

BIOLOGICAL CONDITIONS FOR OSCILLATIONS AND CHAOS GENERATED BY MULTISPECIES COMPETITION

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Abstract. We investigate biological mechanisms that generate oscillations and chaos in multispecies competition models. For this purpose, we use a competition model concerned with competition for abiotic essential resources. Because phytoplankton and plants consume quite a number of abiotic essential resources, the model is particularly relevant for phytoplankton communities and terrestrial vegetation. We show that the predicted dynamics depend crucially on the relationship between the resource requirements and the resource consumption characteristics of the species. More specifically, the model predicts that competition generates (1) stable coexistence if species consume most of the resources for which they have high requirements, (2) oscillations and chaos if species consume most of the resources for which they have intermediate requirements, and (3) competitive exclusion with a winner that depends on the initial conditions if species consume most of the resources for which they have low requirements. The theoretical predictions are compared with available data on resource utilization patterns of phytoplankton species.

Key words: biodiversity; chaos; complex dynamics; heteroclinic cycle; limit cycle; multispecies competition models; nutrient limitation; phosphorus; phytoplankton; plant competition; population dynamics; resource competition; silica.

INTRODUCTION

Competition is seldom regarded as a process that may generate oscillations and chaotic fluctuations in species abundances. Yet in the 1970s it was shown that the competition models introduced by Lotka (1932) and Volterra (1928) can exhibit oscillations with three competing species (Gilpin 1975, May and Leonard 1975, Coste et al. 1978), chaos with four species (Arneodo et al. 1982), and in fact any kind of dynamical behavior if five or more species are involved (Smale 1976). Following this line of argument, it is tempting to suggest that competitive chaos should be widespread. It is well known that such nonequilibrium dynamics can favor species coexistence (Levins 1979, Armstrong and McGehee 1980, Sommer 1985), given the right kinds of nonlinearities (Chesson 1994). Thus, fluctuations generated by competition may contribute to the world's biodiversity (Huisman and Weissing 1999, 2000).

It is not clear, however, whether oscillations and chaos are indeed a common feature in competition models. Lotka-Volterra competition models are not mechanistic; they neither specify what the species are competing for, nor how the species compete (Stewart and Levin 1973, Abrams 1975, León and Tumpson 1975, Schoener 1976, Tilman 1987). It is therefore difficult to grasp from Lotka-Volterra competition theory under what biological circumstances competition will generate nonequilibrium dynamics.

Recently, we showed that another class of competition

models, based on competition for abiotic resources (Tilman 1982, Grover 1997), can also generate oscillations and chaos if multiple species compete for multiple resources (Huisman and Weissing 1999, 2000, 2001). Resource competition models are models that link the population dynamics of competing species with the dynamics of the resources that these species are competing for. An attractive feature of resource competition models is that they use the biological traits of species to predict the time course of competition. Hence, it becomes possible to pinpoint the mechanisms that underlie nonequilibrium dynamics in competition models. In this paper, we analyze the biological mechanisms that drive multispecies competition to oscillations and chaos.

THE MODEL

The competition model analyzed in this paper is concerned with abiotic essential resources. Essential resources are resources that are required for growth. For instance, light, water, nitrogen, phosphorus, and iron are all abiotic essential resources for phytoplankton and plant species.

Consider n species and k resources. Let N_i denote the population abundance of species i , and let R_j denote the availability of resource j . The population dynamics of the species depend on the resource availabilities. The resource availabilities, in turn, depend on the resource supply rates and the amounts of resources consumed by the organisms. We assume that the specific growth rate of a species is determined by the resource that is most limiting, as in Von Liebig's (1840) "Law of the Minimum". This gives the following model (León and Tumpson 1975, Tilman 1982, Huisman and Weissing 1999):

$$\frac{dN_i}{dt} = N_i(\min[p_{1i}(R_1), \dots, p_{ki}(R_k)] - m_i)$$

$$i = 1, \dots, n \tag{1a}$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^n c_{ji}N_i \min[p_{1i}(R_1), \dots, p_{ki}(R_k)]$$

$$j = 1, \dots, k. \tag{1b}$$

Here min is the minimum function, $p_{ji}(R_j)$ is the specific growth rate of species i given the availability of resource j , m_i is the specific loss rate of species i , D is the resource turnover rate, S_j is the supply of resource j , and c_{ji} is the content of resource j in species i .

We assume that the specific growth rates in Eqs. 1a and 1b are governed by the Monod equation (Monod 1950)

$$p_{ji}(R_j) = \frac{r_i R_j}{K_{ji} + R_j} \tag{2}$$

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

The model has been tested extensively using competition experiments with phytoplankton species (Tilman 1977, 1981, Holm and Armstrong 1981, Sommer 1985, 1986, Kilham 1986, van Donk and Kilham 1990, Rothhaupt 1996, Huisman et al. 1999).

DEFINITIONS AND TERMINOLOGY

The following definitions and terminology are used throughout the paper. We say that a species is limited by resource j if its specific growth rate is determined by resource j . More precisely, a species i is limited by resource j if

$$\min[p_{1i}(R_1), \dots, p_{ki}(R_k)] = p_{ji}(R_j) \quad j \in 1, \dots, k. \tag{3}$$

We summarize the competitive ability of a species for a resource j by its resource requirement R_{ji}^* (Armstrong and McGehee 1980, Tilman 1982). More specifically, R_{ji}^* is defined as the availability of resource j at which the specific growth rate of species i , when limited by resource j , equals its specific loss rate. Using Eq. 2, this gives the following expression:

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

We say that a species has the lowest requirement for a resource if it has a lower R^* for this resource than other species. That is, if $R_{ji}^* < R_{jk}^*$ for all $k \neq i$ then species i has the lowest requirement for resource j .

We say that a species consumes most of a resource if it has a higher content of this resource than other species. Thus, if $c_{ji} > c_{jk}$ for all $k \neq i$ then species i consumes most of resource j .

GENERAL RESULTS

This section extends the graphical approach developed by Tilman (1980, 1982) to multiple species and

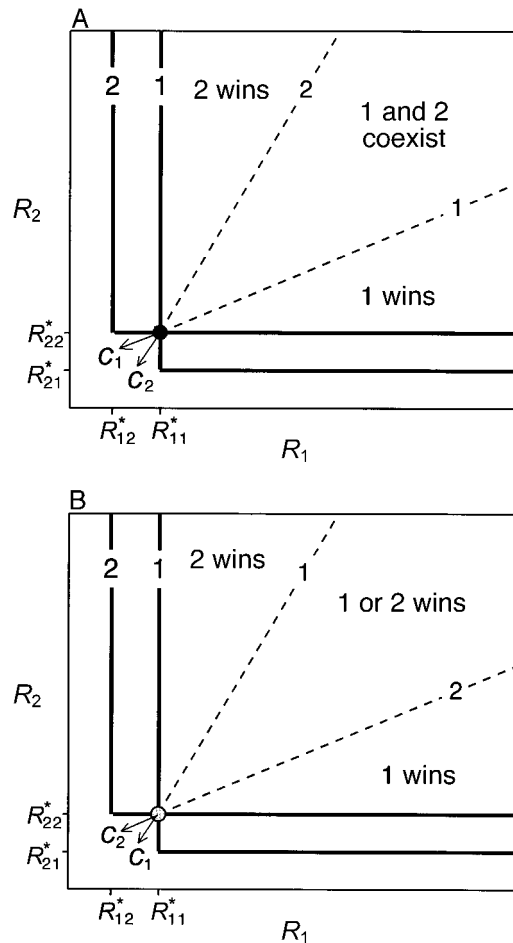


FIG. 1. Graphical approach applied to two species competing for two resources (Tilman 1980). The graphs show zero isoclines (solid lines) of species 1 and species 2 in resource space. Intersection of the zero isoclines, at (R_{11}^*, R_{22}^*) , gives the resource combination at which equilibrium coexistence is possible. The coexistence equilibrium is feasible only if the supply point falls within the region spanned by the two dashed lines. The slopes of these dashed lines equal the slopes of the species' consumption vectors. (A) The consumption vector of species 2 is steeper than that of species 1. Coexistence is stable and the two species coexist. (B) The consumption vector of species 1 is steeper than that of species 2. Coexistence is unstable, and the winner depends on the initial conditions.

multiple resources. The graphical approach is based on zero isoplanes, consumption vectors, and supply points. As an illustration, Fig. 1 shows graphs of two species competing for two resources. It will be convenient to compare all derivations below with the two species–two resource case depicted in this figure.

Resource space.—Try to imagine a multidimensional “resource space” delineated by the axes R_1, R_2, \dots, R_k . The combination of resource availabilities at which a species remains stationary can be drawn as a surface in resource space. This surface will be called the zero isoplane of a species, and is given by the resource

requirements R_i^* (solid lines in Fig. 1). For all combinations of resource availability above the zero isoplane of a given species, this species will increase. For all combinations of resource availability below its zero isoplane, this species will decrease.

The consumption vector of a species is a vector in resource space. This vector has the resource contents of a species as its elements. That is, the consumption vector of species i is given by $\mathbf{c}_i = (c_{i1}, \dots, c_{ik})$.

The supply point is a point in resource space. It indicates the equilibrium resource availabilities in the absence of any species. Thus, the supply point is given by the coordinates (S_1, \dots, S_k) .

Coexistence.—Species can coexist at equilibrium if their zero isoplanes intersect (as in Fig. 1). More precisely, we can derive the following rule: *equilibrium coexistence is possible only if each species becomes limited by the resource for which it has, compared to its competitors, the highest requirement.*

The mathematical proof underlying this result is simple. Suppose that a species remains stationary (i.e., $dN_i/dt = 0$) while limited by a resource for which one of its competitors has the highest requirement. Then this competitor cannot remain stationary but will decrease. Hence, the system would not be at equilibrium. This ends the proof.

Since only one species can have the highest requirement for a given resource, this coexistence rule immediately implies: *at equilibrium, at most k species can coexist on k resources.*

Let us therefore assume that we have k species and k resources, and that each species has the highest requirement for one of the resources. For notational convenience, we label the species such that species 1 has the highest requirement for resource 1, species 2 has the highest requirement for resource 2, and so on. The coexistence equilibrium is then given by the unique resource combination $(R_{11}^*, \dots, R_{kk}^*)$. Graphically, the coexistence equilibrium is the point in resource space at which the zero isoplanes of all species intersect.

In addition to the condition that each species has the highest requirement for one of the resources, equilibrium coexistence also requires that the equilibrium abundances of all species are positive. In graphical terms, it can be shown that all k species have positive equilibrium abundances only if the supply point, when plotted in resource space, falls within a positive cone that is spanned by k straight lines (dashed lines in Fig. 1). These straight lines originate from the equilibrium resource combination $(R_{11}^*, \dots, R_{kk}^*)$, and the directions of these lines correspond to the directions of the species' consumption vectors. A formal derivation of this result is in Appendix A.

Biological interpretation.—The results obtained so far can be interpreted as follows. First, equilibrium coexistence requires intersection of the isoplanes. That is, coexistence requires trade-offs in resource requirements: species with high requirements for one resource

should have low requirements for another resource. Second, coexistence depends on the directions of the consumption vectors. That is, coexistence is more likely if species differ substantially in their consumption characteristics. Third, coexistence depends on the position of the supply point. That is, resource supply rates should be such that different species can become limited by different resources.

Stability conditions.—So far, all multispecies results are similar to the two species–two resource case analyzed by León and Tumpson (1975), Tilman (1980), and Hsu et al. (1981). Stability conditions are more complicated for multiple species, however. Conditions for the local stability of the multispecies equilibrium are derived in Appendix B.

SPECIFIC RESULTS

This section considers various scenarios with k species and k resources. We assume (1) that each species has the highest requirement for one resource, and (2) that the supply point falls within the cone spanned by the consumption vectors. In other words, we consider only scenarios for which an internal coexistence equilibrium exists. This allows us to focus on the stability aspects of multispecies competition.

Several species competing for one resource

Prediction 1: The species that has the lowest requirement for the limiting resource (i.e., the species with lowest R_{1i}^) will displace all other species.*—The origin of this prediction can be traced back to at least the classic work of Volterra (1928). Further elaborations of this prediction were presented by, among others, Stewart and Levin (1973), Hsu et al. (1977), Armstrong and McGehee (1980), and Tilman (1982).

Two species competing for two resources

Prediction 2: (1) If each species consumes most of the resource for which it has the highest requirement, the two species stably coexist; (2) If each species consumes most of the resource for which it has the lowest requirement, the winner depends on the initial conditions.—These predictions were derived by León and Tumpson (1975), Taylor and Williams (1975), Tilman (1980), and Hsu et al. (1981). The predictions can be interpreted graphically, from the configuration of the zero isoclines and consumption vectors. Fig. 1A corresponds to Prediction 2.1, in which the coexistence equilibrium is stable. Fig. 1B corresponds to Prediction 2.2, in which the coexistence equilibrium is unstable.

Three species competing for three resources

Prediction 3: (1) If each species consumes most of the resource for which it has the highest requirement, the three species stably coexist; (2) If each species consumes most of the resource for which it has the intermediate requirement, the system generates species oscillations; (3) If each species consumes most of the

resource for which it has the lowest requirement, the winner depends on the initial conditions.—These predictions rely on local stability analysis (Appendix B).

Using our labeling conventions, suppose that the zero isoplanes of three species are arranged in the following way:

$$\begin{aligned}
 R_{11}^* &> R_{12}^* > R_{13}^* \\
 R_{22}^* &> R_{23}^* > R_{21}^* \\
 R_{33}^* &> R_{31}^* > R_{32}^*.
 \end{aligned}
 \tag{5}$$

Prediction 3.1 assumes that each species consumes most of the resource for which it has the highest requirement. Given Eq. 5, this implies

$$\begin{aligned}
 c_{11} &> c_{12} \geq c_{13} \\
 c_{22} &> c_{23} \geq c_{21} \\
 c_{33} &> c_{31} \geq c_{32}.
 \end{aligned}
 \tag{6}$$

Appendix B shows that, in this case, the three-species equilibrium is locally stable, whereas the monoculture equilibria and two-species equilibria are locally unstable. This yields stable coexistence of all three species (Fig. 2A).

Prediction 3.2 assumes that each species consumes most of the resource for which it has intermediate requirements. Given Eq. 5, this implies

$$\begin{aligned}
 c_{12} &> c_{13} \geq c_{11} \\
 c_{23} &> c_{21} \geq c_{22} \\
 c_{31} &> c_{32} \geq c_{33}.
 \end{aligned}
 \tag{7}$$

Appendix B shows that, in this case, the three-species equilibrium is locally unstable. In addition, it can be shown, using geometrical arguments in resource space, that two-species equilibria do not exist and that all monoculture equilibria are unstable. The species cannot settle at any equilibrium, because none of the equilibria is stable! A typical time course is shown in Fig. 2B. How are these oscillations generated? Suppose that we start with species 1. Species 1 consumes most of resource 3, and becomes limited by resource 3. Species 2 has a lower requirement for resource 3, and invades, but becomes limited by resource 1. Species 3 has a lower requirement for resource 1, and invades, but becomes limited by resource 2. Species 1 has a lower requirement for resource 2, and invades, and so on. In other words, each species invades one species but is excluded by a next species.

Limit cycles.—Prediction 3.2 generates two kinds of oscillations: limit cycles and heteroclinic cycles. Limit cycles have constant frequency. Fig. 3A shows a limit cycle of relatively small amplitude. Such a situation, where none of the species comes close to extinction, is called “permanent coexistence”. A formal criterion for permanent coexistence in three-species models was derived by Hutson and Law (1985). Define λ_{ab} as the

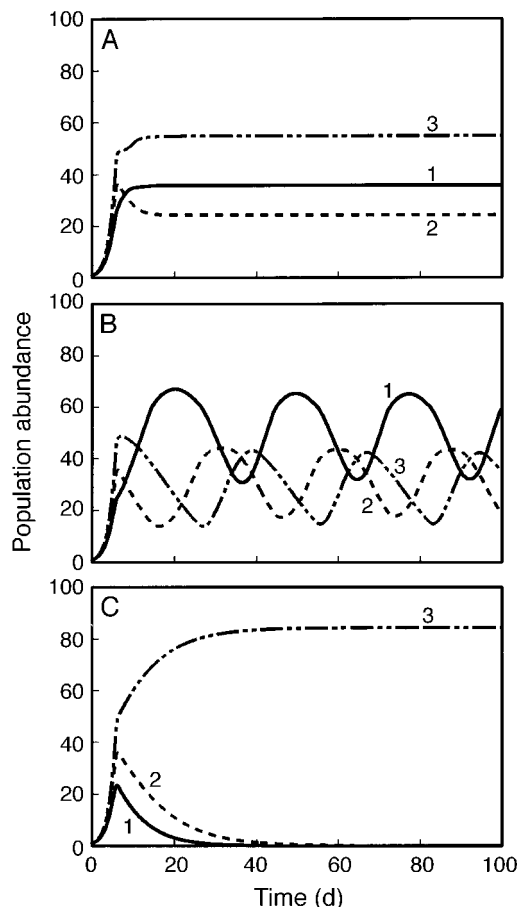


FIG. 2. Three species competing for three resources: (A) stable coexistence; (B) species oscillations; (C) competitive exclusion where the winner depends on the initial conditions. Parameter values are in Appendix C.

net growth rate of species b when grown in an equilibrium monoculture of species a

$$\lambda_{ab} = \min[p_{1b}(R_{1a}^m), \dots, p_{kb}(R_{ka}^m)] - m_b \tag{8}$$

where R_{ja}^m is the availability of resource j in an equilibrium monoculture of species a . If λ_{ab} is positive, species b can invade the monoculture of species a . Conversely, if λ_{ba} is negative, species a cannot invade the monoculture of species b . Hutson and Law (1985) showed that three-species coexistence is permanent if

$$\lambda_{12}\lambda_{23}\lambda_{31} > -\lambda_{21}\lambda_{32}\lambda_{13}. \tag{9}$$

The terms on the left-hand side of Eq. 9 are the (positive) net growth rates of the invading species, whereas the terms on the right-hand side are the (negative) net growth rates of the displaced species. Hence, this criterion states that limit cycles are generated if the product of the invasion rates is higher than the product of the displacement rates.

The permanence criterion in Eq. 9 can be translated into species traits. Consider one of the three species.

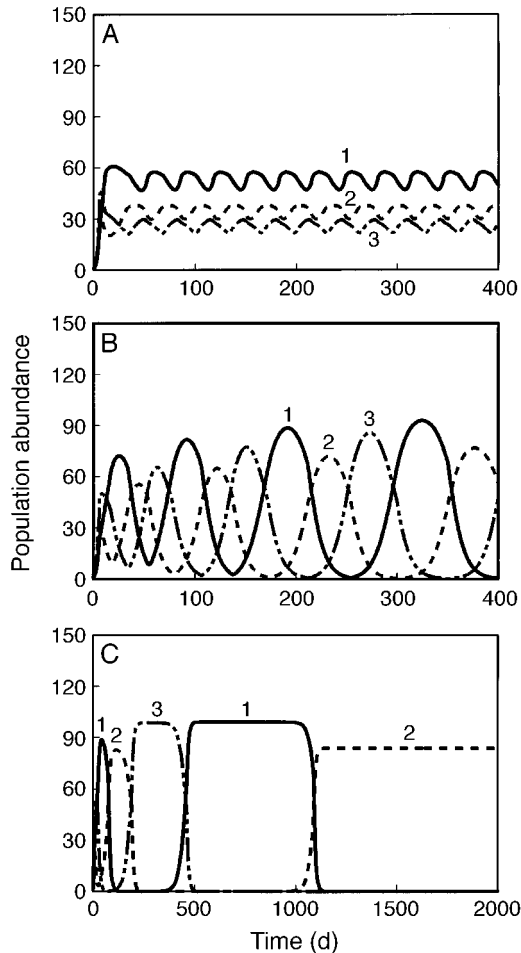


FIG. 3. Species oscillations on three resources: (A) limit cycle and permanent coexistence; (B) on the edge of permanence; (C) heteroclinic cycle and impermanent coexistence. Parameter values are in Appendix C.

This focal species can be invaded by one species, and displaces another species. If, for the resource that limits the focal species, the R^* of the invading species is much lower and the R^* of the displaced species is only slightly higher than the R^* of the focal species, then invasion is fast and displacement is slow. If this argument holds for all three species, then Eq. 9 is satisfied. That is, coexistence is permanent and competition generates limit cycles (Fig. 3A).

Fig. 3B shows an example where invasion rates equal displacement rates. The cycles are on the edge of permanence.

Heteroclinic cycles.—If the inequality in Eq. 9 is reversed, then invasion is slow and displacement is fast. In this case, Prediction 3.2 generates heteroclinic cycles (Fig. 3C). Heteroclinic cycles are cycles that connect unstable equilibria. In our system, the heteroclinic cycle moves from the monoculture equilibrium of species 1, to the monoculture equilibrium of species 2, to the monoculture equilibrium of species 3, back to spe-

cies 1, and so on. In fact, trajectories never truly hit the monoculture equilibria but spiral ever closer towards them. The closer the trajectory approaches a monoculture equilibrium, the longer it stays in the neighborhood of this equilibrium. Consequently, the cycle period lengthens. That is, heteroclinic cycles do not have a constant frequency but they slow down (Fig. 3C). Yet, the system never settles at a monoculture equilibrium since all monoculture equilibria are unstable. Technically, this is called “impermanent coexistence” (Huston and Law 1985) because the species do not really coexist but each time dominance is taken over by a new species.

A practical implication of heteroclinic cycles is that, in the real world, these cycles ultimately collapse because species go extinct when their abundances stay near zero for too long. Since this extinction would be driven by demographic stochasticity, it is hard to predict which of the species would go extinct and which would gain dominance.

Prediction 3.3 assumes that each species consumes most of the resource for which it has the lowest requirement. Given Eq. 5, this implies

$$\begin{aligned} c_{13} &> c_{12} \geq c_{11} \\ c_{21} &> c_{23} \geq c_{22} \\ c_{32} &> c_{31} \geq c_{33}. \end{aligned} \quad (10)$$

Appendix B shows that, in this case, the three-species equilibrium is locally unstable. In addition, it can be shown that two-species equilibria exist but are unstable. All three monoculture equilibria are stable, however. This implies that the dynamics lead to competitive exclusion, where the winner depends on the initial conditions. A typical time course is shown in Fig. 2C.

Competition for more than three resources

A mathematical analysis of local stability for more than three species and more than three resources is beyond the scope of the present paper. Instead, we investigated the cases with four species competing for four resources and with five species competing for five resources by means of extensive numerical simulations.

In many simulations, we found similar dynamics as for three species competing three resources. We observed stable coexistence if each species consumes most of the resource for which it has the highest requirement (as in Predictions 2.1 and 3.1). We observed a winner that depends on the initial conditions if each species consumes most of the resource for which it has the lowest requirement (as in Predictions 2.2 and 3.3). We observed oscillations, in the form of limit cycles and heteroclinic cycles, if each species consumes most of the resource for which it has the second-lowest requirement (as in Prediction 3.2). In the latter case, our simulations suggest that the occurrence of limit cycles

versus heteroclinic cycles depends on the invasion rates versus the displacement rates, as in Prediction 3.2.

In addition, our simulations also revealed other possible outcomes.

Prediction 4 (four species on four resources): If each species consumes most of the resource for which it has the second-highest requirement, one species pair displaces the other species pair. Which species pair wins, depends on the initial conditions.—In this scenario, the four species divide in two species pairs, and compete as species pairs against each other. That is, a species that consumes most of the resource for which it has the second-highest requirement prevents invasion of the species that has the highest requirement. So, species 1 prevents invasion of species 2, 2 prevents invasion of 3, 3 prevents invasion of 4, and 4 prevents invasion of 1. As a consequence, species 1 and 3 can form a coalition against species 2 and 4. Conversely, species 2 and 4 can form a coalition against species 1 and 3. Our simulations show that one of the two species pairs becomes dominant, and prevents invasion of the other species pair. Which of the two species pairs becomes dominant depends on the initial conditions.

Prediction 5 (five species on five resources): (1) If each species consumes most of the resource for which it has the second-highest requirement, the system generates species-pair oscillations with switching partners; (2) If each species consumes most of the resource for which it has the intermediate requirement, the system generates chaos.—Prediction 5.1 produces a cyclic succession of species pairs, in which species switch partners. Consider species 2 and 5 in Fig. 4. Species 3 invades this partnership, displaces species 2, and forms a new pair with species 5. Next, species 1 invades, displaces species 5, and forms a new pair with species 3. Next, species 4 invades, displaces species 3, and forms a new pair with species 1, and so on. Depending on the rates of invasion and displacement, the species-pair oscillations can be either limit cycles (Fig. 4A) or heteroclinic cycles (Fig. 4B).

Prediction 5.2 considers a scenario in which each species consumes most of the resource for which two of the five species have higher requirements and two other species have lower requirements. This leads to chaos (Figs. 5 and 6). Whenever a species begins to become dominant, two species will be displaced and two other species can invade. The two invading species invade at different rates. Hence, trajectories have a tendency to diverge. Divergence of trajectories is one of the characteristic features of chaos.

In Fig. 5, invasion and displacement rates are more or less comparable. The species go up and down without any true regularity. Numerical simulations reveal that the trajectories show sensitive dependence on initial conditions. The chaotic attractor is shown in Fig. 5B.

In Fig. 6, some species invade fast while other species invade slowly. Now there is an oscillating sub-

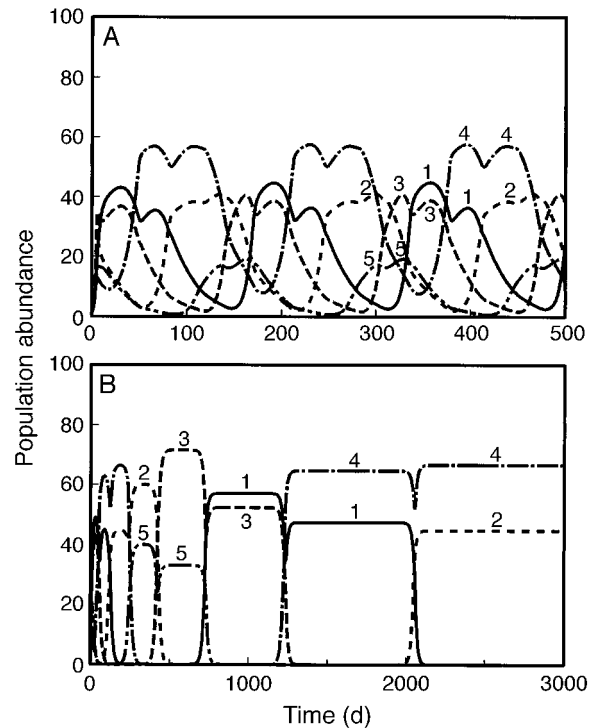


FIG. 4. Species-pair oscillations with switching partners on five resources: (A) limit cycle; (B) heteroclinic cycle. Parameter values are in Appendix C.

system of three species (species 1, 3, 4). Species 5 slowly invades, and destroys the three-species oscillations. Other species invade species 5, with sudden eruptions of species 2 and 4. Via various roundabouts, the system returns to the three-species oscillations, and the whole story starts anew. Although this suggests some regularity, the system is in fact chaotic. The duration of the three-species oscillations does not show any regularity (Fig. 6A). Fig. 6B shows the chaotic attractor.

DISCUSSION

Our results confirm previous findings (Gilpin 1975, May and Leonard 1975, Smale 1976, Huisman and Weissing 1999, 2001) that multispecies competition can lead to a plethora of dynamical phenomena. In addition to predictions of classic competition theory, like stable coexistence and competitive exclusion, we observed that multispecies competition may generate limit cycles (Figs. 2, 3), heteroclinic cycles (Fig. 3), collaboration of species pairs, species-pair oscillations with switching partners (Fig. 4), and competitive chaos (Figs. 5, 6). We emphasize that these findings are based on competition for abiotic resources. Complex dynamics in models in which predators compete for biotic prey are already well established (Gilpin 1979, Abrams and Shen 1989, Vandermeer 1993, Lundberg et al. 2000). In these latter models, complex dynamics are

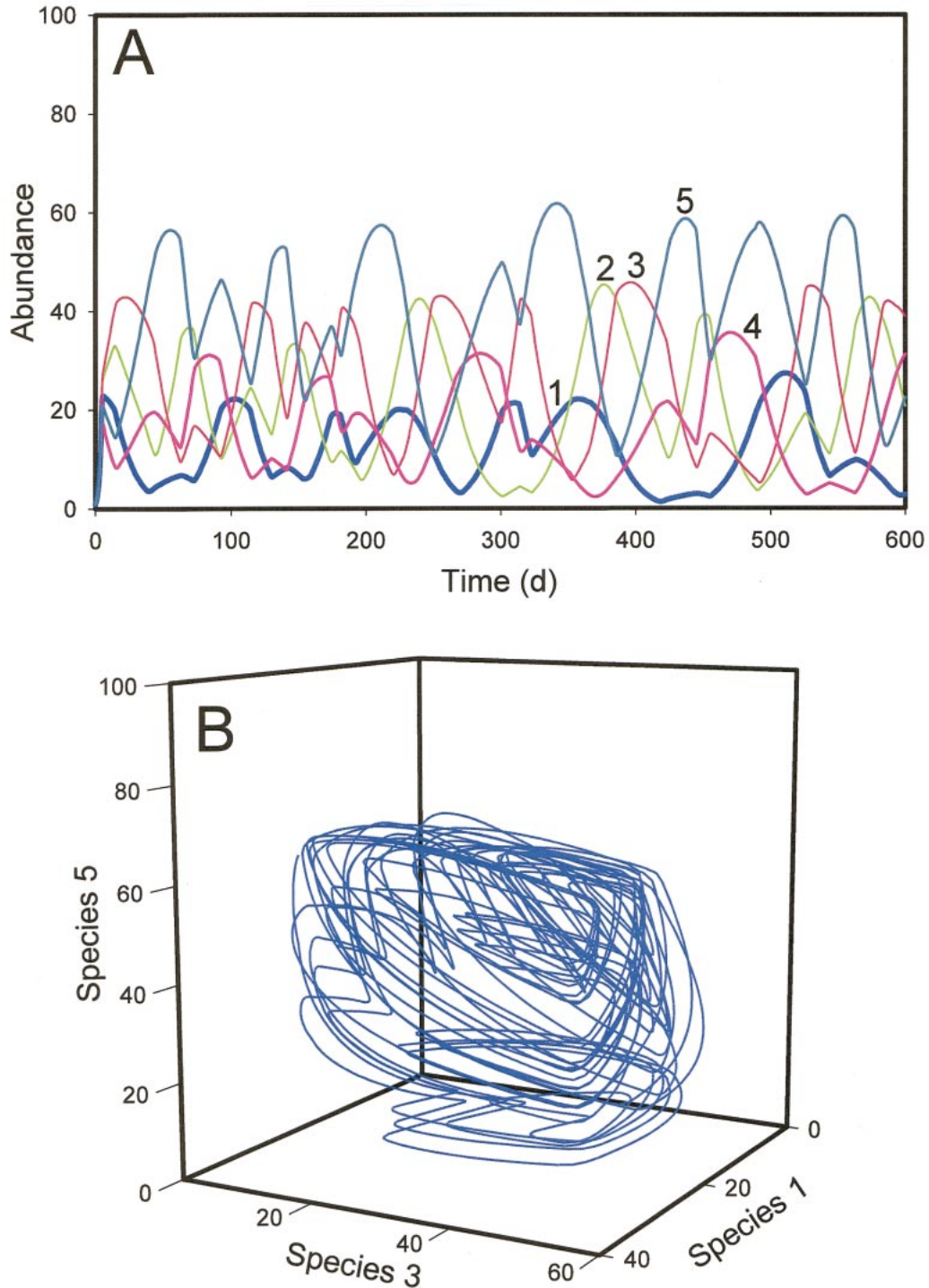


FIG. 5. Competitive chaos on five resources: (A) time course; (B) chaotic attractor, depicted for three of its five dimensions. The trajectory is drawn for the period from $t = 2000$ to $t = 5000$. Parameter values are in Appendix C.

usually generated by predator-prey cycling. In the model that we investigated, however, complex dynamics are generated by purely competitive interactions.

The nonequilibrium dynamics that we observed are well known in other dynamical systems with a similar

mathematical structure as our competition model. They are induced by nontransitive interactions (A beats B, B beats C, C beats A), as in the rock-scissors-paper game (Weissing 1991). Nontransitive interactions leading to nonequilibrium dynamics have been described

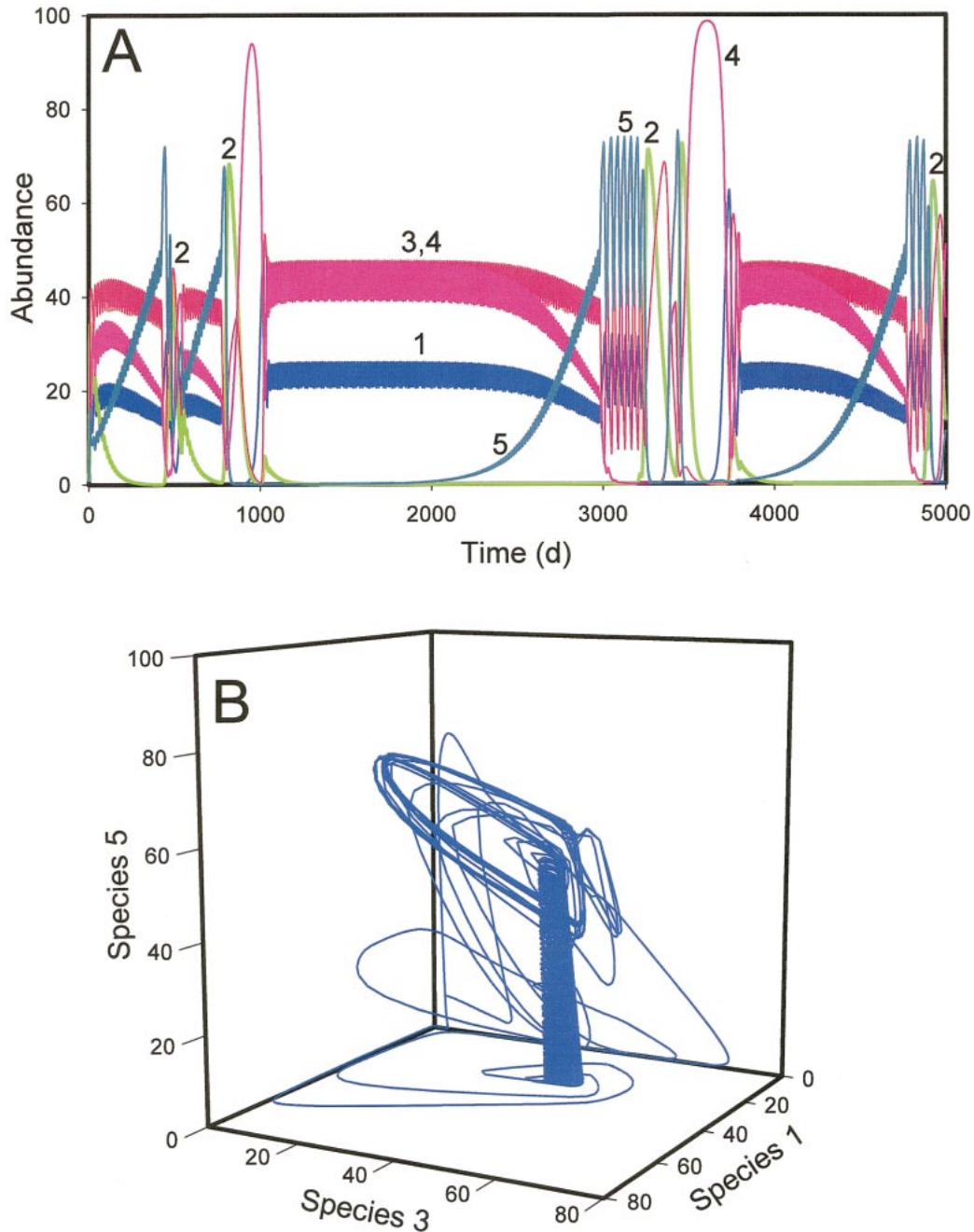


FIG. 6. Competitive chaos on five resources: (A) time course; (B) chaotic attractor, depicted for three of its five dimensions. The trajectory is drawn for the period from $t = 2000$ to $t = 8000$. Parameter values are in Appendix C.

in various research fields, including behavioral ecology (Sinervo and Lively 1996), population genetics (Stadler 1996), immunology (Nowak et al. 1995), sociobiology (Nowak and Sigmund 1993), and the social sciences (Shubik 1982). Gilpin (1975) and Buss and Jackson (1979) provide early discussions on the potential role of nontransitive interactions in interspecific competition. In competitive systems, nontransitivities occur if “variants” that are good invaders when rare are not

resistant against new invaders when common. Such systems may settle at a coexistence equilibrium. But if all equilibria are unstable, the system cannot settle at equilibrium and thus remains in permanent motion.

Robustness of the predictions

To establish the robustness of our model predictions, we ran numerous additional simulations in which we slightly altered the assumptions.

One assumption of the model is that specific growth rates are governed by Monod equations. The derivations in the appendices are independent of the Monod equation, however. Therefore, qualitatively, our results should also apply to other mathematical expressions for the specific growth rates. For example, we found similar dynamics and the same classification of predictions when we used linear expressions for the specific growth rates in our simulations [i.e., $p_{ji}(R_j) = a_{ji}R_j$] instead of the nonlinear Monod equation. This demonstrates that oscillations and chaos are not caused by the nonlinearity of the Monod equation.

Another assumption is the use of Liebig's Law of the Minimum. It is known that some essential resources do not follow this minimum law but show interactive effects. Iron and nitrate, for example, are limiting resources for phytoplankton in various oceanographic regions (e.g., Martin et al. 1994, Blain et al. 1997). Because iron is an essential component of the enzymes nitrate and nitrite reductase (Timmermans et al. 1994), iron and nitrate do not obey Liebig's Law of the Minimum but have interactive effects on phytoplankton growth (Price et al. 1991, Maldonado and Price 1996). We found similar dynamics and the same classification of predictions, however, when we used a multiplicative function in our simulations instead of a minimum function. Hence, the predictions do not hinge on Liebig's Law of the Minimum.

An aspect that we did not investigate so far is resource storage. Storage-based models can predict other outcomes of competition than models without resource storage (Grover 1990, 1991a). Moreover, experiments and field data show that storage-based models often provide a better description of competition in fluctuating environments than competition models without resource storage (Grover 1991b, Sommer 1991, Dubocou et al. 1998). Internal storage of resources buffers organisms against external fluctuations in resource availability. Therefore, one might argue that resource storage dampens oscillations created by competition and reduces opportunities for chaotic fluctuations. On the other hand, resource storage adds additional nonlinearity to the model that may generate new oscillatory behavior. What the net effect of resource storage will be is an interesting open question.

Finally, the model is based on the assumption that there is a continuous supply of resources. Long-term removal of resources from the system or species-specific effects on resource supply rates may complicate resource-consumer interactions, and will need further investigation.

Testability of the predictions

An advantage of resource competition models, when compared to Lotka-Volterra competition theory, is that the model predictions can be interpreted in terms of biological mechanisms. Because the theory developed here concerns abiotic essential resources, and because

plants and phytoplankton require quite a number of abiotic essential resources, the model predictions seem most relevant for phytoplankton and plant communities. Our results show that the conditions that generate the various behaviors have a clear ecological interpretation. The following three questions should be addressed:

1) How many resources are limiting? If species compete for one or two abiotic resources, theory predicts a stable outcome of competition. If species compete for more than two abiotic resources, theory predicts that competition may generate nonequilibrium dynamics.

2) What are the trade-offs in resource requirements? If one species has the lowest requirements for all resources, theory predicts that it will exclude all other species. Complex dynamics generated by competition for abiotic resources are predicted only if there are trade-offs in resource requirements: a species that has a low requirement for one resource, should have intermediate or high requirements for other resources.

3) How are resource requirements and resource consumption related? Our results show that the dynamics depend on the rank order of the resource requirements of the species versus the rank order of their resource consumption. Even for only three species and three resources the number of possible rankings is overwhelming. There are 3! different ways to order three species according to their resource requirements for a single resource. Hence, there are $3!^3 = 216$ different ways to order the resource requirements of three species for three resources. Similarly, there are 216 different ways that three species can be ordered for their resource consumption. Hence, even with only three species and three resources, the number of possible scenarios is hopelessly large. We have thus analyzed only a small fraction of all possible scenarios. Nevertheless, our results indicate that the model predictions can be summarized by a few rules of thumb. First, if species consume most of the resource for which they have high requirements, each species tending to dominance can be invaded by all other species. In this way, deviations from equilibrium are brought back to equilibrium, and stable species coexistence is to be expected. Second, if species consume most of the resource for which they have intermediate requirements, a species tending to dominance can be invaded by some species but excludes several other species. In this case, species oscillations and chaotic fluctuations should be widespread. Third, if species consume most of the resource for which they have low requirements, a species tending to dominance would deprive all other species from their resources. In this case, competition should lead to competitive exclusion where the winner depends on the initial conditions.

Application to phytoplankton

As an illustration, this section attempts to apply the three basic questions just formulated to phytoplankton communities.

First, how many resources are limiting? Traditionally, phosphorus, nitrogen, silica, and light are considered the most important limiting resources for phytoplankton. In the past few years, numerous other resources have also been identified as limiting factors. Iron is now regarded a major limiting factor in several oceanographic regions (Martin et al. 1994, De Baar et al. 1995, Behrenfeld et al. 1996). Other trace metals recently found limiting in freshwater and marine environments include cadmium, cobalt, copper, and zinc (Stoddard 1987, Coale 1991, Granéli and Risinger 1994, Morel et al. 1994, Lee et al. 1995). In dense phytoplankton blooms, inorganic carbon can become a major limiting resource (Bermanfrank et al. 1994, Klemmer et al. 1995, Ibelings and Maberly 1998).

Do these limiting resources operate in concert or in isolation? Elser et al. (1990) reviewed enrichment experiments with nitrogen and phosphorus in freshwater lakes of North America. They selected a total of 80 lake-years. None of these lake-years responded to nitrogen addition only, two lake-years responded to phosphorus addition only, and 39 lake-years responded to combined addition of nitrogen and phosphorus. Hence, this study shows that, at the community level, limitation by two resources appears more common than limitation by a single resource. Note that Elser et al. (1990) considered only nitrogen and phosphorus; they did not report on other potentially limiting resources. Sommer (1986, 1988) investigated nutrient limitation of Antarctic marine phytoplankton. Bioassay experiments identified nitrogen and silica as limiting nutrients. Light was inferred as a third limiting factor. Note that three limiting resources is only a minimum estimate, because Sommer's study did not test for limitation by iron or other trace nutrients. Sommer (1989, 1991, 1993) studied resource limitation in several German lakes. In Großer Binnensee, nitrogen was the most important limiting nutrient, phosphorus was next, silica limitation was observed once, and light was inferred as a fourth limiting factor (Sommer 1989). In Schöhsee, the nutrients nitrogen, phosphorus and silica were all found to be limiting (Sommer 1991). In Plußsee, silica, nitrogen, and light were identified as limiting resources (Sommer 1993). Hence, in these German lakes at least three resources per lake were identified as limiting. Sterner (1994) investigated nutrient limitation in a freshwater reservoir in Texas, USA. He found significant effects of nitrogen, phosphorus, and a trace-nutrient mixture. Again, three limiting resources is a minimum estimate for this reservoir, because Sterner did not distinguish between the various trace nutrients, and did not test for limitation by light or inorganic carbon. Fisher et al. (1999) investigated resource limitation of phytoplankton in Chesapeake Bay, USA. They found that waters in southern Chesapeake Bay were primarily N limited. In contrast, waters in northern Chesapeake

Bay had a light-phosphorus-nitrogen limitation, and in some cases silica limitation as well. Escaravage et al. (1996) filled mesocosms with seawater from the Oosterschelde estuary, The Netherlands. Resource limitation in these mesocosm experiments alternated between nitrogen, phosphorus, and silica limitation (Escaravage et al. 1996). Again, three limiting resources is a minimum estimate for this study, because light, carbon, and trace nutrients were not investigated. In conclusion, on the basis of this small literature survey, multiple resource limitation of phytoplankton communities seems widespread.

Second, what are the trade-offs in resource requirements? We went through the literature in search for R^* values. We found proper data sets to test for trade-offs between (1) phosphorus requirements vs. silica requirements, and (2) nitrate requirements vs. silica requirements. R^* values for phosphorus and silica of freshwater diatom species were obtained from Kilham et al. (1977), Tilman (1977, 1981), Kilham (1984), and van Donk and Kilham (1990). We use their data gathered at 20°C, and calculated R^* values for a loss rate of $m_i = 0.25/d$. The data reveal a significant negative correlation between the R^* values for phosphorus and the R^* values for silica (Fig. 7A; Spearman rank correlation test: $r_s = -0.72$, $N = 9$, $P < 0.05$). This demonstrates a clear trade-off. Diatom species with high silica requirements have low phosphorus requirements. Conversely, diatom species with high phosphorus requirements have low silica requirements.

R^* values for nitrate and silica were obtained from Sommer's (1986) study of marine diatom species from Antarctic waters. Sommer's data were obtained at 0°C, and we calculated the R^* s, assuming again a loss rate of $m_i = 0.25/d$. As for phosphorus and silica above, this reveals a significant trade-off between nitrate requirements and silica requirements (Fig. 7B; Spearman rank correlation test: $r_s = -1$, $N = 5$, $P < 0.05$). Diatom species with high silica requirements have low nitrate requirements. Conversely, diatom species with high nitrate requirements have low silica requirements.

Thus, the available data show trade-offs between the resource requirements of phytoplankton species, at least for the combinations phosphorus-silica and nitrate-silica. We have not found sufficient data to test for other trade-offs in resource requirements, e.g., the combinations nitrogen-phosphorus, nitrogen-light, or iron-light.

Third, how are resource requirements and resource consumption related? We looked for paired data on R^* s (as measure of resource requirements) and cellular nutrient contents (as measure of resource consumption) of phytoplankton species. We found proper data for silica and for phosphorus. Silica data of diatoms were drawn from Tilman (1977, 1981), Tilman et al. (1981), Kilham (1984), and Van Donk and

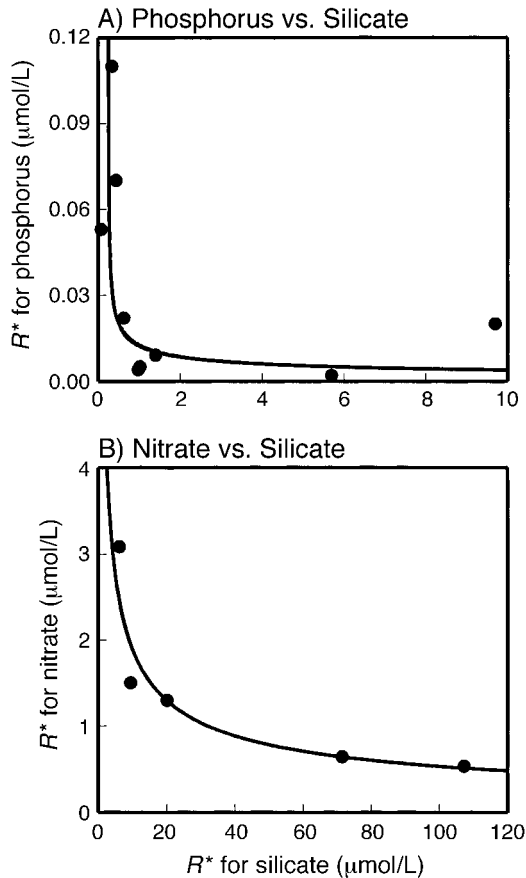


FIG. 7. Trade-offs between resource requirements. Each dot is a different species. (A) Phosphorus requirements vs. silica requirements, based on nine freshwater diatom species; (B) nitrate requirements vs. silica requirements, based on five marine diatom species. Data sources: (A) Kilham et al. (1977), Tilman (1977, 1981), Kilham (1984), van Donk and Kilham (1990); (B) Sommer (1986).

Kilham (1990). Silica data of a scaled chrysophyte were obtained from Sandgren et al. (1996). We use the data gathered at 20°C. R^* values are calculated for loss rates of $m_i = 0.25/d$. Silica contents are expressed as pmol Si per cell. This reveals a significant positive correlation between the R^* s for silica and the cellular silica contents (Fig. 8A; Spearman rank correlation test: $r_s = 0.95$, $N = 9$, $P < 0.002$). That is, species that consume a lot of silica have high silica requirements, and species that consume little silica have low silica requirements. If all resources would show the same pattern as silica, theory predicts that competition for multiple resources favors stable coexistence.

Phosphorus data were obtained from Grover (1989), who screened freshwater species for their phosphorus-dependent growth kinetics. Grover's data were obtained at 12°C. R^* values are calculated for loss rates of $m_i = 0.25/d$. Cellular phosphorus contents are expressed as fmol P per unit cell volume.

In contrast to silica, there is no significant correlation between the R^* s for phosphorus and the cellular phosphorus contents (Fig. 8B; Spearman rank correlation test: $r_s = 0.28$, $N = 11$, ns). In fact, the highest cellular phosphorus contents were found in species with an intermediate R^* for phosphorus. If all resources would show the same pattern as phosphorus, theory predicts that multispecies competition may favor complex dynamics.

Thus, silica and phosphorus show a different correlation pattern between resource requirements and resource consumption. We have not found sufficient data to test for correlation patterns for other important resources, like nitrogen, iron, carbon, and light.

In conclusion, should we expect multispecies competition to generate stable communities or complex dynamics? On the basis of the available data, we can neither confirm nor reject the hypothesis of complex

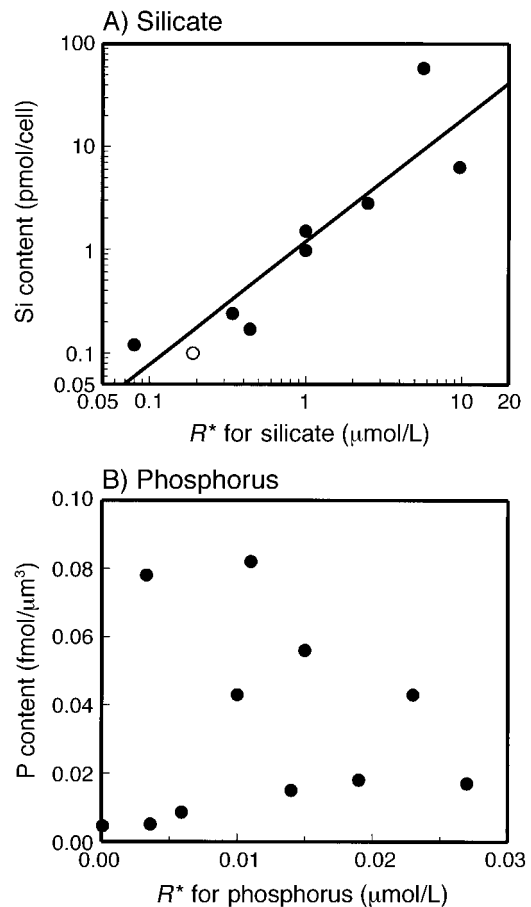


FIG. 8. Resource consumption versus resource requirements. Each dot is a different species. (A) Species with high silica contents have high silica requirements, based on eight diatom species (closed circles) and 1 chrysophyte (open circle). (B) No relation between phosphorus contents and phosphorus requirements, based on 11 freshwater phytoplankton species. Data sources: (A) Tilman (1977, 1981), Tilman et al. (1981), Kilham (1984), van Donk and Kilham (1990), Sandgren et al. (1996); (B) Grover (1989).

dynamics in phytoplankton communities. Two ingredients for complex dynamics are clearly present. It appears quite common that phytoplankton assemblages are limited by more than two resources. Furthermore, at least for the data sets that have been gathered so far, there are trade-offs between the resource requirements of phytoplankton species (Fig. 7). Concerning the third point, however, the relation between resource requirements and resource consumption is not so obvious. If most resources would show the same pattern as silica (Fig. 8A), theory predicts that competition should lead to stable phytoplankton communities. If most resources would show the same pattern as phosphorus (Fig. 8B), theory predicts that multispecies competition may generate complicated non-equilibrium dynamics. More data, for more species and especially for more limiting resources, would be most welcome.

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APPENDIX A

This appendix derives conditions for the existence of a multispecies coexistence equilibrium, and is available in ESA's Electronic Data Archive: *Ecological Archives* E082-029-A1.

APPENDIX B

This Appendix derives conditions for the local stability of a multispecies coexistence equilibrium, and is available in ESA's Electronic Data Archive: *Ecological Archives* E082-029-A2.

APPENDIX C

This appendix provides the parameter values used in our simulations. Simulations are based on a fourth-order Runge-Kutta procedure. The model is parameterized for phytoplankton, with a time scale expressed in days. For parsimonious reasons, we used $r_i = 1/d$ and $m_i = D = 0.25/d$ for all species. These values are within a typical range for phytoplankton species. Initial conditions are $R_j(0) = S_j$ and $N_i(0) = 1$ in all simulations. Half-saturation constants and resource contents are given below, using the notation of matrix algebra. Half-saturation constants, K_{ji} , are in matrix **K**. Resource contents, c_{ji} , are in matrix **C**. Different columns represent different species; different rows represent different resources.

Fig. 2A:

$$\mathbf{K} = \begin{pmatrix} 1 & 0.6 & 0.3 \\ 0.3 & 1 & 0.6 \\ 0.6 & 0.3 & 1 \end{pmatrix} \quad \mathbf{C} = \begin{pmatrix} 0.07 & 0.04 & 0.04 \\ 0.08 & 0.10 & 0.08 \\ 0.10 & 0.10 & 0.14 \end{pmatrix}$$

(resource supply: $S_1 = 6, S_2 = 10, S_3 = 14$).

Fig. 2B: as Fig. 2A, except

$$\mathbf{C} = \begin{pmatrix} 0.04 & 0.07 & 0.04 \\ 0.08 & 0.08 & 0.10 \\ 0.14 & 0.10 & 0.10 \end{pmatrix}$$

Fig. 2C: as Fig. 2A, except

$$\mathbf{C} = \begin{pmatrix} 0.04 & 0.04 & 0.07 \\ 0.10 & 0.08 & 0.08 \\ 0.10 & 0.14 & 0.10 \end{pmatrix}$$

Fig. 3A:

$$\mathbf{K} = \begin{pmatrix} 1 & 0.9 & 0.3 \\ 0.3 & 1 & 0.9 \\ 0.9 & 0.3 & 1 \end{pmatrix} \quad \mathbf{C} = \begin{pmatrix} 0.04 & 0.07 & 0.04 \\ 0.08 & 0.08 & 0.10 \\ 0.14 & 0.10 & 0.10 \end{pmatrix}$$

(resource supply: $S_1 = 6, S_2 = 10, S_3 = 14$).

Fig. 3B: as Fig. 3A, except $K_{12} = K_{23} = K_{31} = 0.5$.

Fig. 3C: as Fig. 3A, except $K_{12} = K_{23} = K_{31} = 0.4$.

Fig. 4A:

$$\mathbf{K} = \begin{pmatrix} 1 & 0.8 & 0.4 & 0.3 & 0.2 \\ 0.2 & 1 & 0.8 & 0.4 & 0.3 \\ 0.3 & 0.2 & 1 & 0.8 & 0.4 \\ 0.4 & 0.3 & 0.2 & 1 & 0.8 \\ 0.8 & 0.4 & 0.3 & 0.2 & 1 \end{pmatrix}$$

$$\mathbf{C} = \begin{pmatrix} 0.04 & 0.07 & 0.04 & 0.04 & 0.04 \\ 0.08 & 0.08 & 0.10 & 0.08 & 0.08 \\ 0.10 & 0.10 & 0.10 & 0.14 & 0.10 \\ 0.03 & 0.03 & 0.03 & 0.03 & 0.05 \\ 0.09 & 0.07 & 0.07 & 0.07 & 0.07 \end{pmatrix}$$

(resource supply: $S_1 = 6, S_2 = 10, S_3 = 14, S_4 = 4, S_5 = 9$.
Fig. 4B: as Fig. 4A, except $K_{12} = K_{23} = K_{34} = K_{45} = K_{51} = 0.6$).

Fig. 5:

$$\mathbf{K} = \begin{pmatrix} 0.45 & 0.35 & 0.30 & 0.24 & 0.23 \\ 0.22 & 0.45 & 0.35 & 0.30 & 0.27 \\ 0.27 & 0.22 & 0.45 & 0.35 & 0.30 \\ 0.30 & 0.24 & 0.22 & 0.45 & 0.35 \\ 0.35 & 0.30 & 0.22 & 0.20 & 0.45 \end{pmatrix}$$

$$\mathbf{C} = \begin{pmatrix} 0.04 & 0.04 & 0.07 & 0.04 & 0.04 \\ 0.08 & 0.08 & 0.08 & 0.10 & 0.08 \\ 0.10 & 0.10 & 0.10 & 0.10 & 0.14 \\ 0.05 & 0.03 & 0.03 & 0.03 & 0.03 \\ 0.07 & 0.09 & 0.07 & 0.07 & 0.07 \end{pmatrix}$$

Resource supply: $S_1 = 6, S_2 = 10, S_3 = 14, S_4 = 4, S_5 = 9$.

Fig. 6: as Fig. 5, except

$$\mathbf{K} = \begin{pmatrix} 0.40 & 0.36 & 0.32 & 0.20 & 0.19 \\ 0.18 & 0.32 & 0.30 & 0.24 & 0.23 \\ 0.20 & 0.10 & 0.45 & 0.35 & 0.22 \\ 0.32 & 0.12 & 0.10 & 0.45 & 0.44 \\ 0.50 & 0.22 & 0.20 & 0.18 & 0.80 \end{pmatrix}$$