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 extent 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 Huismann 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-

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satisfaction 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 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 \(Q_{ji}\)

\[
\begin{align*}
\frac{dN_i}{dt} &= N_i(\mu_i(Q_{1i}, Q_{2i}, Q_{3i}) - m_i) \quad (4.1a) \\
\frac{dQ_{ji}}{dt} &= f_{ji}(R_j) - \mu_i(Q_{1i}, Q_{2i}, Q_{3i})Q_{ji} \quad (4.1b) \\
\frac{dR_j}{dt} &= \phi_j(R_j) - \sum_{i=1}^{3} f_{ji}(R_j)N_i \quad (4.1c)
\end{align*}
\]

\(i, j = 1, 2, 3\)

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.
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 $f_{ji}(R_j)$

$$f_{ji}(R_j) = \frac{v_{ji}R_j}{K_{ji} + R_j}$$

The mechanistic justification of this equation is similar to Holling’s type II functional response (Aksnes and Egge, 1991), being $v_{ji}$ 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

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

where the resource supply point $S = (S_1, \ldots, S_3)$ 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 $\mu_i = \mu_{i1}(Q_{1i}^*) = m_i$, this quota requirement is

$$Q_{ji}^* = \frac{r_i q_{ji}}{r_i - m_i}$$

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 $i$

$$R_{ji}^* = \frac{K_{ji}m_i Q_{ji}^*}{v_{ji} - m_i Q_{ji}^*} = \frac{K_{ji}m_i r_i q_{ji}}{v_{ji}(r_i - m_i) - m_i r_i q_{ji}}$$

The three planes $R_1 = R_{1i}^*$, $R_2 = R_{2i}^*$, $R_3 = R_{3i}^*$ with $R_j \geq R_{ji}^*$ 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)
\[ \begin{align*}
\phi_1(R_1) &= f_{11}(R_1)N_1 + f_{12}(R_1)N_2 + f_{13}(R_1)N_3 \\
\phi_2(R_3) &= f_{21}(R_1)N_1 + f_{22}(R_1)N_2 + f_{23}(R_1)N_3 \\
\phi_3(R_3) &= f_{31}(R_1)N_1 + f_{32}(R_1)N_2 + f_{33}(R_1)N_3
\end{align*} \]

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

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

11. The resource turnover vector \( \Phi = (\phi_1, \phi_2, \phi_3) \) is parallel and opposite to the total consumption vector \( \sum f_i N_i \) at the ZNGI of the species whose equilibrium is considered, being \( f_i = (f_{1i}, f_{2i}, f_{3i}) \) 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 \( R = (R_1, R_2, R_3) \) lies in one of the planar faces of \( i \)'s ZNGI; thus \( R_j = R_{ji}^* \) for the limiting resource, and \( R_k > R_{ki}^* \) for the non-limiting resources \( k \neq j \). The resource turnover vector \( \Phi \) 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, \( R = (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3) \). This is shown for the \( R_1R_2 \) plane in Figure 2.1A. The equilibrium density of the monoculture \( \tilde{N}_i \) satisfies all equations in (4.7) for \( N_{ji} = 0 \)

\[ \phi_j(\tilde{R}_j) = f_{ji}(\tilde{R}_j)\tilde{N}_i \]  

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

\[ \tilde{N}_i = \min\left( \frac{\phi_1(R_{1i}^*)}{f_{1i}(R_{1i}^*)}, \frac{\phi_2(R_{2i}^*)}{f_{2i}(R_{2i}^*)}, \frac{\phi_3(R_{3i}^*)}{f_{3i}(R_{3i}^*)} \right) \]

Substituting \( \tilde{N}_i \) in the equations corresponding to non-limiting resources of (4.8) we fully specify the resource level point \( \tilde{R} = (\tilde{R}_1, \tilde{R}_2, \tilde{R}_3) \), and substituting the \( \tilde{R}_j \) in equation (4.1b) with \( \tilde{Q}_{ji} = 0 \) 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 $\Phi$ vector points to the resource supply point $S$; and the slope of the consumption vector $f_i$ varies along the ZNGI, it aligns with the ZNGI as resources increase. The resource equilibrium level $\tilde{R}$ 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 form 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 $f_2$ is higher than the slope of $f_1$ (C). When each species consume comparatively less of the resource that limits its own growth the equilibrium is unstable, here when the slope of $f_2$ is smaller than the slope of $f_1$. 

\[ \mu_i - m_i > 0 \]
\[ \mu_i - m_i < 0 \]
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

\[
R_{11}^* > R_{12}^* > R_{13}^* \\
R_{22}^* > R_{23}^* > R_{21}^* \\
R_{33}^* > R_{31}^* > R_{32}^* 
\]

(4.10)

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

1. \((R_1 = R_{11}^*, R_2 = R_{22}^*, R_3 > R_{31}^*) \cup (R_1 > R_{11}^*, R_2 = R_{22}^*, R_3 = R_{31}^*)\) for species 1 limited by resource 1 or 3, and species 2 limited by resource 2

2. \((R_1 = R_{11}^*, R_2 > R_{23}^*, R_3 = R_{33}^*) \cup (R_1 = R_{11}^*, R_2 = R_{23}^*, R_3 > R_{33}^*)\) for species 1 limited by resource 1, and species 3 limited by resource 2 or 3

3. \((R_1 > R_{12}^*, R_2 = R_{22}^*, R_3 = R_{33}^*) \cup (R_1 = R_{12}^*, R_2 > R_{22}^*, R_3 = R_{33}^*)\) 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 \(R_1R_2\) 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 \(v_{ji}, K_{ji}, q_{ji}\), 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

\[
\begin{align*}
R_{11}^* &= R_{22}^* = R_{33}^* = A \\
R_{12}^* &= R_{23}^* = R_{31}^* = B \\
R_{13}^* &= R_{21}^* = R_{32}^* = C
\end{align*}
\] (4.11)

\[A > B > C\] (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

\[
\begin{bmatrix}
    v_{11} & v_{12} & v_{13} \\
    v_{21} & v_{22} & v_{23} \\
    v_{31} & v_{32} & v_{33}
\end{bmatrix} =
\begin{bmatrix}
    u & v & w \\
    w & u & v \\
    v & w & u
\end{bmatrix}
\] (4.13)

where

\[0 < u < 1, \ 0 < v < 1, \ w = 1 - u\] (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 \(j\)).
4.3 Analysis and Results

Figure 4.2: Bifurcation plots for species 1. (A) For $v = 0.25$ the three-species equilibrium displays a sub-critical Hopf bifurcation and unstable periodic orbits. (B) For $v = 0.75$ the periodic branch arising from the bifurcation changes from unstable to stable, see Fig. 4.4 for details. Spi(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

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

(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 by 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 of 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
4.3 Analysis and Results

Figure 4.3: Competitive oscillations. (A) For $u = 0.47$ in Fig. 4.2 A 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 $N_1 N_2 N_3$ 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 $K_{ij} = K$ the resource equilibrium conditions (4.7) for each case are

$$X_A = uN_1 + vN_2 + wN_3$$
$$X_C = wN_1 + uN_2 + vN_3$$
$$X_B = vN_1 + wN_2 + uN_3$$

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

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
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 4.3 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 4.4: Enlarged portion of Figure 4.3B 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.
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. 4.3B). 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 $1 \to 2 \to 3 \to 1$. 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 $R_j = \Lambda$

$$f_{ji}(\Lambda) = \frac{v_{ji}A}{K_{ji} + A} = \frac{xA}{K + A}$$

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

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

(4.16)

satisfying the same consumption rate $f_{ji}(\Lambda)$. Indeed, there is an infinite number of ways to pick $(v_{ji}, K_{ji})$ resulting in the same three-species equilibrium configuration for consumption patterns $f_{ji}(\Lambda)$, resources $\tilde{R}_1 = \tilde{R}_2 = \tilde{R}_3 = \Lambda$ and densities $\tilde{N}_1 = \tilde{N}_2 = \tilde{N}_3 = \tilde{N}$ as before. Sampling $K_{ji}$ from a uniform random distribution in the interval $[0, 2\Lambda]$, the corresponding $v_{ji}$ have means $\bar{v}_{11} = \bar{v}_{22} = \bar{v}_{33} = u, \bar{v}_{12} = \bar{v}_{31} = \bar{v}_{31} = v$ and $\bar{v}_{13} = \bar{v}_{21} = \bar{v}_{32} = w$ ($w = 1 - u$). 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 $v_{ji}$ 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 $1 \rightarrow 3 \rightarrow 2 \rightarrow 1$ 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 $v_{ji}$ 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 $1 \rightarrow 2 \rightarrow 3 \rightarrow 1$. Since $v_{ji}$ and $K_{ji}$ are variable, so 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.
4.3 Analysis and Results

A

$u=0.47 \quad v=0.25$

B

$u=0.58 \quad v=0.75$

Figure 4.6: Simulations with $K_{ji}$ sampled from the uniform distribution $[0,0.01]$ and $v_{ji}$ 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 $v_{ji}$ 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 $v_{ji}$ 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 $v_{11}, v_{22}, v_{33}$ (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 $v_{12}, v_{23}, v_{31}$ (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
$v_{ji}$ 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 ex-
pected 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 in-
terdependency 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 equilib-
rium 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 ac-
curate prediction of competitive outcomes a difficult task, even when the number of species
is as 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 hete-
roclinic 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

\[
\begin{align*}
t' &= Dt, \quad R'_j = R_j/S, \quad Q'_{ji} = Q_{ji}/q, \quad N'_i = qN_i/S \\
\end{align*}
\]

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

\[
\begin{align*}
\frac{dN'_i}{dt} &= N'_i(\mu'_i - m') \\
\frac{dQ'_{ji}}{dt} &= v'_j g(R'_j) - \mu'_i Q'_{ji} \\
\frac{dR'_j}{dt} &= (1 - R'_j) - \sum_{i=1}^{n} v'_j g(R_j) N'_i \\
\mu'_i &= r' \min_j \left(1 - \frac{q'_{ji}}{Q'_{ji}}\right), \quad g(R'_j) = \frac{R'_j}{K' + R'_j}
\end{align*}
\]

with parameters

\[
\begin{align*}
r' &= r/D, \quad m' = m/D, \quad q'_{ji} = q_{ji}/q, \quad v'_j = v_{ji}/Dq, \quad K' = K/S
\end{align*}
\]

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

Appendix: Parametrization for bifurcation analysis
Appendix: Parametrization for bifurcation analysis

\[
\{R_{ji}\} = \begin{bmatrix} A & B & C \\ C & A & B \\ B & C & A \end{bmatrix}, \{v_{ji}\} = \begin{bmatrix} u & v & w \\ w & u & v \\ v & w & u \end{bmatrix}
\]

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 \( \hat{N}_i = (1-A)/(g(A)(1+v)) = 0.84/(1+v) \). \( \hat{R}_i \) 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

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Appendix: Parametrization for bifurcation analysis

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 ---
Appendix: Parametrization for bifurcation analysis