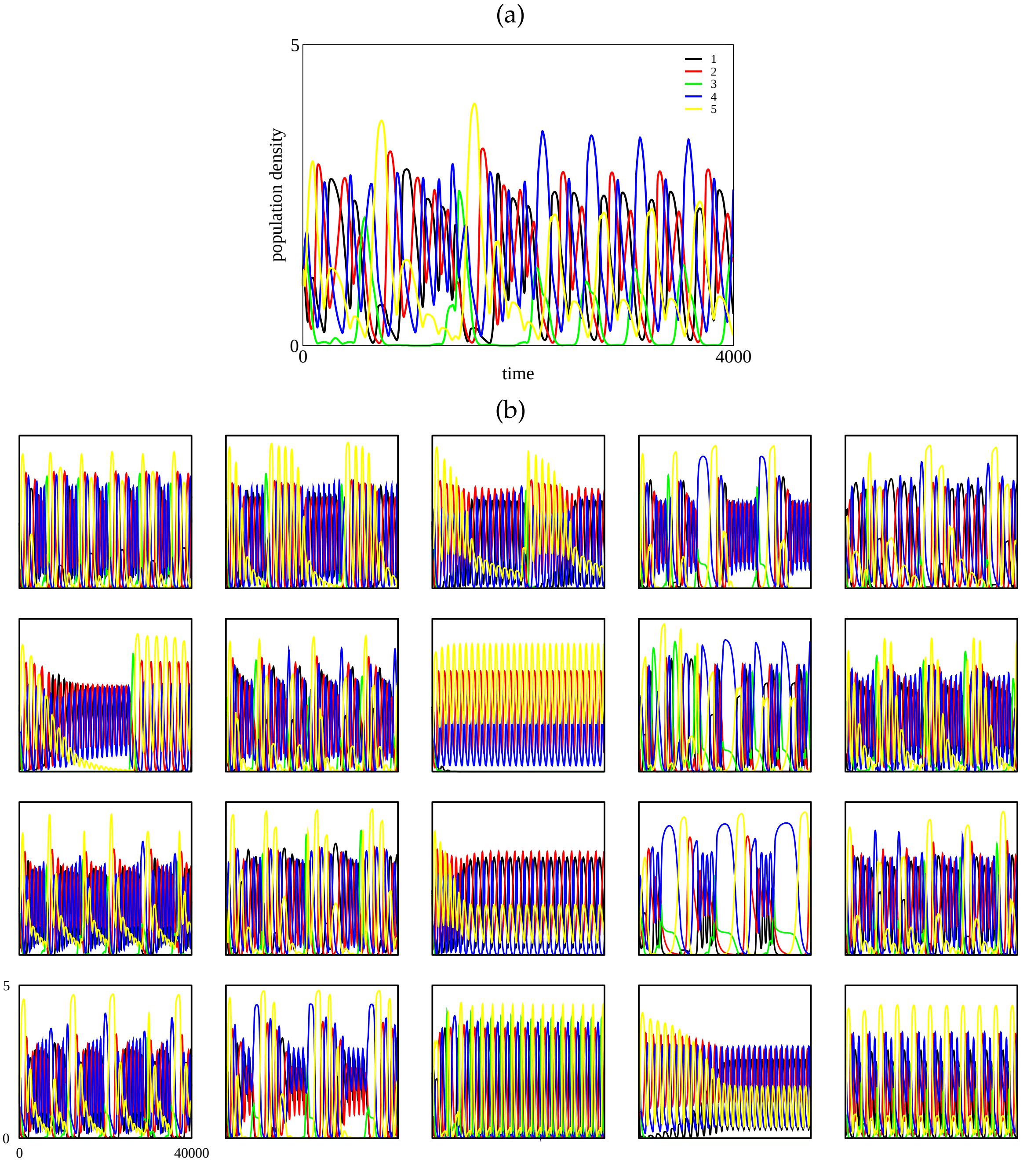


Figure 7.2: Competition of five species for five resources in the absence (a) and presence (b) of resource storage. The simulations are all based on a specific configuration of resource requirements and consumption patterns ((7.5) in the text). Each species tends to consume most of those resources, for which it has intermediate requirements. (a) The model with no storage is fully specified by the parameter combination (7.5). As predicted by rules of thumb, the system exhibits (chaotic) oscillations. (b) The storage model is only partly specified by resource requirements and consumption patterns. The 20 panels show simulation runs for randomly chosen realizations of the storage model, which are all compatible with the imposed parameter configuration (7.5). Some of these simulations display similar dynamics as the model without storage, others display regular oscillations, and even the extinction of one or two species. The time scale of the dynamics of the storage model (shown in the lower left panel) is considerably longer compared with its non-storage equivalent.

criteria do not depend on the functional form of the underlying model parameters μ_i, f_{ji} and ϕ_j. Hence, the results are quite robust and not dependent on details.

In contrast with the model without storage (where the consumption rates are assumed to be constant), the consumption matrix $[f_{ji}]$ of the storage model is not fixed, but varying from one equilibrium to the next: the matrix $[f_{ji}]$ may be identical to the matrix $[c_{ji}]$ in (7.5) at the 5-species equilibrium, but it can have a totally different structure at any of the 4-, 3- ... and 1-species equilibria. Thus, the "rules of thumb" regarding consumption become local rules in the storage model.

As shown in Chapter 4, another important aspect varying from one equilibrium to the next is the identity of the limiting resource. In an n-species equilibrium, each species must be limited by a different resource: that resource, for which it has the highest requirement. In the neighborhood of other equilibria with fewer than n species, a species may be limited by a different resource than in the n-species equilibrium. As a consequence, the dynamics becomes strongly dependent on the initial conditions. Such changes in resource limitation become important whenever more than three resources are considered. They are not an exclusive feature of the storage model, but a consequence of framing essential resources in terms of Liebig's law. However, since both theory and experiments on resource competition tend to focus on the special case of two resources, this issue has not received the attention it deserves (Zhang, 1991; Hu and Zhang, 1993).

As the dimensionality of the system increases, both in species and in resources, the long term dynamics becomes more dependent on the initial conditions, even in the absence of deterministic chaos. But the consumption patterns can be still responsible for major features of the competitive dynamics, since they determine the tendency for displaying non-equilibrium dynamics, which affecs biodiversity in shorter time scales. For example, it may happen that the long term deterministic attractor of a system is an equilibrium state where one species exclude all others. However, transitory oscillations can delay the approach to such state of low diversity, and thus maintain a high number of species. In case of storage models such delays can be considerable (Fig. 7.2).

Comparisons of competition models

Without or with storage, resource competition models share many dynamical features with the much simpler multispecies Lotka-Volterra model for competition. All three models can exhibit multiple stable states, stable and unstable limit cycles, and chaos (Gilpin, 1975; May and Leonard, 1975; Smale, 1976; Arneodo et al., 1982; Zeeman, 1993). As I showed in Chapter 5, the equilibrium states and local stability of resource competition models (with and without storage) depend on the structure of the consumption matrix ($[c_{ji}]$ or $[f_{ji}]$), whereas in Lotka-Volterra models equilibrium and stability are governed by the *community matrix*; the matrix of competition coefficients. These matrices can be related to each other, although the form of the relationship depends on the mechanistic details of the consumer-resource interaction.

In view of these similarities between the mechanistic resource competition models and the phenomenological Lotka-Volterra model, we can generalize the "rules of thumb" of resource competition (Huisman and Weissing, 2001) as rules of thumb relating the relative intensity of inter- and intra-specific competition:

1. weak interspecific competition leads to stable coexistence at equilibrium;
2. strong interspecific competition leads to competitive exclusion with the winner depending on the initial conditions;
3. intermediate interspecific competition can lead to all of the above, but also to competitive oscillations and chaos.

In the Lotka-Volterra model, interspecific competition is considered "weak" when the intraspecific coefficients of the community matrix tend to be higher than the interspecific coefficients; it is considered "strong" if the opposite is true. In resource competition models, interspecific competition is "weak" if each species has the strongest effect (via consumption) on its ‘own’ limiting resource than on the limiting resources of other species; it is "strong" if the opposite is true.

Scenarios of "intermediate" interspecific competition, are more difficult to define. Intermediate could mean that all interspecific effects are of similar magnitude. In terms of resource competition that would be roughly equivalent to a situation where the consumption ratios for each species are comparable. Without knowing the resource requirements, it is difficult to determine if such situations lead to equilibrium non-equilibrium or non-equilibrium dynamics.

The other "intermediate " scenario occurs when each species tends to impose strong effects on a given subset of its competitors and weak effects on the rest, such that the average effects are approximately similar for all species. Under resource competition, this is achieved when each species tends to display high consumption rates for the most critical resources of some species, and low consumption rates for the most critical resources of the rest. In a minimal community of three species this results a non-transitive hierarchy of competitive dominance, like in the Rock-Scissors-Paper game where Rock blunts Scissors, Scissors cuts Paper, and Paper captures Rock (Weissing, 1991). As long as all three strategies are present, no one is a clear winner and they chase each other forever; thus they coexist. Incomplete dominance as in the Rock-Scissors-Paper game, has been invoked to explain the maintenance of biodiversity not just in the context of resource competition, but in more general ecological and evolutionary contexts (Buss and Jackson, 1979; Sinervo and Lively, 1996; Kerr et al., 2002; Laird and Schamp, 2006). In order to survive, organisms do not have to be superior for all characteristics; it suffices to compensate weaknesses in some aspects with strengths in other aspects.

Like in the Lotka-Volterra model, the outcome of resource competition is the consequence of the dominance relationships among the species, independently of the mechanistic details of resource consumption. This does not mean that mechanistic detail is unimportant; such detail is required in order to explain how the dominance relationships arise in the first place. This is reminiscent of the description for the ideal gas given at the beginning of this chapter. *Classical thermodynamics* can tell us what is the relation between pressure and volume a given temperature, but what is exactly temperature? Enter *statistical mechanics*: temperature is a measure of the mean kinetic energy of the gas particles. Classical thermodynamics is phenomenology, statistical mechanics gives the explanation.

Non-transitivity as in the Rock-Scissors-Paper game appears to be an essential feature for competitive oscillations. Interestingly, competitive oscillations can occur between two species, where non-transitivity is ruled out by definition. In Chapter 6 this was explored by means of a plant-soil interaction model in which the competitive displacement of one plant by another turns the winning plant vulnerable to invasion at a later time. In this plant-soil model, the state of the soil community (composed of mutualists, consumers and parasites) leads to a switch in plant dominance in a predictable and cyclical way.

7.2 FOOD WEBS

I focused on purpose on competition for essential and abiotic resources. This choice makes growth rates easy to model, and interactions among resources (like competition among prey species) can be neglected. Although complex, the major features of the competitive dynamics are explainable by a few rules of thumb. However, these rules might be overshadowed by interactions across trophic levels, since in the real world competitive communities are embedded in food webs. In this context, are there competitive oscillations on substitutable resources? Does competition among the resources affects consumer dynamics? Are competitive oscillations affected, suppressed, enhanced by predation or herbivory?

In this section will try to approach these questions by means of a simple but realistic example considering competing plants and competing herbivores, linked in a food web by means of the Rosenzweig-MacArthur equations (Rosenzweig, 1971)

$$\begin{aligned}\frac{dN_i}{dt} &= N_i\left\{\frac{c\sum_j e_{ji}p_{ji}R_j}{1+h\sum_j p_{ji}R_j} - m\right\}\\ \frac{dR_j}{dt} &= rR_j\left\{1-\frac{\sum_k a_{jk}R_k}{K}\right\} - \sum_i \frac{cp_{ji}R_jN_i}{1+h\sum_k p_{ki}R_k}\end{aligned} \tag{7.6}$$

N_i and R_j denote the densities of herbivores and plants respectively. Plants compete according to the Lotka-Volterra model, where r is the intrinsic rate of growth and K is the carrying capacity. a_{jk} are the competition coefficients, i.e. the ratio of the effect of plant k on plant j with respect to the effect of plant j on itself, which is assumed to be one $(a_{jj} = 1)$. Plants are substitutable resources for the herbivores. They are consumed according to Holling's type II functional response, where c is the attack rate, h is the resource handling time and p_{ji} is the proportion of resource j in the diet of consumer i, a measure of the foraging effort. The parameter e_{ji} is the conversion yield of resource j into biomass of consumer i (Grover, 1997), and m is the constant mortality rate of the consumers.

This Rosenzweig-MacArthur model has the link structure of a small food web embedded in a larger one as in Figure 7.3. There are three types of interactions to consider. The first is competition among the herbivores which can lead to competitive oscillations (Huisman and Weissing, 1999). The second is competition among plants which can lead to competitive oscillations too (Gilpin, 1975; May and Leonard, 1975). And the third are the plant-herbivore interactions, which may lead to prey-predator oscillations (Rosenzweig and MacArthur, 1963).

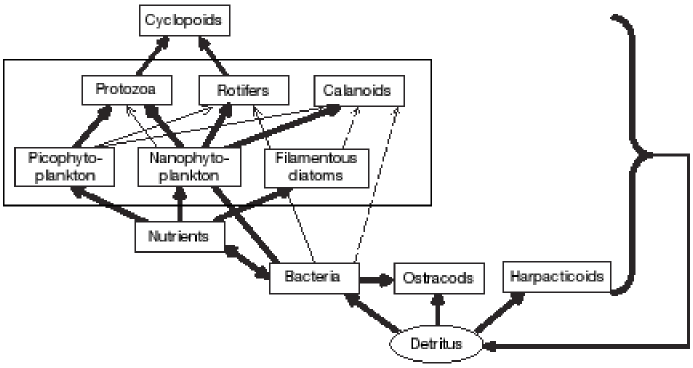


Figure 7.3: An experimental food web studied by Benincà et al. (2008) which displays chaotic dynamics. The "sub-web" formed by primary producers and their consumers (rectangle) has the same consumer-resource link structure as the Rosenzweig-MacArthur model (eqns. 7.6) discussed in the text.

Effects of lower trophic levels

Let us turn our attention to the consumer species. Complex dynamics like competitive oscillations require trade-offs, e.g. higher requirements for certain resources must be balanced by low requirements for others. In chapters 1 - 4 we employed parameter matrices to express such trade-offs (as in section 2). The same can be done for this model. Consider three consumers and three resources and the following parameters

$$[e_{ji}] = \begin{bmatrix} \epsilon & 0 & 1-\epsilon \\ 1-\epsilon & \epsilon & 0 \\ 0 & 1-\epsilon & \epsilon \end{bmatrix}, [p_{ji}] = \begin{bmatrix} \pi & 0 & 1-\pi \\ 1-\pi & \pi & 0 \\ 0 & 1-\pi & \pi \end{bmatrix}, [a_{jk}] = \begin{bmatrix} 1 & \alpha & \alpha \\ \alpha & 1 & \alpha \\ \alpha & \alpha & 1 \end{bmatrix} \tag{7.7}$$

where each herbivore consumes only two out of three resources, or alternatively each pair of herbivores only competes for one resource. A trade-off exists, in which the high conversion yield of one resource is compensated by a low conversion yield for the other ($0 < \epsilon < 1$). A second trade-off concerns the diet, in which the high consumption of one resource is compensated by the low consumption of the other resource ($0 < \pi < 1$).

Let us assume that plants do not compete ($\alpha = 0$), and that each plant is the most nutritive resource for a different herbivore: plant 2 for herbivore 1, plant 3 for herbivore 2, and plant 1 for herbivore 3 ($\epsilon < 1/2$). In Figure 7.4a, where the herbivore diets are biased towards the most nutritive resource ($\pi < 1/2$) the system develops competitive oscillations. These are not predator-prey oscillations because: (1) the carrying capacity is too low to sustain predator-prey oscillations ("paradox of enrichment" Rosenzweig, 1971), (2) there is a regular sequence of invasions and displacements and (3) the elimination of one herbivore destroys the cycle and leads to a community dominated by one herbivore (the elimination of one plant also destroys the cycle, but herbivores can coexist since their resources are substitutable). In Figure 7.4b the diet has switched such that the less nutritive resource is favored ($\pi > 1/2$). This makes the competitive oscillations short lived, and they are replaced by a predator-prey cycle. Interestingly, this parametrization does not allow sustained

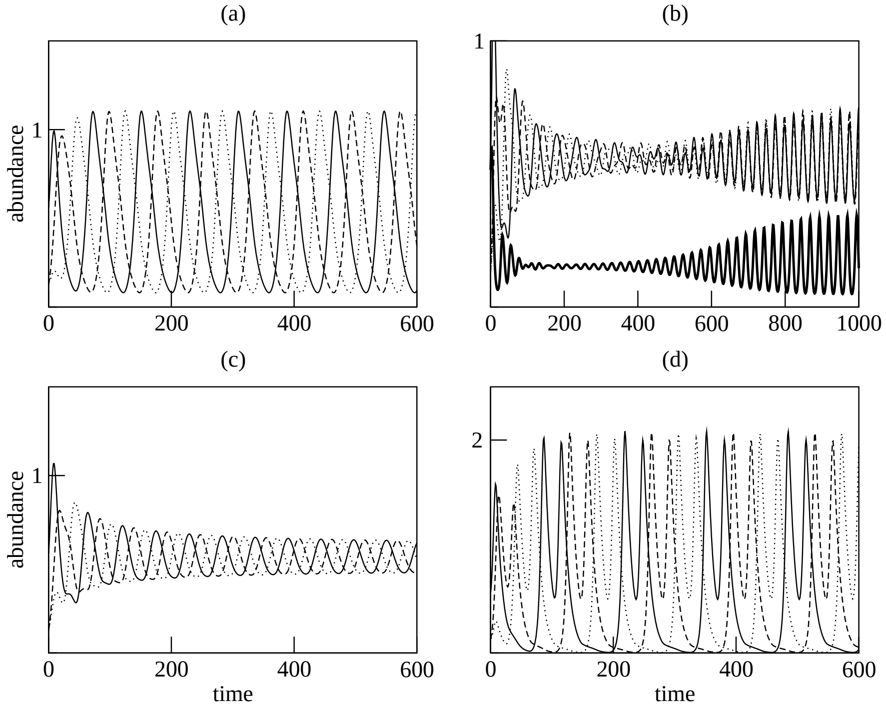


Figure 7.4: Dynamics of the Rosenzweig-MacArthur model of three competing herbivore species (linetypes correspond to species) feeding on three competing plant species. (a) Reference scenario that is characterized by the parameter setting $r = K = c = h = 1, m = 0.1$; and e_{ji}, p_{ji}, a_{ji} given by (7.7) with $\epsilon = 0.4$, $\pi = 0.1$ and $\alpha = 0$. Here the plants do not compete and herbivory is biased towards the most nutritive resource. In this scenario the herbivores display competitive oscillations. (b) The herbivores diet changes to $\pi = 0.7$, which is now biased towards the less nutritive resource. As a consequence the competitive oscillations are substituted by a predator-prey oscillation, in which the community of herbivores act as if they were a single herbivore (the thick line shows the average plant density). (c) If the plants are allowed to compete in part b (by setting $\alpha = 0.1$), the herbivore's competitive oscillations are restored, but the amplitude is lower than the in reference scenario. (d) Raising the carrying capacity to $K = 2$ in the reference scenario induces predator-prey oscillations, which combine with the competitive oscillations.

predator-prey oscillations for any pair herbivore-plant. Instead, the oscillation is between the community of herbivores acting as a single predator, and the plant community acting as a single prey.

In Figure 7.4c the plants are allowed to compete with each other ($\alpha > 0$). We can see that competitive oscillations develop again, but this time their amplitudes are smaller than in the case where the plants do not interact. However, starting from a different initial condition (not shown) the oscillations are transitory and the system approaches an equilibrium. This may indicate the existence of a subcritical bifurcation, as discussed in Chapter 4.

Until now, the carrying capacity K was kept low, implying that predator prey oscillations cannot be sustained. It is well known that consumer-resource models develop oscillations when the carrying capacity increases Rosenzweig, 1971, or when the handling (h) time increases. In Figure 7.4d, the carrying capacity was raised and as a consequence the system displays a mixture of competitive and predator- prey oscillations.

Thus, competitive oscillations can develop in competition for substitutable resources. As in competition for essential resources, the type of dynamics depends on the consumption patterns, in this case represented by the matrix $[p_{ji}]$. But in the context of a food web, interactions among the resources can in effect modify and even mask the competitive dynamics in the trophic level under study.

Effects of higher trophic levels

We can also change our perspective by focusing on the plants as the competing species instead of the herbivores. For this purpose consider the following parameter configuration

$$[e_{ji}] = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}, [p_{ji}] = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}, [a_{jk}] = \begin{bmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{bmatrix} \tag{7.8}$$

where the plants display Lotka-Volterra competitive oscillations in the absence of the herbivores when $\beta < 1 < \alpha$ (May and Leonard, 1975). The herbivores are this time specialist consumers. Figure 7.5 shows that competitive oscillations under this scheme are very fragile, because as soon as one of the consumers is gone, the resulting imbalance in herbivory leads to the collapse of the cycle. On the other hand, if herbivores are generalists ($e_{ji} = p_{ji} = 1/3$, not shown) oscillations do not show up at all.

In these examples we clearly see that the competitive dynamics within a trophic level is affected by interactions across trophic levels. In the simple model considered above, the simulations suggest that oscillations are more strongly suppressed by higher than by lower trophic levels. For the sake of simplicity, a symmetric parametrization was chosen, and plant interactions were modeled in a non-mechanistic ways. Thus the model considered above can be improved and extended in various ways.

We have only seen simple forms of coupling between predator-prey and competitive oscillations, like forcing (Fig. 7.4b) and superposition (Fig. 7.4d). Coupled oscillators (Hastings and Powell, 1991; Vandermeer, 1993; Huisman and Weissing, 2001; Benincà et al., 2008) are implied in the onset of chaos (Hastings and Powell, 1991; Vandermeer, 1993; Huisman and Weissing, 2001; Benincà et al., 2008), and they have been found to be respon-

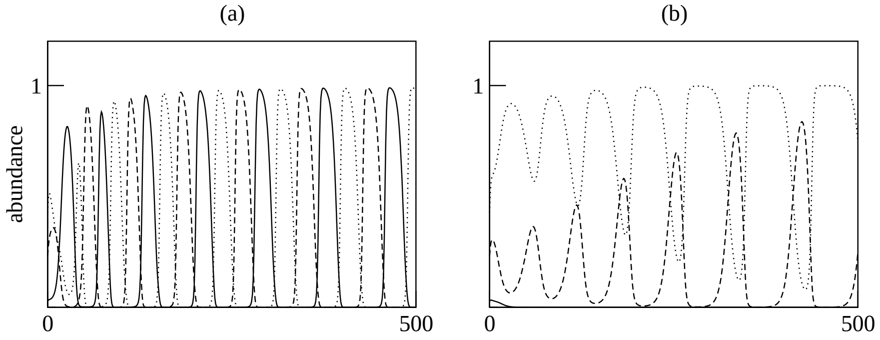


Figure 7.5: Dynamics of three competing plant species (linetypes correspond to species). In the absence of herbivores, the plants can display competitive oscillations. (a) In the presence of three specialist herbivores the consumption pressure is well balanced, and the plant competitive oscillations persist. (b) After the elimination of a single herbivore, the competitive cycle collapses, leaving a system of one herbivore and two plants. Parameters: $r = K = h = 1, m = 0.1, c = 0.7$; and e_{ji}, p_{ji}, a_{ji} given by (7.8) with $\alpha = 0.8, \beta = 1.2$.

sible for the chaotic dynamics displayed by the food web in Figure 7.3 (Benincà et al., 2009). But chaos resulting from the interaction of predator-prey and competitive oscillations is yet to be found.

7.3 METABOLISM

The Metabolic Theory of Ecology (Brown et al., 2004) (MTE) states that large-scale patterns in communities and ecosystems (e.g. community structure, size distributions, biodiversity gradients) reflect the physical constraints imposed on the metabolism of individuals. According to MTE individual metabolic rates M, from microorganisms to whales (Gillooly et al., 2001), scales with body mass/size w and ambient (absolute) temperature T as follows:

$$M = M_0 w^{3/4} e^{-E/k_b T} \tag{7.9}$$

According to this "master equation", the body mass dependence follows Kleiber's law, and the temperature dependence follows the Arrhenius law, where E corresponds to the mean activation energy of biochemical processes (0,6 - 0,7 eV) and k_b is Boltzmann's constant (Moore, 1972). Whether there is a universal metabolic rule is a hotly debated topic in ecology (Agrawal, 2004, special issue on MTE). On the other hand the prospect of a unified metabolic law is appealing, and the master equation of MTE has been already considered in the study of the stability (Brose et al., 2006) and emergence (Loeuille and Loreau, 2005) of complex food webs.

According to MTE the equilibrium population densities scale with body mass and temperature as

$$N \propto \lambda w^{-3/4} e^{E/k_b T} \tag{7.10}$$

where λ is the rate of resource supply (Brown et al., 2004; Savage et al., 2004). By means of simple algebra, several mass and temperature scaling relationships follow, like community metabolism, primary production, even biodiversity (which is not a rate). For example, at a given temperature and resource supply, the total metabolism of a whole population should scale as $N \times M \propto w^{-3/4} \times w^{3/4} = w^0$. In other words, the total metabolism does not depend on body mass (the so-called "energetic equivalence rule"): the energy per unit area used by a population is independent of the body mass of its individuals. This energy equivalence rule has been extended to whole communities (Enquist et al., 1998; Allen et al., 2002): it implies that the energy consumption of a community is independent of the body mass distribution of its constituent populations.

It is important to realize that the main predictions of MTE (like the energy equivalence rule) were derived in a highly simplified manner, without paying attention to the intricacies of ecological interactions. In this section, I will show that such 'details' may matter a lot. At the same time I will show how to integrate the microscopic details of resource consumption and competition dynamics with the basic assumptions of MTE.

Populations

Although the MTE acknowledges the effects of resource availability, it ignores the underlying mechanisms of consumer-resource interactions. Using the Droop (7.2), uptake (7.3) and chemostat (7.4) equations in the resource storage model (7.1), I will illustrate why such level of detail is relevant.

In the equilibrium, the density of a single consumer species that is limited by a single resource is given by

$$N = D\,(S - R^*)\,\frac{r - m}{rmq} \tag{7.11}$$

where the resource requirement R^* is related to the basic model parameters as follows

$$R^* = \frac{Krmq}{\nu(r - m) - rmq} \tag{7.12}$$

In principle, all these parameters (r, m, ν, K, q) may be dependent on body size and temperature. It is a standard assumption of MTE, that the specific growth rate r and the specific death rate m are proportional to mass specific metabolism $(r, m \propto M/w)$:

$$r = r_0 w^{-1/4} e^{-E/k_b T} \tag{7.13a}$$

$$m = m_0 w^{-1/4} e^{-E/k_b T} \tag{7.13b}$$

In phytoplankton, resource consumption is a surface- and diffusion-limited process. According to the mechanistic model of Aksnes and Egge (1991), it is plausible to assume that the maximal consumption rate ν and the half-saturation constant for consumption K scale with body mass and temperature as follows:

$$\nu = \nu_0 w^{2/3} e^{-E/k_b T} \tag{7.14a}$$

$$K = K_0 w^{1/3} \frac{e^{-E/k_b T}}{d(T)} \tag{7.14b}$$

In line with MTE, I made the assumption that the temperature dependence of ν is described by the Arrhenius equation. In contrast, K is affected by molecular diffusion. I assumed that the diffusion coefficient $d(T)$ is an linearly increasing function of temperature; which implies that K increases with T but at a lower pace than ν.

There is currently no causal theory that explains how the threshold quota q depends on body mass and temperature. Two studies (Grover, 1989; Irwin et al., 2006) indicate that q is positively related to body mass. Let us therefore for the moment assume a generic relationship like this

$$q = q_0 w^{\gamma} f(T) \tag{7.15}$$

where $f(T)$ accounts for the (hitherto unknown) effect of temperature.

If we now substitute equations (7.13a, 7.13b, 7.14a, 7.14b, 7.15) in (7.12) and subsequently in (7.11), we obtain a relationship between equilibrium population density N and body mass and temperature. At first sight, this relationship is much more complicated than equation (7.10), which is one of the most basic predictions of MTE. However, equation (7.10) might still hold by approximation.

In order to see whether this is the case, let us make the plausible assumption that in our simple storage model the resource input concentration is much higher than the resource requirements of our consumer species $(S \gg R^*)$. In this case, equation (7.11) simplifies to

$$N \approx DS \left[\frac{r_0 - m_0}{r_0 m_0 q_0}\right] \frac{w^{1/4-\gamma} e^{E/k_b T}}{f(T)} \tag{7.16}$$

Now the result has at least some resemblance with the prediction of MTE. For example, density is directly proportional to the resource supply rate if $\lambda \equiv DS$. However, mass and temperature dependencies do not agree with (7.10). According to the scarce evidence available (Grover, 1989; Irwin et al., 2006) the allometric coefficient of the threshold quota q is lower than one, around $\gamma \approx 0.7$; thus $N \propto w^{-0.45}$ which implies that population energy use $N \times M$ scales with mass as $w^{0.3}$ and the energetic equivalence rule does not follow. With respect to temperature dependence the situation is unclear because we do not know the form of $f(T)$.

From this very simple consumer-resource model we can conclude that the dependence of population densities on body mass and temperature is much more intricate than MTE suggest – even if one systematically applies the line of argumentation typically used by MTE.

Communities

The Metabolic Theory of Ecology ignores or caricaturizes the role of competitive interactions. In order to study this issue, we have to integrate resource competition models with metabolic dependencies. For the purpose of illustration, I will here replace the storage based model of multispecies competition by the much simpler model without storage:

$$\begin{aligned}\frac{dN_i}{dt} &= N_i\{\mu_i(R_1,\ldots,R_m) - m_i\}\\ \frac{dR_j}{dt} &= D(S_j - R_j) - \sum_i c_{ji}\mu_i(R_1,\ldots,R_m)N_i \qquad (7.17)\\ \mu_i(R_1,\ldots,R_m) &= r_i \min_j\left[\frac{R_j}{H_{ji}+R_j}\right]\end{aligned}$$

The growth rates μ_i are functions of the resource densities in the external environment, which are modeled by combining Liebig's law of the minimum and the Monod equation. r_i is the maximum growth rate of species i under resource saturation, and H_{ji} is the half-saturation constant for the growth of species i on resource j. c_{ji} is the fixed resource content of resource j in an individual of species i. The remaining parameters (m_i, D, S_j) have the same meaning as in the storage based model.

As indicated by (7.10) MTE predicts that density scales with size as $N_i \propto w_i^{-3/4}$. In a stable community the densities of the competitors $\hat{N}_i$ must satisfy the following system of linear equations

$$D(S_j - \hat{R}_j) = \sum_i c_{ji}m_i\hat{N}_i \qquad (7.18)$$

implying that no more species than resources can coexist at equilibrium (principle of competitive exclusion). Thus, the derivations that follow apply to communities with low diversity. The equilibrium concentration of resource j corresponds to the maximum requirement of resource j among all consumers $\hat{R}_j = \max_i[R^*_{ji}]$. For model (7.17) the resource requirements are given by

$$R^*_{ji} = \frac{r_i H_{ji}}{r_i - m_i}$$

Following MTE, the specific growth and death rates are proportional to mass specific metabolism (M_i/w_i): $r_i = r_o w^{-1/4} e^{-E/k_bT}$ and $m_i = m_o w^{-1/4} e^{-E/k_bT}$. On the other hand, there is no theory explaining how half-saturation constants for growth scale with body mass and temperature. (In contrast, the half-saturation constants for consumption in the storage model do have a mechanistic interpretation, allowing to make judicious guesses on their dependency on body mass and temperature.). Following common practice (Vasseur and McCann, 2005; Lopez-Urrutia et al., 2006), I therefore assume that the H_{ji} are constant and not dependent on body mass or temperature. As a consequence R^*_{ji}, and thus $\hat{R}_j$ in (7.18) are as well independent of both body mass and temperature.

Given that c_{ji} is defined as the amount of resource j contained in an individual of species i, it is reasonable to assume that c_{ji} represents a fraction of the body mass, that is

$$c_{ji} = \gamma_{ji} w_i,\ \gamma_{ji} < 1$$

where γ_{ji} can be defined as a compositional or stoichiometric coefficient. As in the case of the half-saturation constant, let us assume that c_{ji} is independent of temperature.

At equilibrium, the population densities (which are given by the linear equations (7.18)) must be of the form

$$\hat{N}_i = \left[\frac{DG_i}{m_o}\right] w_i^{-3/4} e^{E/k_b T} \tag{7.19}$$

Here G_i is the determinant of the matrix of stoichiometric coefficients γ_{ji}, but after the substitution of the i-th column by the vector of differences between the resource supply and equilibrium concentrations $(S_1 - \hat{R}_1, S_2 - \hat{R}_2, \ldots)^T$. As an illustration, consider two species competing for two resources in a rich environment (where $S_j \gg R^*_{ji}$). In such a situation, the terms G_1 and G_2 are of the form:

$$G_1 = \frac{S_1\gamma_{22} - S_2\gamma_{12}}{\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21}},\ G_2 = \frac{S_2\gamma_{11} - S_1\gamma_{21}}{\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21}} \tag{7.20}$$

but for more than two species and resources, the G_i are even more complex.

Equation (7.19) displays a similar mass and temperature dependence as predicted by the MTE in (7.10), in the sense that N_i scales with mass to the $-3/4$, and with temperature as in the Arrhenius law. However, the dependence of the G_i on the resource supplies (S_j) and on the stoichiometric coefficients (γ_{ji}) is nonlinear and complicated. As a result, it is uncertain whether the term in square brackets of (7.19) is close to a common factor, i.e. a "universal constant", for all species involved. Thus, there is not *a priori* reason to assume that a plot of $\log(N)$ versus $\log(w)$ or T^{-1} will reveal a linear relationship as predicted by MTE. In other words, the effects of resource and species stoichiometry can obscure the effects of the Kleiber and Arrhenius laws.

Real world scenarios

The density-mass relationship (7.19) is restricted to homogeneous environments where the number of species is limited by the number of resources. In reality, environments can be spatially heterogeneous, thus allowing the coexistence of a much higher number of species than resources, provided there are trade-offs in resource requirements and consumption (Tilman, 1982). The rationale is as follows: consider n species competing for two resources, in a region fractionated into several sites. Each site x differs in the resource input concentrations of the two resources $S_1(x), S_2(x)$. Thus, each site x can harbor 2, 1 or 0 plant species from the pool of n. If two species, for example $i = a, b$ coexist in site x, their equilibrium densities $\hat{N}_a(x)$ and $\hat{N}_b(x)$ are the solutions of (7.18). If there is enough variation in resource supply ratios all species pair equilibrium combinations are feasible at the regional scale. The resource ratios also determine the numerical representation of each species at the local level, thus the details of their distribution say which species, and thus which body masses become more frequent in the regional scale.

To see if the density-mass relationship (7.10) predicted by MTE holds in highly diverse ecosystems, I performed a simulation that considers 100 species competing for two essential resources according to the resource competition model (7.17), in an heterogeneous environment. Such environment consists of 10000 sites, each with resource supply concentrations

S_j taken from a normal distribution with a mean of 10 and standard deviation of 2. I will assume that the environment has a homogeneous temperature.

The species body masses were generated according to $w_i = 10^{u\Delta}$ where u is uniformly distributed in $[0, 1]$ and $\Delta = 1, \dots, 10$ is the order of magnitude of body mass variation. A small amount of site specific variation was introduced as a normal deviate with mean zero and standard deviation $0.1w_i$.

To promote local coexistence of at least two species for some combinations of resource supplies I imposed the following conditions. (1) The resource requirements were sampled uniformly along the trade-off line $R^*_{1i} + R^*_{2i} = 1$. (2) The resource contents where generated according to the ratios $c_{2i}/c_{1i} = R^*_{2i}/R^*_{1i}$, such that each species consume resources in proportion to its requirements. In addition the actual values of c_{1i} and c_{2i} are fractions of the species body mass, something that is achieved by introducing a linear trade-off $c_{1i} + c_{2i} = 0.2w_i$ (i.e. resource contents make 20% of the body mass). Thus, body size determines the total amount of resource contents, but not their relative proportions or stoichiometry.

Let N_i be the total density of species i, which is the sum of the densities of i in all the sites where it is present, alone or coexisting with a competitor. According to MTE a double logarithmic plot of N_i versus w_i must produce a line with slope of $-3/4$, independently of the local effects and competition. Figure 7.6 shows the slopes of these density-mass relationships for many simulations, plotted against the order of magnitude of the body mass variation (Δ). For small body mass ranges the resulting slopes are highly variable, with a tendency for values higher than $-3/4$, and in very few cases even positive. The dispersion decreases as the body mass range increases, and the slopes accumulate around $-3/4$ at the end of the axis, as predicted by MTE. Surprisingly, the amount of variation explained by body mass remains high along the axis of mass variation (around 70-80%).

We can conclude that body mass is an important factor in structuring communities (suggested by the coefficient of determination). However, under low ranges of mass variation the body mass dependence does not reflect the quarter power law of the mass-metabolism scaling exponent (7.9), indeed the relationship tends to be weaker in most cases. Most competitive interactions take place among similarly sized organisms, within 3 orders of magnitude in size variation. This means that functional traits (e.g. consumption ratios) and locality (e.g. supply concentrations), play the most important roles in structuring real communities Tilman et al. (2004), obscuring the metabolic dependence suggested by MTE.

This simulation and the results from the previous sections illustrate that the predictions of MTE are very sensitive to simplifying assumptions regarding physiology, interactions and scale. Of course, I made a made a number of simplifying assumptions regarding these factors, for example:

1. The consumption ratios match the requirement ratios, so competition is weak. According to Loeuille and Loreau (2006) increased competition within food webs results in density-mass slopes that are more negative than $-3/4$.

2. Competition is limited to two resources, which leads to equilibrium dynamics only. For three and more resources oscillations and chaos are possible, and there can be many alternative stable states. Does allometry has any relevance under such complex scenarios?

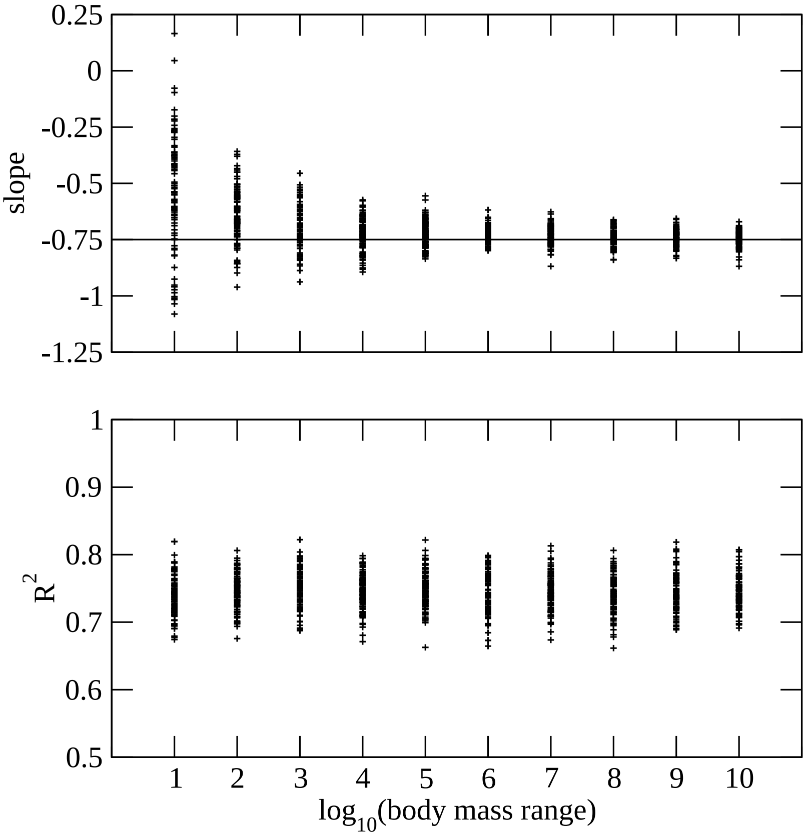


Figure 7.6: Density-mass relationships in competitive communities. The top panel indicate the slopes of the double logarithmic plots of density vs mass, for 100 simulated communities, each consisting of 100 species competing for 2 resources in an heterogeneous environment. They are plotted against the order of magnitude of the variation in body mass. According the Metabolic Theory of Ecology, the slopes must be close to $-1/4$ (horizontal line). The bottom panel shows the coefficients of determination of the density-mass relationships above.

3. Species stoichiometry is independent of body mass. The reality is that consumption ratios $c_{ji} : c_{ki}$ are mass dependent. For example, heavier plants (trees) have much more carbon per total weight than lighter plants (weeds).

This simulation and relationships like (7.16) and (7.19) can be seen as first attempts towards a statistical description of communities that integrates MTE, consumer resource interactions, and resource competition theory, one of my original goals.

Temperature

Many parameters of the models discussed in this chapter are physiological rates (maximum growth rates, maximum consumption rates, mortalities) which in turn depend on biochemical processes. Thus the exponential increase of these rates with temperature could be explained by the Arrhenius law, although there are other relationships and mechanisms (Ahlgren, 1987) that may fit rates vs temperature equally well (Brauer et al., 2009).

However, realistic models of temperature dependence must also account for positive and negative effects on biological rates. It is true that starting from low temperatures, warming increases reaction rates (Fig. 7.7a) enhancing metabolism. But biological rates are mediated by enzymes, which means that after some point further warming results in alterations of protein structure, rapid loss of activity, and irreversible denaturation. Physiological rates display a dome or bell shaped response to temperatures (Fig. 7.7b), with optima that are species specific (Tilman et al., 1981; Savage et al., 2004). Both views, the monotonic increase "à la Arrhenius", and the "dome shaped" describing the temperature niche, can be reconciled if each species spans a portion of an exponentially increasing curve (Fig. 7.7b, Eppley, 1972; Gillooly et al., 2002). But this of course would imply that a universal temperature dependency (Gillooly et al., 2001), if such thing exist, is a very complex emergent phenomenon and not the direct manifestation of the Arrhenius law.

We could leave aside this issue and just plug in the Arrhenius function in dynamical models (e.g. Vasseur and McCann, 2005; Lopez-Urrutia et al., 2006). But, there is still the problem that there are temperature dependent parameters which are not rates, or that result from combining rates. For them, the dependence on temperature cannot be described by means of a simple Arrhenius factor. In the storage model for example, resource uptake is limited by diffusion, the rate of which scales linearly with temperature. As a result, the half-saturation constant of consumption K scales with temperature at a lower rate than the maximum consumption rate ν, and for low resource concentrations the overall rate of consumption ($f \approx \nu/K$) becomes directly proportional to temperature (Aksnes and Egge, 1991).

In the Monod equation the half-saturation constant is known to increase or to decrease with temperature (Tilman et al., 1981; Nedwell and Rutter, 1994; Rutter and Nedwell, 1994). To illustrate how simple functional relationships like the Monod equation could lead to complex temperature dependencies, I will consider an analogy with enzyme kinetics. According to a Michaelis-Menten mechanism (Moore, 1972), population growth can be represented by an autocatalytic reaction scheme

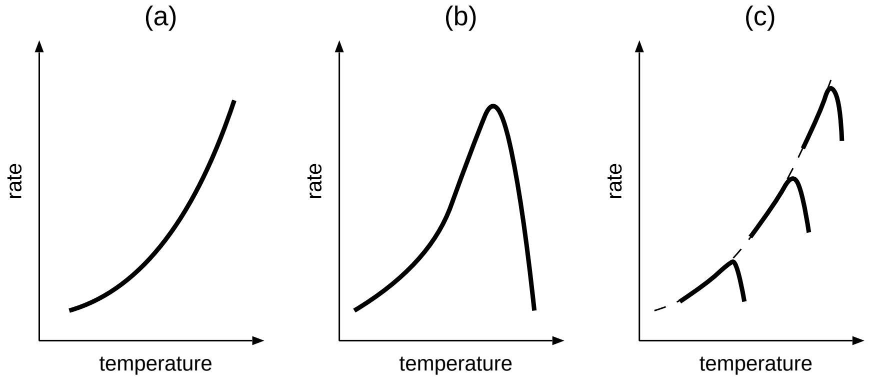


Figure 7.7: (a) The rates of simple chemical reactions increase monotonically with temperature. (b) The rates of enzyme based reactions increase with temperature until a maximum is attained. Further warming results in rapid loss of enzyme activity. Physiological rates should respond in similar ways. (c) The initial positive response to temperature of different species can be described by a common exponential envelope (dashed curve) (Eppley, 1972).

$$R + N \underset{k_2}{\overset{k_1}{\rightleftharpoons}} RN \overset{k_3}{\rightarrow} 2N \tag{7.21}$$

where R represents a substrate unit and N an autoreplicating enzyme; but for us ecologists they are resources and individuals respectively. The reversible reaction on the left corresponds to the process of resource consumption and the irreversible reaction on the right corresponds to reproduction. Consumption results in the formation of an intermediate complex RN (in analogy to the quota in the storage model) with rate constant k_1. RN can be destroyed with rate constant k_2 (analogous to excretion or respiratory losses), or it can be converted into a new individual with rate constant k_3 and the population doubles. By assuming a quasi steady state approximation for RN concentration, the specific growth rate of the population will be

$$\mu = \frac{rR}{H + R}$$

where

$$r = k_3,\ H = \frac{k_2 + k_3}{k_1}$$

are the maximum growth rate and the half-saturation constant respectively.

Using Arrhenius's law $k_i = A_i \exp\left(-E_i/k_b T\right)$ we can see that the maximum growth rate behaves according to the predictions of MTE. However, for the half-saturation constant

$$H = \frac{A_2 e^{-E_2/k_b T} + A_3 e^{-E_3/k_b T}}{A_1 e^{-E_1/k_b T}}$$

where small differences in E_i can result in the net increase, decrease or both with respect to temperature.

Temperature can influence community dynamics in different ways. Through the physiological rates, warming can shorten the time scales of ecological processes (Brown et al., 2004), and trigger stability changes in simple food chains (Vasseur and McCann, 2005). However, the net effects of temperature in multispecies community models can be very difficult to asses, because temperature changes many parameters simultaneously. Just in the Monod model, on the one hand variation in growth and mortality parameters influence the local stability of equilibria; on the other hand variation in the half saturation parameters determine resource requirements and thus the existence of equilibria.

7.4 CONCLUDING REMARKS

Multispecies competition models display very complex dynamics, with strong dependence on the initial conditions. However, despite the many degrees of freedom, it seems that a few rules of thumb can be used to predict the major features of the competitive dynamics. If these rules are robust to the underlying mechanistic assumptions (e.g. resource storage, resource classification, functional responses), we may be able to summarize the most important features of individual and population level interactions, simplify complexity, and make community ecology a more predictive science. It is still an open question if the complex dynamics induced by competition manifest under more realistic circumstances, in which the competitors belong to whole food webs. The first steps towards answering these issues were presented in this chapter.

As shown in the last sections, an integration of the Metabolic Theory of Ecology and multispecies resource competition theory is achievable and can be fruitful. Such integration reveals that consumer resource interactions, competition and ecological stoichiometry add significant amounts of variation in populations sizes, not explained by allometry and temperature. These exercises also highlight an important complication, which is that an important number of size and temperature dependent parameters are not biological rates, thus they cannot be adequately modeled by means of simple relationships as suggested by the Metabolic Theory of Ecology.

BIBLIOGRAPHY

Abrams, P. A. (1983). Arguments in favor of higher order interactions. *American Naturalist*, 121(6):887–891.

Agrawal, A. A. (2004). The Metabolic Theory of Ecology. *Ecology*, 85:1790–1791.

Ahlgren, G. (1987). Temperature functions in biology and their application to algal growth constans. *Oikos*, 49(2):177–190.

Aksnes, D. L. and Egge, J. K. (1991). A theoretical model for nutrient uptake in phytoplankton. *Marine Ecology Progress Series*, 70:65–72.

Allen, A. P., Brown, J. H., and Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297:1545–1548.

Armstrong, R. A. and McGehee, R. (1976). Coexistence of two competitors on one resource. *Journal of Theoretical Biology*, 56:499–502.

Armstrong, R. A. and McGehee, R. (1980). Competitive exclusion. *American Naturalist*, 115:151–170.

Arneodo, A., Coullet, P., Peyraud, J., and Tresser, C. (1982). Strange attractors in volterra equations for species in competition. *Journal of Mathematical Biology*, 14:153–157.

Ayala, F. J., Gilpin, M. E., and Ehrenfeld, J. G. (1973). Competition between species: theoretical models and experimental tests. *Theoretical Population Biology*, 4:331–356.

Baer, S. M., Li, B., and Smith, H. L. (2006). Multiple limit cycles in the standard model of three species competition for three essential resources. *Journal of Mathematical Biology*, 52:745–760.

Begon, M., Townsend, C. R., and Harper, J. L. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell, Malden, MA, 4 edition.

Benincà, E., Huisman, J., Heerkloss, R., Jöhnk, K. D., Branco, P., Van Nes, E. H., Scheffer, M., and Ellner, S. P. (2008). Chaos in a long-term experiment with a plankton community. *Nature*, 451:822–825.

Benincà, E., Jöhnk, K. D., Heerkloss, R., and Huisman, J. (2009). Coupled predator-prey oscillations in a chaotic food web. *Ecology Letters*, 12:1367–1378.

Bever, J. D. (1994). Feedback between plants and their soil communities in an old field community. *Ecology*, 75:1965–1977.

Bever, J. D. (1999). Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecology Letters*, 2:52–61.

Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist*, 157:465–473.

Bever, J. D., Westover, K. M., and Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, 85:561–573.

Bolker, B. M., Pacala, S. W., and Neuhauser, C. (2003). Spatial dynamics in model plant communities: what do we really know? *American Naturalist*, 162(2):135–148.

Bonanomi, G., Giannino, F., and Mazzoleni, S. (2005). Negative plant-soil feedback and species coexistence. *Oikos*, 111:311–321.

Bradley, D. J., Gilbert, G. S., and Martiny, J. B. H. (2008). Pathogens promote plant diversity through a compensatory response. *Ecology Letters*, 11:461–469.

Brauer, V. S., de Jonge, V. N., Buma, A. G. J., and Weissing, F. J. (2009). Does universal temperature dependence apply to communities? An experimental test using natural marine plankton assemblages. *Oikos*, 118:1102–1108.

Brose, U., Williams, R. J., and Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9:1228–1236.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 87:1771–1789.

Burmaster, D. E. (1979). The continuous culture of phytoplankton: mathematical equivalence among three steady-state models. *American Naturalist*, 113:123–134.

Buss, L. W. and Jackson, J. B. C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist*, 113:223.

Callaway, R. M., Thelen, G. C., Rodriguez, A., and Holben, W. E. (2004). Soil biota and exotic plant invasion. *Nature*, 427:731–733.

Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. (1985). Cascading trophic interactions and lake productivity. *BioScience*, 35:634–639.

Case, T. (2000). *An Illustrated Guide to Theoretical Ecology*. Oxford University Press.

Clodong, S. and Blasius, B. (2004). Chaos in a periodically forced chemostat with algal mortality. *Proceedings of the Royal Society of London B*, 271:1617–1624.

Cohen, J. E., T. Luczak, C. M. N., and Zhou, Z.-M. (1990). Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka-Volterra cascade model. *Proceedings of the Royal Society of London B*, 240:607–627.

Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290:699–700.

De Deyn, G. B., Raaijmakers, C., Zoomer, H. ., Berg, M. P., de Ruiter, P. ., Verhoef, H. A., Bezemer, T. M., and van der Putten, W. H. (2003). Soil invertebrate fauna enhances grassland succession and diversity. *Nature*, 422:711–713.

de Leenheer, P., Levin, S. A., and Sontag, E. D. Klausmeier, C. A. (2006). Global stability in a chemostat with multiple nutrients. *Journal of Mathematical Biology*, 52:419–438.

Di Toro, D. M. (1980). Applicability of cellular equilibrium and Monod theory to phytoplankton growth kinetics. *Ecological Modelling*, 8:201–218.

Droop, M. R. (1970). Vitamin B12 and marine ecology. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 20:629–636.

Droop, M. R. (1973). Some thoughts on nutrient limitation in algae. *Journal of Phycology*, 9:264–272.

Ducobu, H., Huisman, J., Jonker, R. R., and Mur, L. R. (1998). Competition between a prochlorophyte and a cyanobacterium under various phosphorous regimes: comparison with the Droop model. *Journal of Phycology*, 34:467–476.

Enquist, B. J., Brown, J. H., and West, G. B. (1998). Allometric scaling of plant energetics and population density. *Nature*, 395:163–165.

Eppinga, M. B., Rietkerk, M., Dekker, S. C., De Ruiter, P. C., and Van der Putten, W. H. (2006). Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. *Oikos*, 114:168–176.

Eppley, R. W. (1972). Temperature and phytoplankton growth in the sea. *Fishery bulletin*, 70:1063–1085.

Eppstein, M. J., Bever, J. D., and Molofsky, J. (2006). Spatio-temporal community dynamics induced by frequency dependent interactions. *Ecological Modelling*, 197:133–147.

Eppstein, M. J. and Molofsky, J. (2007). Invasiveness in plant communities with feedbacks. *Ecology Letters*, 10:253–263.

Ermentrout, B. (2002). *Simulating, Analyzing, and Animating Dynamical Systems: A Guide to XPPAUT for Researchers and Students*. Society for Industrial and Applied Mathematics, Philadelphia, 1st edition.

Fussmann, G. F., Ellner, S. P., and Hairston Jr., N. G. (2003). Evolution as a critical component of plankton dynamics. *Proceedings of the Royal Society of London B*, 270(1519):1015–1022.

Galassi, M., Davies, J., Theiler, J., Gough, B., Jungman, G., Booth, M., and Rossi, F. (2004). *Gnu Scientific Library: Reference Manual*. Network Theory Ltd., 1.6 edition.

Gause, G. F. (1934). *The Struggle for Existence*. Williams & Wilkins, Baltimore, MD.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293:2248–2251.

Gillooly, J. F., Charnov, E. L., West, G. B., Savage, V. M., and Brown, J. H. (2002). Effects of size and temperature on developmental time. *Nature*, 417:70–73.

Gilpin, M. E. (1975). Limit cycles and competition in communities. *American Naturalist*, 109:51–60.

Gilpin, M. E. and Justice, K. E. (1972). Reinterpretation of the invalidation of the principle of competitive exclusion. *Nature*, 236:273–301.

Grover, J. P. (1989). Influence of cell shape and size on algal competitive ability. *Journal of Phycology*, 25:402–405.

Grover, J. P. (1991). Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. *American Naturalist*, 138:811–835.

Grover, J. P. (1992). Constant- and variable-yield models of population growth: responses to environmental variability and implications for competition. *Journal of Theoretical Biology*, 158:409–428.

Grover, J. P. (1997). *Resource Competition*. Chapman & Hall, London.

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist*, 94:421–425.

Hall, E. K., Neuhauser, C., and Cotner, J. B. (2008). Toward a mechanistic understanding of how natural bacterial communities respond to changes in temperature in aquatic ecosystems. *ISME J*, 2:471–481.

Halliday, D. and Resnick, R. (1974). *Fundamentals of Physics*. Wiley International.

Hardin, G. (1960). The competitive exclusion principle. *Science*, 131:1292–1297.

Harper, J. L. (1977). *Plant Population Biology*. Academic Press, New York.

Hastings, A. and Powell, T. (1991). Chaos in a three-species food chain. *Ecology*, 72(3):896–903.

Hofbauer, J. and Sigmund, K. (1988). *The Theory of Evolution and Dynamical Systems*. Cambridge University Press.

Hofbauer, J. and So, J. W. H. (1994). Multiple limit cycles for three dimensional Lotka-Volterra equations. *Applied Mathematics Letters*, 7:65–70.

Holling, C. S. (1959). The components of predation as revealed by a study of small mammal predation predation of the european pine sawfly. *Canadian Entomologist*, 91:293–320.

Hsu, S.-B., Hubbell, S. P., and Waltman, P. (1977). A mathematical theory for single-nutrient competition in continuous cultures of micro-organims. *SIAM J. Appl. Math.*, 32(2):366–383.

Hu, S. and Zhang, D.-Y. (1993). The effects of initial population density on the competition for limiting nutrients in two freshwater algae. *Oecologia*, 96(4):569–574.

Huisman, J., Johansson, A. M., Folmer, E. O., and Weissing, F. J. (2001). Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecology Letters*, 4:408–411.

Huisman, J. and Weissing, F. J. (1999). Biodiversity of plankton by species oscillations and chaos. *Nature*, 402:407–410.

Huisman, J. and Weissing, F. J. (2001). Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology*, 82:2682–2695.

Huisman, J. and Weissing, F. J. (2002). Oscillations and chaos generated by competition for interactively essential resources. *Ecological Research*, 17:175–181.

Hutchinson, G. E. (1961). The paradox of the plankton. *American Naturalist*, 95:137–145.

Irwin, A. J., Finkel, Z. E., Schofield, O. M. E., and Falkowski, P. G. (2006). Scaling-up from nutrient physiology to the size-structure of phytoplankton communities. *Journal of Plankton Research*, 28:459–471.

Kerr, B., Riley, M. A., Feldman, M. W., and Bohannan, B. J. M. (2002). Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature*, 418:171–174.

Klausmeier, C. A., Litchman, E., Daufresne, T., and Levin, S. A. (2004a). Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature*, 249:171–174.

Klausmeier, C. A., Litchman, E., Daufresne, T., and Levin, S. A. (2008). Phytoplankton stoichiometry. *Ecological Research*, 23:479–485.

Klausmeier, C. A., Litchman, E., and Levin, S. A. (2004b). Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnology and Oceanography*, 49:1463–1470.

Klironomos, J. N. (2003). Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, 84:2292–2301.

Kooijman, S. A. L. M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, 2nd edition.

Kulmatiski, A., Beard, K. H., Stevens, J. R., and Cobbold, S. M. (2008). Plant-soil feedbacks: a meta-analytical review. *Ecology Letters*, 11:980–992.

Laird, R. A. and Schamp, B. S. (2006). Competitive intransitivity promotes species coexistence. *American Naturalist*, 168:182–193.

Lange, K. and Oyarzun, F. J. (1992). The attractiveness of the Droop equations. *Mathematical Biosciences*, 111:261–278.

Legovic, T. and Cruzado, A. (1997). A model of phytoplankton growth on multiple nutrients based on the Michaelis-Menten-Monod uptake, Droop's growth and Liebig's law. *Ecological Modelling*, 99:19–31.

León, J. A. and Tumpson, D. (1975). Competition between two species for two complementary or substitutable resources. *Journal of Theoretical Biology*, 50:185–201.

Li, B. (2001). Periodic coexistence in the chemostat with three species competing for three essential resources. *Mathematical Biosciences*, 174:27–40.

Li, B. and Smith, H. L. (2003). Periodic coexistence of four species competing for three essential resources. *Mathematical Biosciences*, 184:115–135.

Li, B. and Smith, H. L. (2007). Global dynamics of microbial competition for two resources with internal storage. *Journal of Mathematical Biology*, 55:481–515.

Loeuille, N. and Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the USA*, 102:5761–5766.

Loeuille, N. and Loreau, M. (2006). Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecology Letters*, 9:171–178.

Lopez-Urrutia, A., San Martin, E., Harris, R. P., and Irigoien, X. (2006). Scaling the metabolic balance of the oceans. *Proceedings of the National Academy of Sciences of the USA*, 103:8739–8744.

Lotka, A. J. (1925). *Elements of Physical Biology*. Williams & Wilkins Company, Baltimore.

MacArthur, R. H. (1969). Species packing, and what interspecies competition minimizes. *Proceedings of the National Academy of Sciences of the USA*, 64:1369–1371.

MacArthur, R. H. (1970). Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, 1:1–11.

MacArthur, R. H. and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Martinez, N. D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, 61(4):367–392.

May, R. M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton Landmarks in Biology. Princeton University Press, Princeton.

May, R. M. and Leonard, W. J. (1975). Nonlinear aspects of competition between three species. *SIAM Journal of Applied Mathematics*, 29:243–453.

Mills, K. E. and Bever, J. D. (1998). Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. *Ecology*, 79:1595–1601.

Monod, J. (1950). La technique de culture continue, theorie et applications. *Annales d'Institute Pasteur*, 79:390–410.

Moore, W. J. (1972). *Physical Chemistry*. Prentice Hall, 5th edition.

Morel, F. (1987). Kinetics of nutrient uptake and growth in phytoplankton. *Journal of Phycology*, 23:137–150.

Morin, P. J., Lawler, S. P., and Johnson, E. A. (1988). Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology*, 69:1401–1409.

Murray, J. D. (2002). *Mathematical Biology I: An Introduction*, volume 17 of *Interdisciplinary Applied Mathematics*. Springer, 3 edition.

Nabi, I. (1981). On the Tendencies of Motion. *Science and Nature*, 4:62–66.

Nedwell, D. B. and Rutter, M. (1994). Influence of temperature on growth rate and competition between two psychrotolerant Antarctic bacteria: low temperature diminishes affinity for substrate uptake. *Applied and Environmental Microbiology*, 60:1984–1992.

Olff, H., Hoorens, B., de Goede, R. G. M., van der Putten, W. H., and Gleichman, J. M. (2000). Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. *Oecologia*, 125:45–54.

Oyarzun, F. J. and Lange, K. (1994). The attractiveness of the Droop equations II. Generic uptake and growth functions. *Mathematical Biosciences*, 121:127–139.

Passarge, J., Suzanne, H., Escher, M., and Huisman, J. (2006). Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? *Ecological Monographs*, 76:57–72.

Redfield, A. C. (1958). The biological control of chemical factors in the environment. *American Scientist*, 46:205–221.

Revilla, T. A. and Weissing, F. J. (2008). Nonequilibrium coexistence in a competition model with nutrient storage. *Ecology*, 89:865–877.

Reynolds, H. L., Packer, A., Bever, J. D., and Clay, K. (2003). Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology*, 84:2281–2291.

Rosenzweig, M. L. (1971). The paradox of enrichment. *Science*, 171:385–387.

Rosenzweig, M. L. and MacArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *American Naturalist*, 97:209–223.

Rutter, M. and Nedwell, D. B. (1994). Influence of changing temperature on growth rate and competition between two psychrotolerant Antarctic bacteria: competition and survival in non-steady-state temperature environments. *Applied and Environmental Microbiology*, 60:1993–2002.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., and Charnov, E. L. (2004). Effects of body size and temperature on population growth. *American Naturalist*, 163(3):429–441.

Schippers, P., Verschoor, A. M., Vos, M., and Mooij, W. M. (2001). Does "supersaturated coexistence" resolve the "paradox of the plankton"? *Ecology Letters*, 4:404–407.

Schoener, T. W. (1976). Alternatives to Lotka-Volterra competition: models of intermediate complexity. *Theoretical Population Biology*, 10:309–333.

Sinervo, B. and Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380(rock-paper-scissors, lizards, selection):240–243.

Smale, S. (1976). On the differential equations of species in competition. *Journal of Mathematical Biology*, 3:5–7.

Smith, H. L. (1995). *Monotone Dynamical Systems*. American Mathematical Society, Providence.

Smith, H. L. and Waltman, P. (1994). Competition for a single limiting resource in continuous culture: the variable-yield model. *SIAM Journal of Applied Mathematics*, 54:1113–1131.

Soler, R., Bezemer, T. M., Van Der Putten, W. I. M. H., Vet, L. E. M., and Harvey, J. A. (2005). Root herbivore effects on above-ground herbivore, parasitoid and hyperparasitoid performance via changes in plant quality. *Journal of Animal Ecology*, 74:1121–1130.

Sterner, R. W. and Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.

Strang, G. (1988). *Linear Algebra and its Applications*. Thomson Learning, 3 edition.

Strobeck, C. (1973). N species competition. *Ecology*, 54:650–654.

Thingstad, T. F. (1987). Utilization of N,P, and organic C by heterotrophic bacteria. I. Outline of a chemostat theory with a consistent concept of 'maintenance' metabolism. *Marine Ecology Progress Series*, 35:99–109.

Tilman, D. (1977). Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*, 58:338–348.

Tilman, D. (1980). Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist*, 116:362–393.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton.

Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press.

Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C., and Lehman, C. (2004). Does metabolic theory apply to community ecology? it's a matter of scale. *Ecology*, 85:1797–1799.

Tilman, D., Mattson, M., and Langer, S. (1981). Competition and nutrient kinetics along a temperature gradient: An experimental test of a mechanistic approach to niche theory. *Limnology and Oceanography*, 26:1020–1033.

Turpin, D. H. (1988). Physiological mechanisms in phytoplankton resource competition. In Sandgren, C. D., editor, *Growth and Reproductive Strategies of Freshwater Phytoplankton*, chapter 8, pages 316–368. Cambridge University Press, Cambridge, New York.

Umbanhowar, J. and McCann, K. S. (2005). Simple rules for the coexistence and competitive dominance of plants mediated by mycorrhizal fungi. *Ecology Letters*, 8:247–252.

van der Heijden, M. G. A., Bardgett, R. D., and van Straalen, N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, 11:296–310.

van der Heijden, M. G. A., Boller, T., Wiemken, A., and Sanders, I. R. (1998). Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology*, 79(6):2082–2091.

van der Heijden, M. G. A., Wiemken, A., and Sanders, I. R. (2003). Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytologist*, 157:569–578.

van der Putten, W. H., Bardgett, R. D., de Ruiter, P. C., Hol, W. H., Meyer, K. M., Bezemer, T. M., Bradford, M. A., Christensen, S., Eppinga, M. B., Fukami, T., Hemerik, L., Molofsky, J., Schädler, M., Scherber, C., Strauss, S. Y., and Vos, M. Wardle, D. A. (2009). Empirical and theoretical challenges in aboveground-belowground ecology. *Oecologia*. online.

van der Putten, W. H. and Van der Stoel, C. D. (1998). Plant parasitic nematodes and spatio-temporal variation in natural vegetation. *Applied Soil Ecology*, 10:253–262.

van der Putten, W. H., Van Dijk, C., and Peters, B. A. M. (1993). Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, 362(6415):53–56.

van der Putten, W. H., Vet, L. E. M., Harvey, J. A., and Wäckers, F. (2001). Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology and Evolution*, 16:547–554.

Vandermeer, J. (1993). Loose coupling of predator-prey cycles: entrainment, chaos, and intermitency in the classic Macarthur consumer-resource equations. *American Naturalist*, 141:687–716.

Vasseur, D. and McCann, K. (2005). Mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *American Naturalist*, 166:184–198.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature*, 118:558–560.

Von Liebig, J. (1840). *Die Organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie*. Friedrich Vieweg, Braunschweig.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setala, H., van der Putten, W. H., and Wall, D. H. (2004). Ecological Linkages Between Aboveground and Belowground Biota. *Science*, 304:1629–1633.

Weinstein, E. W. (2003). *CRC Concise Encyclopedia of Mathematics*. Chapman & Hall/CRC, 2 edition.

Weissing, F. J. (1991). Evolutionary Stability and Dynamic Stability in a Class of Evolutionary Normal Form Games. In Selten, R., editor, *Game Equilibrium Models I. Evolution and Game Dynamics*, pages 27–97. Springer Verlag.

Williams, R. J. and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404:180–183.

Yeates, G. W. (1999). Effects of plants on nematode community structure. *Annual Review of Phytopathology*, 37:127–149.

Zeeman, M. L. (1990). Hopf bifurcations in competitive three-dimensional Lotka-Volterra systems. Technical Report 622, IMA Preprint Series.

Zeeman, M. L. (1993). Hopf bifurcations in competitive three-dimensional Lotka-Volterra systems. *Dynamics and Stability of Systems*, 8:189–216.

Zhang, D. (1991). Exploitation competition and coexistence of two plant populations on a number of growth-limiting resources. *Ecological Modelling*, 53:263–279.