

Oscillations and chaos generated by competition for interactively essential resources

JEF HUISMAN^{1*} AND FRANZ J. WEISSING²

¹*Aquatic Microbiology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands and*

²*Center for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

Recent theory shows that: (i) competition between multiple species for multiple resources may generate oscillations and chaotic fluctuations in species abundances; and (ii) these non-equilibrium dynamics may favor a high biodiversity. These findings were based on Liebig's Law of the Minimum, which assumes that each species is limited by only one resource at a time. In reality, however, resources can have interactive effects on growth. Here, we investigate whether competition for interactively essential resources may generate oscillations and chaos as well. Our results show that competition for interactively essential resources may, indeed, exhibit dynamics of similar complexity. This illustrates the wide potential for non-equilibrium dynamics generated by multispecies competition, and suggests that competitive chaos may occur on a wide variety of different resource types.

Key words: biodiversity; chaos; coexistence; competition model; resource competition.

INTRODUCTION

In 1887, on the occasion of his 60th birthday, King Oscar II of Sweden organized a scientific contest to address an intriguing question: Is the solar system stable? Do the planets of our solar system remain in the orbits they are currently occupying, will they slowly spiral towards the sun, or will they gradually wander off in space? Poincaré, a French mathematician, was inspired by the problem. He made a number of discoveries that drastically changed our understanding of dynamical systems. In particular, Poincaré found that the dynamics of two bodies encircling each other is well behaved, but that the dynamics of three, or more, interacting bodies is so entangled that their trajectories may become irregular and unpredictable (Poincaré 1892). Poincaré's pivotal con-

tributions to the so-called 'three-body problem' marked the first steps in chaos theory.

Like astronomers, biologists are often confronted with complex interactions between different entities. Yet, most competition theory developed by theoretical biologists over the past century was concerned with competition between two species only (e.g. Lotka 1932; Gause 1934). Textbook theory predicts that competition between two species generally leads to a stable outcome where, depending on the circumstances, either one species survives or else both species coexist (Tilman 1982). In sharp contrast to the emphasis of biological theory on competition between two species, the biodiversity in natural communities is generally overwhelming. A single milliliter of water or a single microgram of soil may contain hundreds of different species. It is questionable whether the simple rules deduced from the two-species theory will be generally applicable to competition in such highly diverse communities. Recently, we followed an earlier trail (Gilpin 1975; May & Leonard 1975; Smale 1976) indicating that multispecies competition can, indeed, be considerably more complex than

*Author to whom correspondence should be addressed. Email: jef.huisman@science.uva.nl

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two-species competition. Model simulations revealed that multispecies competition for three, or more, resources may lead to oscillations and chaotic fluctuations in species abundances (Huisman & Weissing 1999, 2001a). Mathematical proofs support these simulation results (Huisman & Weissing 2001b; Li 2001; Smith & Li 2001). These non-equilibrium dynamics, in turn, may allow the coexistence of many species on a few limiting resources. Hence, competitively induced non-equilibrium dynamics, ‘competitive chaos’ in short, may provide a potential explanation for the biodiversity of many communities (Huisman & Weissing 1999, 2000; Huisman *et al.* 2001).

The results of Huisman and Weissing (1999, 2000, 2001a, 2001b) were based on one specific class of competition models. More specifically, the model assumed Von Liebig’s (1840) Law of the Minimum. According to Liebig’s Law, the growth rate of a species is fully determined by the resource that is most limiting. Resources that obey Liebig’s Law are frequently referred to as perfectly essential resources (*sensu* Tilman 1982). One may criticize Liebig’s Law on both biological and mathematical grounds. From a biological point of view, it is known that several essential resources do not follow Liebig’s Law but show interactive effects. Such resources are called interactively essential resources (*sensu* Tilman 1982). Iron and nitrogen are good examples. Iron is a component of the enzymes nitrate reductase and nitrite reductase (Timmermans *et al.* 1994). As a consequence, the combination of iron and nitrate does not obey Liebig’s Law but iron and nitrate have interactive effects on phytoplankton growth (Price *et al.* 1991; Maldonado & Price 1996). In fact, many resource combinations might have interactive effects at the physiological level. From a mathematical point of view, the minimum operator commonly used to model Liebig’s Law implies that the growth rate of a species is not a continuously differentiable function of resource availability. One might argue that this mathematical feature introduces model artefacts and, thus, that results obtained with Liebig’s Law might not be robust.

For these reasons, the present paper investigates whether our previous findings on ‘competitive chaos’ are restricted to perfectly essential resources, as in Liebig’s Law, or whether these non-

equilibrium dynamics occur on interactively essential resources as well.

METHODS

The model

We consider a number of n species competing for k resources. Let N_i denote the abundance of species i , and let R_j denote the availability of resource j . The dynamics of the species and resources are described by the following competition model (León & Tumpson 1975; Tilman 1982; Huisman & Weissing 1999):

$$\frac{dN_i}{dt} = N_i(\mu_i(R_1, \dots, R_k) - m_i) \quad i = 1, \dots, n \quad (1a)$$

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

Here $\mu_i(R_1, \dots, R_k)$ is the specific growth rate of species i as a function of resource availabilities; m_i is the specific mortality rate of species i ; D is the system’s turnover rate; S_j is the supply concentration of resource j ; and c_{ji} is the content of resource j in species i .

Previously, we considered perfectly essential resources. That is, we assumed that the specific growth rates in Equations 1a and 1b follow a combination of Monod’s (1950) equation and Von Liebig’s (1840) Law of the Minimum (Huisman & Weissing 1999, 2001a, b):

$$\mu_i(R_1, \dots, R_k) = r_i \text{MIN} \left(\frac{R_1}{K_{1i} + R_1}, \dots, \frac{R_k}{K_{ki} + R_k} \right) \quad (2)$$

where r_i is the maximum specific growth rate of species i , K_{ji} is the half-saturation constant for resource j of species i , and MIN is the minimum operator.

In the present paper, we consider interactively essential resources. More specifically, we assume that the specific growth rates are determined by the product of several Monod terms:

$$\mu_i(R_1, \dots, R_k) = r_i \prod_{j=1}^k \frac{R_j}{K_{ji} + R_j} \quad (3)$$

We will summarize the competitive ability of a species i for a given resource j by its resource requirement R_{ji}^* (Tilman 1982). R_{ji}^* is defined as the availability of resource j at which species i remains stationary, assuming that all other resources are in ample supply. That is, according to equations 1a and 3,

$$R_{ji}^* = \frac{m_i K_{ji}}{r_i - m_i}. \quad (4)$$

This shows that, all else being equal, a low half-saturation constant for a particular resource implies a low R_{ji}^* . We will say that the species with lowest R_{ji}^* for a particular resource is the best competitor for that resource (Armstrong & McGehee 1980; Tilman 1982). We will say that a species consumes most of a resource if it has a higher content of this resource than all other species.

The key difference between perfectly essential resources and interactively essential resources can be visualized by means of zero isoclines (Tilman 1982). The zero isocline of a species i , plotted in resource space, indicates all resource availabilities at which species i remains stationary (i.e. $dN_i/dt = 0$). For resource combinations above and to the right of its zero isocline, this species will increase. For resource combinations below and to the left of its zero isocline, this species will decrease. Zero isoclines based on perfectly essential resources have a right angle corner, which indicates a sudden switch from limitation by one resource to limitation by another resource (Fig. 1a). In contrast, zero isoclines based on interactively essential resources have a rounded corner, which indicates a smooth transition from limitation by one resource to limitation by another resource (Fig. 1b).

RESULTS

Competitive oscillations

Consider three species competing for three resources. Even with three species only, it is a tremendous task to investigate all potential parameter combinations in a systematic manner. We, therefore, parametrized the model for phytoplankton species, with a timescale expressed in days (d). To keep the model parametrization as simple as

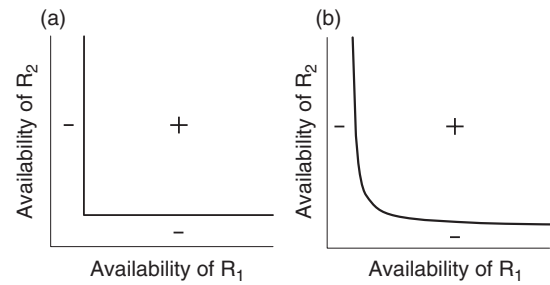


Fig. 1. Zero isoclines for (a) perfectly essential resources and (b) interactively essential resources. Above and to the right of the zero isocline, net growth is positive. Below and to the left of the zero isocline, net growth is negative.

possible, we assume that all species have a maximal specific growth rate of $r_i = 1 \text{ d}^{-1}$, and a specific mortality rate of $m_i = D = 0.25 \text{ d}^{-1}$. Furthermore, we assume that each of the resources has a resource supply concentration of $S_j = 10 \mu\text{mol l}^{-1}$. These parameter values are within the range of typical values for phytoplankton species grown in chemostats (De Nobel *et al.* 1997; Ducobu *et al.* 1998; Huisman *et al.* 1999).

The half-saturation constants, K_{ji} , and resource contents, c_{ji} , are given in matrices \mathbf{K} and \mathbf{C} , respectively. Different columns in these matrices represent different species, and different rows represent different resources. Assuming three species and three resources we consider the following \mathbf{K} matrix and \mathbf{C} matrix.

$$\mathbf{K} = \begin{pmatrix} 1 & \alpha & 0.25 \\ 0.25 & 1 & \alpha \\ \alpha & 0.25 & 1 \end{pmatrix},$$

$$\mathbf{C} = \begin{pmatrix} 0.10 & 0.20 & 0.15 \\ 0.15 & 0.10 & 0.20 \\ 0.20 & 0.15 & 0.10 \end{pmatrix}.$$

According to the \mathbf{C} matrix, species 2 consumes most of resource 1, species 3 consumes most of resource 2, and species 1 consumes most of resource 3. Recall from equation 4 that as we assumed that all species have similar r_i and similar m_i , a species with a low K_{ji} for a particular resource is a strong competitor for that resource. Thus, we can distinguish a number of different scenarios, depending on the value of α in the \mathbf{K} matrix:

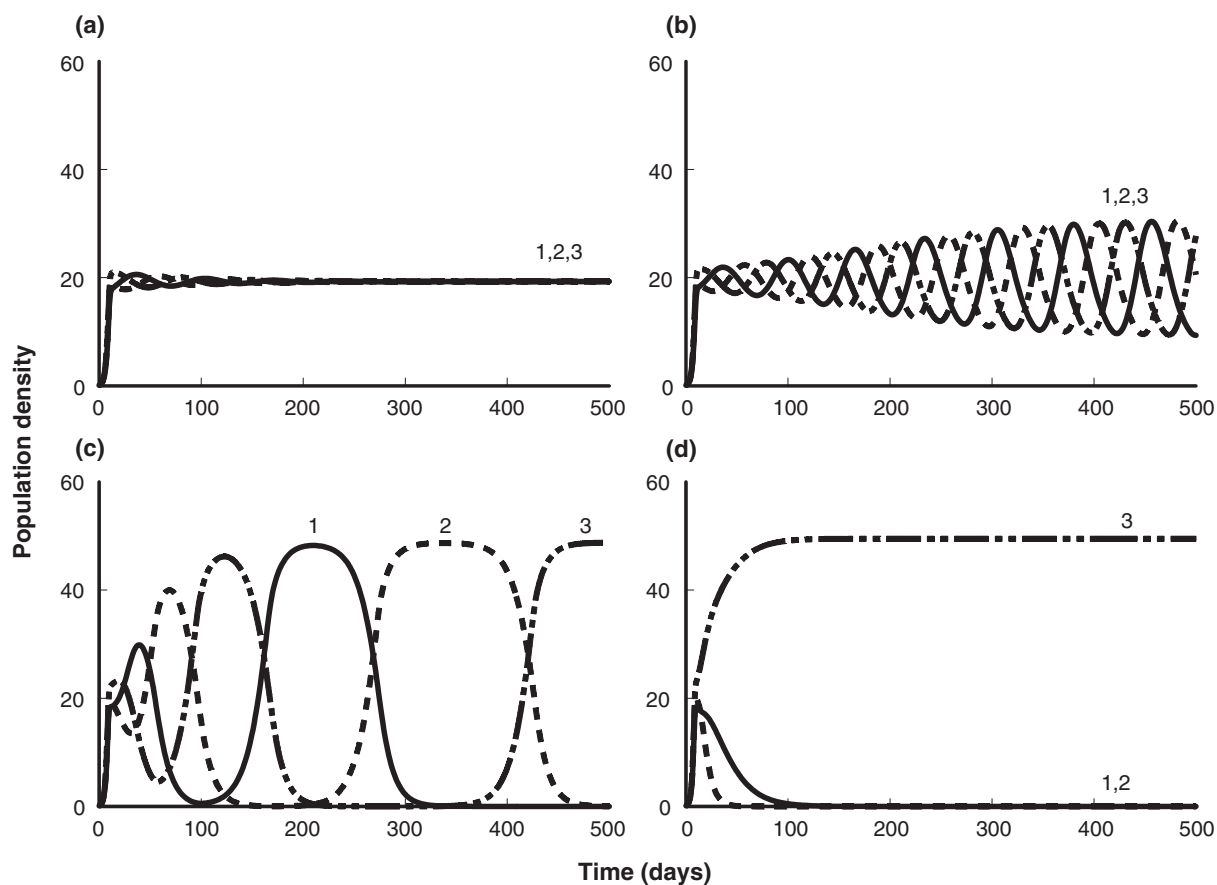


Fig. 2. Competition between three species for three interactively essential resources (1,2,3). (a) Stable coexistence ($\alpha = 1.2$), (b) limit cycle ($\alpha = 0.9$), (c) heteroclinic cycle ($\alpha = 0.5$), (d) competitive exclusion where the winner depends on the initial conditions ($\alpha = 0.2$). Initial conditions: $R_i(0) = S_i$, $N_1(0) = 0.11$, $N_2(0) = 0.12$, $N_3(0) = 0.13$.

Assume $\alpha > 1$ gives a scenario in which each species consumes most of the resource for which it is the worst competitor. In this case, our simulations reveal that competition leads to stable coexistence (Fig. 2a). It is interesting to note from Fig. 2a that the coexistence equilibrium can be approached by means of damped oscillations.

If $1 > \alpha > 0.25$, then each species consumes most of the resource for which it is the intermediate competitor. In this case, most of our simulations reveal that competition generates species oscillations, although some simulations lead to competitive exclusion. The oscillations can be in the form of either limit cycles or heteroclinic cycles. More precisely, if $1 > \alpha > 0.60$, then our simulations indicate that oscillations are in the form of limit cycles (Fig. 2b). Essentially, limit cycles are oscillations with a constant frequency. If $0.60 > \alpha > 0.30$, then our simulations indicate

that oscillations are in the form of heteroclinic cycles (Fig. 2c). Heteroclinic cycles are oscillations that gradually slow down. That is, the cycle period lengthens, but the cyclic movement never stops. If $0.30 > \alpha > 0.25$, then our simulations show that competition leads to competitive exclusion with a winner that depends on the initial conditions.

If $\alpha < 0.25$, then each species consumes most of the resource for which it is the best competitor. In this case, simulations reveal that competition leads to competitive exclusion with a winner that depends on the initial conditions (Fig. 2d).

Non-equilibrium coexistence

It is well known for competition models like equation 1 that, at equilibrium, the number of coexisting species cannot exceed the number of

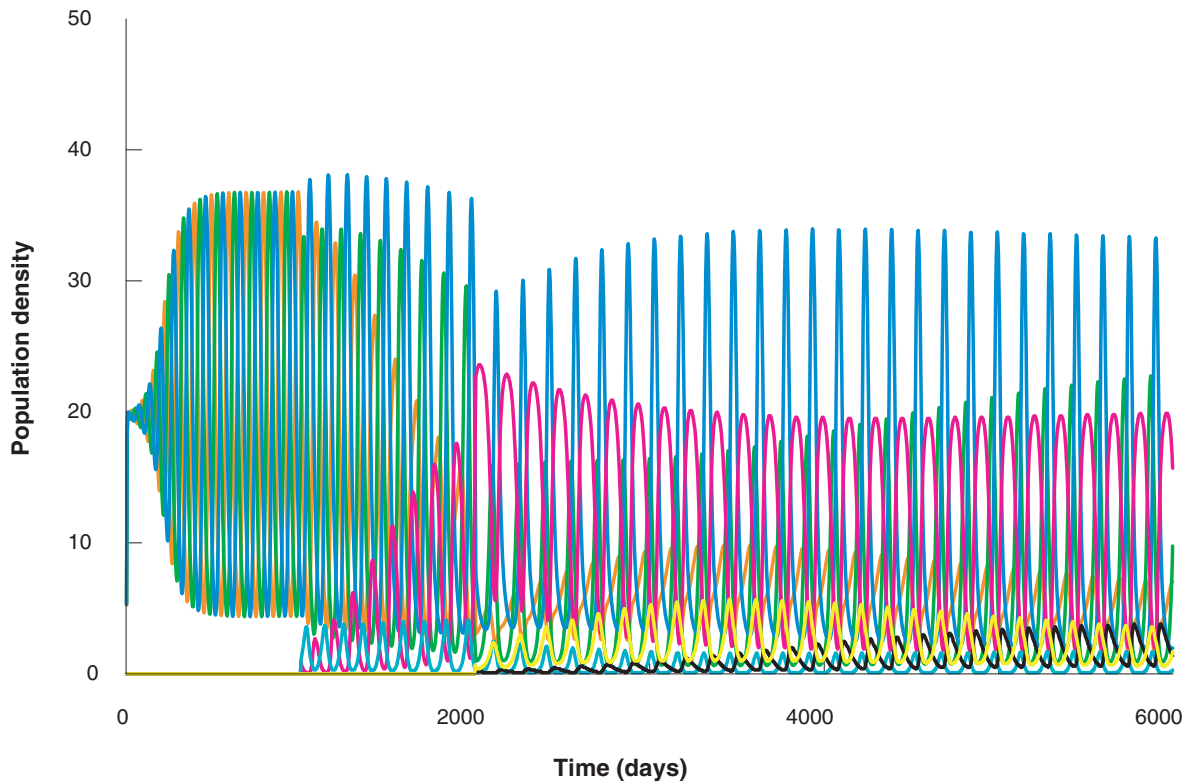


Fig. 3. Non-equilibrium coexistence of seven species on three interactively essential resources. Initial conditions: $R_j(0) = S_j$; species 1–3 start at $t = 0$ days with $N_1(0) = 0.11$, $N_2(0) = 0.12$, $N_3(0) = 0.13$; species 4 and 5 invade at $t = 1000$ days with $N_4(1000) = N_5(1000) = 1.0$; species 6 and 7 invade at $t = 2000$ days with $N_6(2000) = N_7(2000) = 1.0$.

limiting resources (Armstrong & McGehee 1980; Tilman 1982). However, fluctuations in species abundances, even when generated by competition, may allow the coexistence of multiple species on a few resources. Earlier, we found this phenomenon of non-equilibrium coexistence for perfectly essential resources (Huisman & Weissing 1999, 2001a; Huisman *et al.* 2001). Here, we illustrate the same phenomenon for interactively essential resources. Figure 3 shows a specific example of seven species coexisting on three interactively essential resources. The K matrix and C matrix used to generate Fig. 3 are as follows:

$$\mathbf{K} = \begin{pmatrix} 1 & 0.80 & 0.25 & 1.05 & 0.52 & 0.65 & 0.64 \\ 0.25 & 1 & 0.80 & 0.11 & 1.30 & 0.19 & 0.74 \\ 0.80 & 0.25 & 1 & 1.01 & 0.29 & 1.30 & 0.56 \end{pmatrix},$$

$$\mathbf{C} = \begin{pmatrix} 0.10 & 0.20 & 0.15 & 0.29 & 0.24 & 0.29 & 0.41 \\ 0.15 & 0.10 & 0.20 & 0.30 & 0.09 & 0.45 & 0.20 \\ 0.20 & 0.15 & 0.10 & 0.32 & 0.16 & 0.43 & 0.30 \end{pmatrix}.$$

Competitive chaos

On five interactively essential resources, multi-species competition may generate chaos. According to our simulations, competitive chaos on five resources occurs in the great majority of cases that assume that each of the species consumes most of the resource for which it is the intermediate competitor. An example is shown in Fig. 4, which is based on the following K matrix and C matrix:

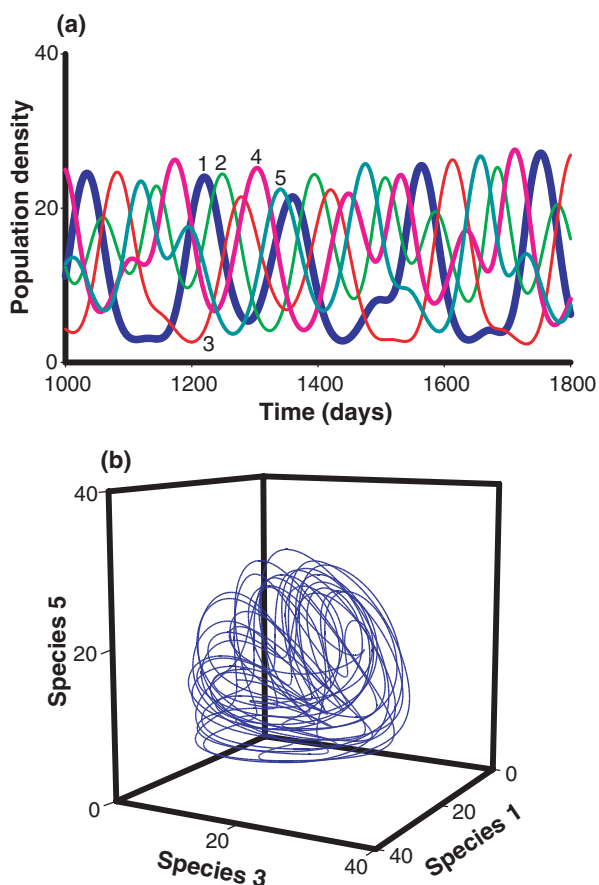


Fig. 4. Competitive chaos on five interactively essential resources. (a) Time course of the species. Initial conditions: $R_j(0) = S_j$, $N_1(0) = 1.1$, $N_2(0) = 1.2$, $N_3(0) = 1.3$, $N_4(0) = 1.4$, $N_5(0) = 1.5$. (b) The corresponding chaotic attractor; the trajectory is plotted for three of the five species, for the period from $t = 1000$ to $t = 5000$ days.

$$\mathbf{K} = \begin{pmatrix} 1.2 & 0.8 & 0.56 & 0.4 & 0.2 \\ 0.2 & 1.1 & 0.8 & 0.56 & 0.4 \\ 0.4 & 0.2 & 1.1 & 0.8 & 0.56 \\ 0.56 & 0.4 & 0.2 & 1.2 & 0.8 \\ 0.8 & 0.56 & 0.4 & 0.2 & 1.1 \end{pmatrix},$$

$$\mathbf{C} = \begin{pmatrix} 0.1 & 0.1 & 0.2 & 0.1 & 0.1 \\ 0.1 & 0.1 & 0.1 & 0.2 & 0.1 \\ 0.1 & 0.1 & 0.1 & 0.1 & 0.2 \\ 0.2 & 0.1 & 0.1 & 0.1 & 0.1 \\ 0.1 & 0.2 & 0.1 & 0.1 & 0.1 \end{pmatrix}.$$

Please note from the \mathbf{K} matrix and \mathbf{C} matrix that this example, indeed, assumes that each of the

species consumes most of the resource for which it is the intermediate competitor.

DISCUSSION

Competition for three or more perfectly essential resources may generate oscillations and chaotic fluctuations in species abundances (Huisman & Weissing 1999, 2001a, 2001b; Li 2001). The present paper shows that similar dynamics can be found on interactively essential resources as well. Hence, the observation that resource competition may generate non-equilibrium dynamics does not hinge on Liebig's Law of the Minimum. Instead, our results indicate that the dynamics of competition depend on the relationship between the resource requirements and the resource consumption characteristics of the species. Generally speaking, we find that competition for interactively essential resources generates: (i) stable coexistence if species consume most of the resources for which they are poor competitors; (ii) non-equilibrium dynamics if species consume most of the resources for which they are intermediate competitors; and (iii) competitive exclusion with a winner that depends on the initial conditions if species consume most of the resources for which they are strong competitors. This is in line with the previous findings for perfectly essential resources (Huisman & Weissing 2001b). We emphasize that these predictions should be interpreted as rules of thumb; they are not mathematical theorems. The rules are not always strictly obeyed (see the case $0.30 > \alpha > 0.25$ discussed above), but do capture the general patterns of literally thousands of simulations.

In conclusion, our findings demonstrate that competitively generated oscillations and chaos are not restricted to perfectly essential resources, but occur on interactively essential resources as well. This suggests that competitively generated non-equilibrium dynamics may occur on a wide variety of different resource types.

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