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LETTER

Towards a solution of the plankton paradox: the importance of physiology and life history

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Abstract

Phytoplankton communities reveal an astonishing biodiversity, whereas classical competition theory seems to suggest that only a few competing species can survive. Recently we suggested a new solution to this plankton paradox. In theory, at least, competition between multiple species can generate complex dynamics that can support a large number of species. How likely is it then, in reality, that competitive chaos indeed promotes biodiversity? To obtain some insight, we simulated multispecies competition according to five different physiological scenarios. For random species parameters, biodiversity was generally low. Assuming plausible physiological trade-offs, the simulations revealed switches back and forth between equilibrium and nonequilibrium dynamics, and a higher biodiversity. An extremely high biodiversity, with sometimes more than 100 species on three resources, was observed in simulations that assumed a cyclic relation between competitive abilities and resource contents. We conclude that physiological and life-history patterns have a major impact on the likelihood of nonequilibrium dynamics and on the biodiversity of plankton communities.

Keywords

Biodiversity, chaos, coexistence, competition model, competitive exclusion, nutrients, phytoplankton, resource competition, supersaturation.

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INTRODUCTION

To what extent does competitive chaos contribute to the world's biodiversity? Earlier we showed that competition for three or more resources can generate oscillations and chaotic fluctuations in species abundances, and that these nonequilibrium conditions may allow the coexistence of many species (Huisman & Weissing 1999, 2000, 2001a,b). This demonstrates that, at least in theory, the astonishing species diversity in phytoplankton communities (Hutchinson 1961) can be explained by fluctuations generated by competitive interactions. Given this proof of principle, how likely is it, in the real world, that nonequilibrium conditions do indeed promote biodiversity? How often will competitive interactions generate nonequilibrium conditions, and how often will this enhance biodiversity?

Recently, Schippers *et al.* (2001) attempted to address these questions. Based on computer simulations with random choices of species parameters, they argued that species coexistence by means of competitive chaos is rare. The choice of random species parameters, however, does not provide much insight into the issue. In reality, species do not have random traits. Species traits are determined by physiological constraints and trade-offs, environmental conditions, and evolutionary forces. Empirical studies reveal that physiological and ecological trade-offs indeed exist in phytoplankton (e.g. Reynolds 1997). For instance, phytoplankton species that are strong competitors for silica are generally poor competitors for phosphorus and nitrogen, and vice versa (Tilman 1982; Sommer 1986; Huisman & Weissing 2001b). Thus, it is important to know how species traits in natural communities are structured. What are physiologically plausible parameter combinations? What are the trade-offs between species parameters? Has evolution selected for particular combinations of species traits? Using extensive computer simulations reflecting several physiological scenarios, we here investigate to what extent particular combinations of physiological traits and life-history patterns affect the likelihood of chaos-enhanced biodiversity.

PHYSIOLOGICAL SCENARIOS

We consider a competition model with a large number of species competing for three essential resources. For a detailed presentation of the model, the reader is referred to Tilman (1982) and Huisman & Weissing (1999, 2001b). It would be a daunting task to vary all model parameters systematically. Here, we focus on six species parameters: the three half-saturation constants, K, and the three resource contents, c, of a species. The Ks are a measure of the competitive abilities, where a low K corresponds to a high competitive ability. The cs reflect the consumption patterns of the species. Huisman & Weissing (2001b) showed that trade-offs between competitive abilities, and the relation between competitive abilities and consumption patterns, are major determinants of the dynamics of multispecies competition. Therefore, we chose combinations of species parameters that reflect the following physiological scenarios:

Scenario 1 Random species parameters. K and c were randomly chosen from a uniform distribution on the intervals [0,1] and [0.04,0.06], respectively.

Scenario 2 Trade-off between competitive abilities. If a species has a low K for one resource, it has a high K for the other resources. This trade-off is compatible with experimental data (Huisman & Weissing 2001b). The trade-off was achieved by choosing the Ks of a species randomly subject to the constraint that their mean equalled 0.5. The c values were again chosen randomly from a uniform distribution in the interval [0.04,0.06].

Scenario 3 Trade-off between competitive abilities, and a negative relation between competitive ability and resource content. The negative relation was obtained by choosing c directly proportional to K and adding some small random noise.

Scenario 4 Trade-off between competitive abilities, and a positive relation between competitive ability and resource content. The positive relation was obtained by choosing c directly proportional to $1 - K$ and adding some small random noise.

Scenario 5 Trade-off between competitive abilities, and a cyclic relation between competitive ability and resource content. That is, species with a high content of resource 1 are strong competitors for resource 2, species with a high content of resource 2 are strong competitors for resource 3, and species with a high content of resource 3 are strong competitors for resource 1.

Resource supply rates were set at $S = 10$ for all three resources. Remaining parameter values were as in Huisman & Weissing (1999).

EXTINCTION AND INVASION

Following Schippers *et al.* (2001), we say that a community is "supersaturated" if the number of species exceeds the number of limiting resources. For each of the five physiological scenarios, we tested the probability of supersaturation using two different approaches: an extinction approach and an invasion approach.

In the extinction approach, we started with 500 species at day 0. Each simulation was run for 100 000 days, to ensure that all transients were removed and the simulations approached the attractor. After 100 000 days we monitored how many species still remained above a threshold abundance of 0.1 and whether the system oscillated. Each scenario was simulated 1000 times.

In the invasion approach we started with a single species at day 0, and once every 50 days a new species was added with a low abundance of 0.1. In each simulation, we monitored during 10 million days how many species persisted above their initial abundance of 0.1. We ran five of these long-term simulations per scenario. The status of the simulations was reported every 1000 days, yielding 50 000 sampling points per scenario.

We note that our simulations assume environmental constancy for thousands of days, which is obviously unrealistic. With this approach, we do not wish to downplay the role of externally imposed nonequilibrium conditions in the real world. Rather, we removed external fluctuations on purpose, to focus on the key issue whether a high biodiversity can be maintained by internally generated nonequilibrium dynamics.

RESULTS

Extinction approach

For random species parameters, 1.6% of the simulations showed sustained fluctuations and supersaturation (Table 1). Assuming trade-offs between competitive abilities (scenario 2), the probability of supersaturation increased to 4.4%. Scenario 3 led mainly to coexistence of three species and to 9.3% supersaturation. Interestingly, in scenario 3 the species were not oscillating in the majority of cases labelled as supersaturation. Instead, neutral coexistence (*sensu* Hubbell 2001) was widespread. Scenario 4 led almost exclusively to dominance of a single species and no supersaturation at all. Scenario 5 yielded a high probability of 36.9% supersaturation. Moreover, in the latter scenario, 3.4% of the simulations showed nonequilibrium coexistence of more than 10 species (Table 1), and a few of these even showed coexistence of more than 20 species.

Invasion approach

Scenario 1 generated a species-poor community (Fig. 1A, Table 2). The number of species generally fluctuated between one and three, with a fourth species only very occasionally. Incorporation of trade-offs between competitive abilities (scenario 2) revealed a different picture (Fig. 1 B, Table 2). During part of the time, species abundances remained at equilibrium and diversity was low.

Table 1 Probability distribution (%) of the number of coexisting species, using the extinction approach

	Number of coexisting species							Mean # of species	Super-saturation
	1	2	3	4	5	6–10	> 10		
Scenario 1	25.0%	43.8%	29.6%	1.4%	0.2%	0.0%	0.0%	2.08	1.6%
Scenario 2	13.6%	23.5%	58.5%	3.9%	0.4%	0.1%	0.0%	2.54	4.4%
Scenario 3	0.2%	6.4%	84.1%	8.4%	0.9%	0.0%	0.0%	3.03	9.3%
Scenario 4	99.7%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	1.00	0.0%
Scenario 5	3.0%	4.3%	55.8%	23.1%	7.0%	3.4%	3.4%	3.90	36.9%

Data are based on 1000 simulations per scenario. Each simulation starts with 500 species, and is run for 100 000 days. Supersaturation occurs if there are more than three coexisting species. In all scenarios except scenario 3, we found species fluctuations in more than 90% of the simulations in which supersaturation was reported.

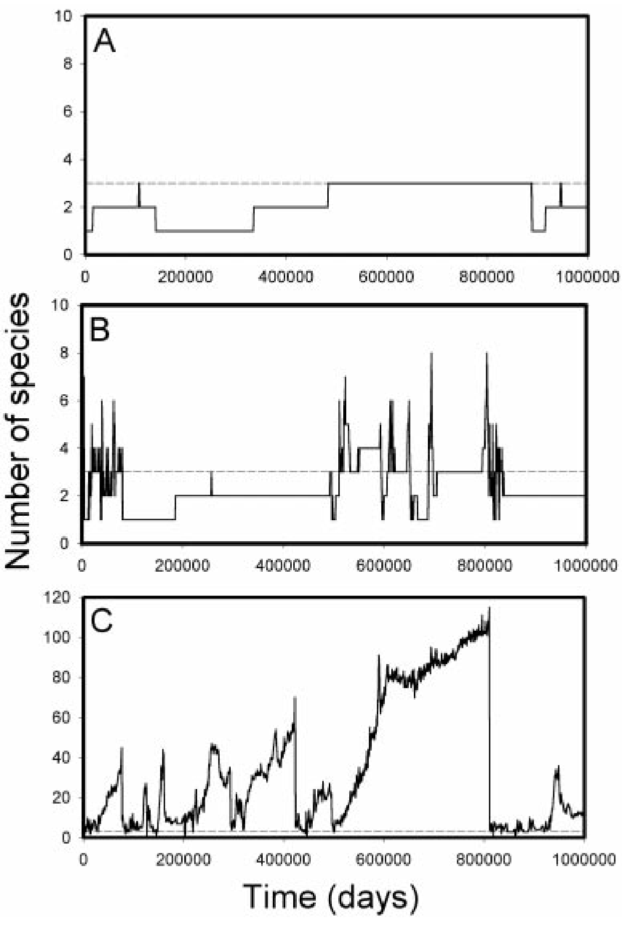

Figure 1 Time course of species diversity. Each simulation starts with a single species, and a new species is added once every 50 days. Simulations were run for a total of 10 million days, though only the first million days are shown here. (A) Random species parameters (scenario 1). (B) Trade-offs in competitive abilities, and random resource contents (scenario 2). (C) Trade-offs ian competitive abilities, and a cyclic relation between competitive ability and resource content (scenario 5). The horizontal dashed lines indicate the border between normal and supersaturated coexistence.

Then, all of a sudden, the species started to oscillate and species diversity increased. Until, suddenly, the whole system collapsed again to equilibrium conditions with a few species. These switches back and forth from equilibrium to nonequilibrium dynamics were observed repeatedly within the simulations. The back and forth switches led to a time average of more than 5% supersaturation in scenario 2, more than 11% supersaturation in scenario 3, and 70% supersaturation in scenario 5. In the latter scenario, species abundances fluctuated wildly, the mean number of species exceeded seven, and occasionally species diversity even increased to more than 100 species (Fig. 1C, Table 2).

DISCUSSION

Our results demonstrate that different assumptions on correlations between species traits lead to completely different predictions on the likelihood that competitive chaos contributes to the world's biodiversity.

Based on random species parameters, as in our scenario 1, Schippers *et al.* (2001; their Table 2) report 0.1% of supersaturation. This low percentage is not surprising, since Schippers *et al.* considered only six, nine or 12 species. The problem of using a few randomly constructed species is that most of these species will have poor parameter combinations, and therefore will be poor competitors. With a larger number of randomly constructed species, a much wider variability in parameter combinations can be sampled. Using 500 random species, we obtained supersaturation in 1.6% of the simulations. Although this figure is still rather small, it is significantly higher than the figure reported by Schippers *et al.* Random species parameters are unlikely to occur in nature, however, and therefore do not provide much insight into the likelihood of supersaturation in the real world.

Incorporation of plausible trade-offs in competitive abilities (Tilman 1982; Sommer 1986; Huisman & Weissing 2001b) increases the likelihood of supersaturation (scenario 2). Given these trade-offs in competitive abilities, our results show that the probability of supersaturation depends on the

Table 2 Probability distribution (%) of the number of coexisting species, using the invasion approach

	Number of coexisting species				Mean # of species	Max # of species	Super-saturation
	1–3	4–10	11–20	> 20			
Scenario 1	99.9%	0.1%	0.0%	0.0%	1.67	5	0.1%
Scenario 2	94.7%	5.3%	0.0%	0.0%	2.02	14	5.3%
Scenario 3	88.4%	11.6%	0.0%	0.0%	3.13	9	11.6%
Scenario 4	100%	0.0%	0.0%	0.0%	1.00	2	0.0%
Scenario 5	30.0%	57.1%	7.2%	5.7%	7.08	115	70.0%

Also shown are the mean number and maximum number of coexisting species. Data are based on five simulations of 10 million days each per scenario. Each simulation starts with one species, and a new species is added once every 50 days. Only those species were counted that exceeded their initial abundance. Supersaturation occurs if there are more than three coexisting species.

relation between competitive abilities and resource contents (scenarios 3–5). One might argue that physiological plausibility would favour scenario 3, which assumes a negative correlation between competitive abilities and resource contents. That is, if a species has a high content of a particular element in its tissue (high c), it is likely that this species needs a high availability of this element in the environment in order to grow adequately (high K, meaning low competitive ability). This pattern is supported by silica data from freshwater diatoms (Huisman & Weissing 2001b). The probability of supersaturation in scenario 3 is about 10%. Scenario 4 assumes the opposite pattern – a positive correlation between competitive ability and resource content – which seems physiologically less plausible than scenario 3. In contrast to scenario 3, scenario 4 predicts that the probability of supersaturation is extremely low: in most cases only one species survives. The physiological plausibility of scenario 5 is not clear. It assumes that a high content of one element facilitates the acquisition of another element in a cyclic manner. Intriguingly, in scenario 5 the probability of supersaturation may reach 37% in the extinction approach and 70% in the invasion approach, and the number of coexisting species can be staggeringly high.

On the basis of these findings, we conclude that physiological and life-history patterns are major determinants of the likelihood that species interactions generate nonequilibrium dynamics, and thereby enhance the biodiversity of natural communities. It will be an important task for future studies in physiology, ecology, and evolution to pinpoint those combinations of species traits that are most widespread in real ecosystems.

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BIOSKETCH

Jef Huisman's research interests include competitive interactions, complex dynamics, biodiversity, the interplay between fluid dynamics and plankton dynamics, phytoplankton ecology, and plant–herbivore interactions.

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