Phylogenetic analyses

For the taxa analysed, all 105 species had *rbcL* sequences, and 93, 88, 98 and 101 species had *atpB*, 18S rDNA, *matR* and *atp1* sequences, respectively (missing data for critical taxa: *Kadsura*: 18S rDNA, *Trimenia*: *atp1*, *Cycas* and *Zamia*: *atpB*, and *Metasequoia* and *Podocarpus*: *matR*). Each taxon had data for at least three out of the five genes. Parsimony (equal weighting) analyses were carried out using PAUP*4.0b2 (ref. 30). To search for islands of shortest trees, a heuristic search was conducted using 1,000 random taxon-addition replicates, one tree held at each step during stepwise addition, TBR branch swapping, steepest descent option in effect. MulTrees option in effect and no upper limit of MaxTrees. Both bootstrap and jackknife (50% character deletion) analyses were conducted using 1,000 resampling replicates and the same tree search procedure as described above except with simple taxon addition. The data matrix is available as Supplementary Information at http://www.nature.com.

All *atp1* and *matR*, and some *atpB*, *rbcL* and 18S rDNA sequences were generated in this study, deposited in GenBank under accession numbers AF197576-AF197815; remaining sequences were from GenBank and ref. 27.

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Biodiversity of plankton by species oscillations and chaos

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Biodiversity has both fascinated and puzzled biologists[1]. In aquatic ecosystems, the biodiversity puzzle is particularly troublesome, and known as the 'paradox of the plankton'[2]. Competition theory predicts that, at equilibrium, the number of coexisting species cannot exceed the number of limiting resources[3–6]. For phytoplankton, only a few resources are potentially limiting: nitrogen, phosphorus, silicon, iron, light, inorganic carbon, and sometimes a few trace metals or vitamins. However, in natural waters dozens of phytoplankton species coexist[2]. Here we offer a solution to the plankton paradox. First, we show that resource competition models[6–10] can generate oscillations and chaos when species compete for three or more resources. Second, we show that these oscillations and chaotic fluctuations in species abundances allow the coexistence of many species on a handful of resources. This model of planktonic biodiversity may be broadly applicable to the biodiversity of many ecosystems.

We consider a well-known resource competition model[6–10] that has been tested and verified extensively using competition experiments with phytoplankton species[8,11–16]. 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 dynamics of the species depend on the availabilities of the resources. The resource availabilities, in turn, depend on the rates of resource supply and the amount of resources consumed by the phytoplankton species. This gives the following model[6–9]:

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

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, ..., R_k)N_i \quad j = 1, ..., k \tag{2}$$

Here $\mu_i(R_1, ..., R_k)$ is the specific growth rate of species i as a function of the 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. We assume that the specific growth rates follow the Monod equation[17], and are determined by the resource that is most limiting according to Liebig's 'law of the minimum'[18]:

$$\mu_i(R_1, ..., R_k) = \min\left(\frac{r_i R_1}{K_{1i} + R_1}, ..., \frac{r_i R_k}{K_{ki} + R_k}\right) \tag{3}$$

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 function. This is a standard formulation used in numerous phytoplankton competition models[6–10].

When solved for equilibrium, this competition model predicts that the number of species cannot exceed the number of limiting resources. More precisely, there are k unknown resource availabilities in equation (1). Hence, in the generic case, the number of equilibrium solutions that satisfy equation (1) with $N_i > 0$ cannot

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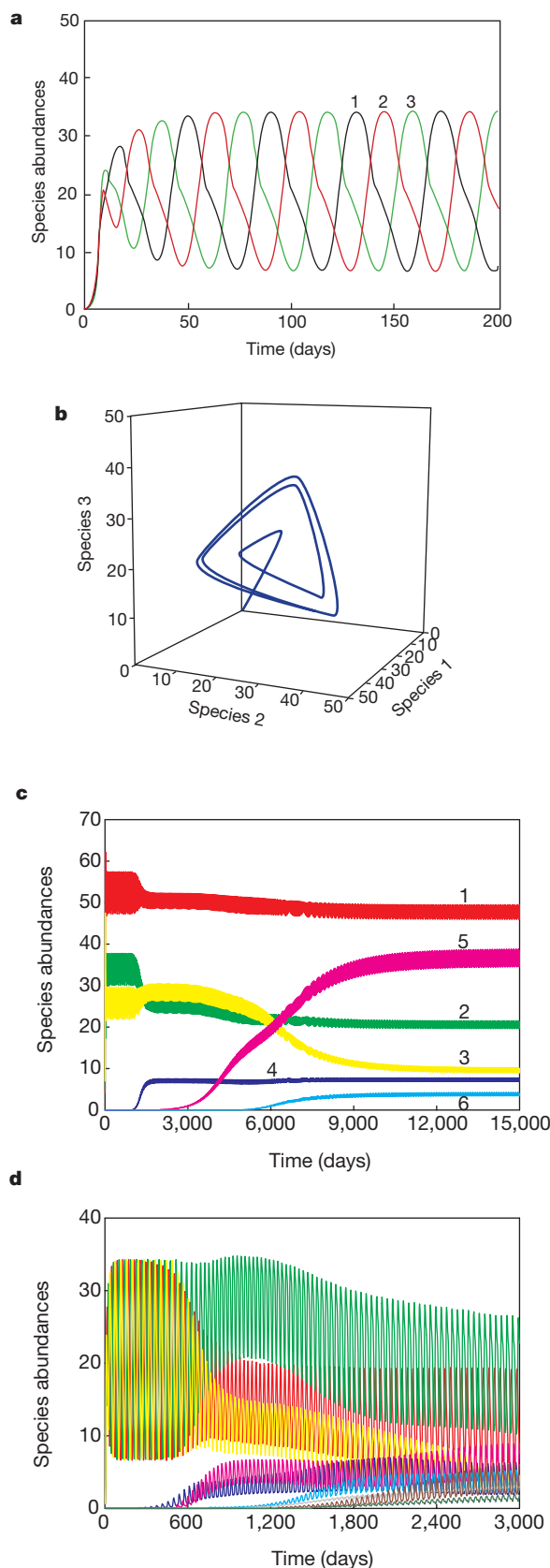
Figure 1 Oscillations on three resources. **a**, Time course of the abundances of three species competing for three resources. **b**, The corresponding limit cycle. **c**, Small-amplitude oscillations of six species on three resources. **d**, Large-amplitude oscillations of nine species on three resources.
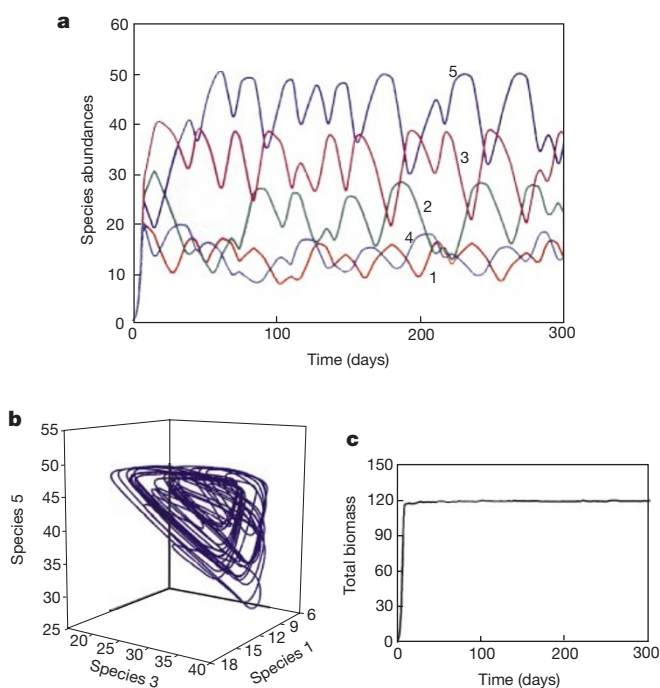

Figure 2 Chaos on five resources. **a**, Time course of the abundances of five species competing for five resources. **b**, The corresponding chaotic attractor. The trajectory is plotted for three of the five species, for the period from $t = 1,000$ to $t = 2,000$ days. **c**, Time course of total community biomass.

exceed k. The surplus of species should be competitively excluded. This leads to the so-called "principle of competitive exclusion"[3–6]: at most $n \leqslant k$ species can coexist on k limiting resources. We note that this principle is based on equilibrium arguments. It assumes that competition leads to a stable species composition.

Several ways to circumvent the competitive exclusion principle and to explain the species diversity of planktonic communities have been proposed[12,19–21]. These solutions usually invoke factors external to the phytoplankton, like selective predators, spatial heterogeneity, or temporal variability caused by fluctuating weather conditions. Here we develop a solution for the plankton paradox that does not invoke external factors. We consider a constant and homogeneous environment, and derive an explanation for biodiversity based on the dynamics of competition itself.

The dynamics of our competition model are well known for one or two limiting resources[6–10]. In a constant environment, the system approaches a stable equilibrium. If all species are limited by the same resource, the strongest competitor displaces all other species and then approaches a monoculture equilibrium. If one species is limited by one resource, and another species by the other resource, then two species may stably coexist. Competition experiments with phytoplankton species support these predictions[8,11–16].

Natural phytoplankton communities, however, are frequently limited by more than two resources[22–24]. What happens if the competition model is extended to three species and three resources? For certain species combinations, three-species competition generates sustained oscillations (Fig. 1a, b). This occurs if the species displace each other in a cyclic fashion. That is, species 1 is the better competitor for resource 1 but becomes limited by resource 2, species
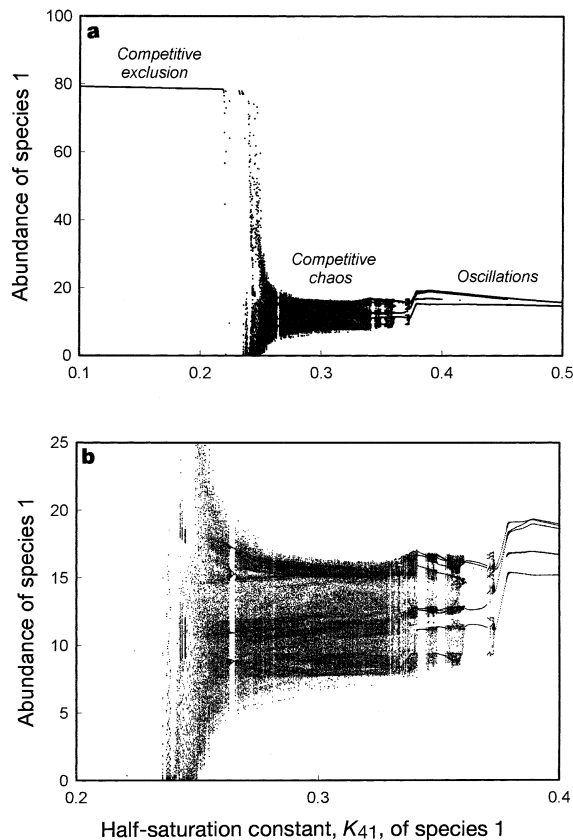
Figure 3 Bifurcation diagram, for five species competing for five resources. The graphs show the local minima and maxima of species 1, plotted during the period from $t = 2,000$ to $t = 4,000$ days, as a function of the half-saturation constant K_{41}. Part of **a** is magnified in **b**.

Figure 4 Competitive chaos and the coexistence of 12 species on five resources. **a**, The abundances of species 1–6; **b**, the abundances of species 7–12.

2 is the better competitor for resource 2 but becomes limited by resource 3, species 3 is the better competitor for resource 3 but becomes limited by resource 1, and so on. The amplitude of the species oscillations may range from small cycles (Fig. 1c) to large oscillations (Fig. 1d), depending on the precise parameter settings. We note that the oscillations are not generated by fluctuating weather conditions or other sources of external variability. The species oscillations are generated by the competition process itself.

Non-equilibrium conditions allow the coexistence of more species than limiting resources[5,12,20]. Hence, it is conceivable that the oscillations generated by competition create an opportunity to increase species diversity. To test this idea, at $t = 1,000$ we added a fourth species to the model simulations (Fig. 1c). This fourth species is able to coexist on the oscillations generated by the three species already present. Also, a fifth species and a sixth species can be sustained. The amplitudes of the oscillations in Fig. 1c are so small that the oscillations would probably go unnoticed behind the noise of any real-world data set. Yet even these small-amplitude oscillations are apparently sufficient for the coexistence of six species on three resources. Similar results were obtained with large-amplitude oscillations (Fig. 1d): in the end, a total of nine species coexist on three resources.

Simulations revealed similar patterns with four limiting resources. For certain species combinations, competition for four resources generates oscillations. These oscillations allow the coexistence of many species on four resources (J.H. and F.J.W., unpublished results).

With five resources, many simulations show irregular species fluctuations (Fig. 2a). The pattern of species replacement never
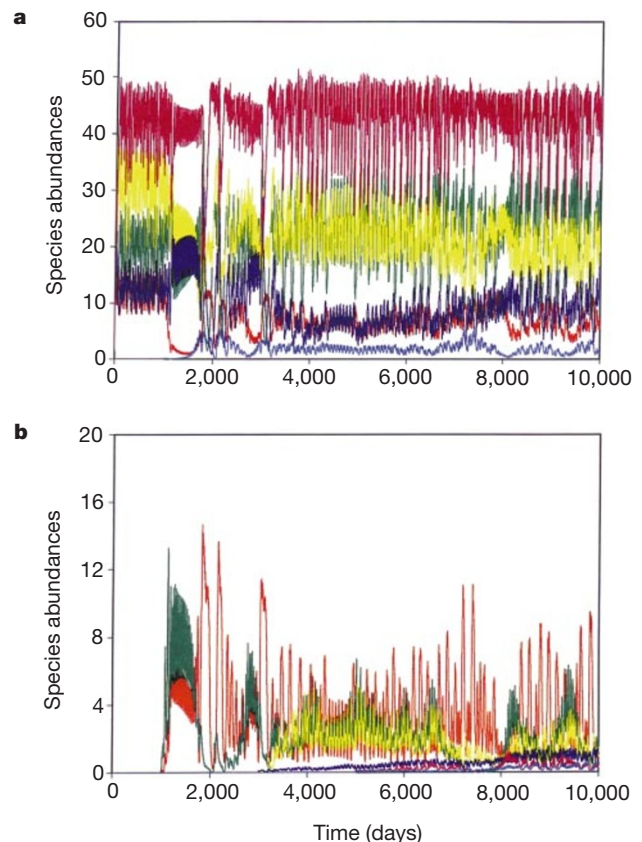
repeats itself. Each time one species tries to become dominant, there are several other species that invade. The species invade at different rates, and, hence, the abundances of the species continuously diverge. Yet all species abundances remain bounded because resources are limited. The continuous divergence of trajectories within a bounded region of phase space is a characteristic feature of chaos (Fig. 2b). In fact, the species dynamics show sensitive dependence on initial conditions. Extensive simulations reveal that trajectories that start with almost identical species abundances slowly diverge, and gradually become completely uncorrelated. The chaotic ups and downs of the individual species abundances go together with a near constancy of total community biomass (Fig. 2c). This supports the hypothesis[25–27] that competition in high-diversity ecosystems may increase the variability at the species level while at the same time it may stabilize global ecosystem properties like total community biomass.

The bifurcation diagram in Fig. 3 illustrates how the model predictions depend on the parameter regime. We choose K_{41}, the half-saturation constant for resource 4 of species 1, as bifurcation parameter. Resource 4 is the resource that most limits the growth rate of species 1. If species 1 is a strong competitor for resource 4 ($K_{41} < 0.2$), species 1 excludes all other species (Fig. 3). If species 1 is a weak competitor for resource 4 ($K_{41} > 0.4$), competition leads to mild oscillations or stable coexistence. Competitive chaos occurs in the intermediate range, where species 1 is an "intermediate competitor" ($0.24 < K_{41} < 0.35$). Given the relatively broad parameter range that leads to chaos, it seems plausible that such competitors indeed occur in real-world plankton communities. We ran numerous additional simulations, with many parameter combinations

(not shown). This confirmed that the pattern in Fig. 3 is quite general: roughly speaking, competitive chaos occurs whenever each species is an intermediate competitor for the resources that most limit its growth rate. Chaotic fluctuations in species abundances allow the coexistence of many more species than limiting resources (Fig. 4).

The possibility that competition models may generate oscillations and chaos was already recognized in the mid 1970s[28–30]. Also, it is well established that non-equilibrium conditions may favour species coexistence[5,12,20]. What is new here is that we found both phenomena in a single competition model. Moreover, our findings do not stem from an artificially constructed model, but are based on one of the standard models of phytoplankton competition[6–16]. We conclude that the biodiversity of plankton communities need not be explained by external factors, but can be based on the competition process itself. Once a plankton community is sufficiently complex to generate its own non-equilibrium dynamics, the number of coexisting phytoplankton species may greatly exceed the number of limiting resources, even in a constant and well-mixed environment. In this sense, the paradox of the plankton is essentially solved.

These findings have some wider implications that go beyond the plankton system studied here. First, within the biological realm, our explanation for planktonic biodiversity may serve as a conceptual model for the biodiversity of many other ecosystems as well. Second, our results demonstrate that competition, in its broadest sense, is not a simple process. Competitive systems may display highly dynamical phenomena, with continuous shifts and changes in species composition. Third, our results show that competition is not necessarily a destructive force. Competitive interactions that generate oscillations and chaos may allow the persistence of a great diversity of competitors on only a few limiting resources. □

Methods

Here we give the parameter values used in the model simulations. Simulations were based on equations (1) and (2), with specific growth rates according to equation (3). The model is parametrized for phytoplankton species, with a timescale expressed in days. We used $r_i = 1 \, d^{-1}$ and $m_i = D = 0.25 \, d^{-1}$ for all species. These are typical values for phytoplankton grown in chemostats[8,11–16]. Initial conditions were $R_j = S_j$ and $N_i = 0.1 + i/100$ for all species i present at $t = 0$. Species added at a later time T started with $N_i = 0.1$ at $t = T$.

Half-saturation constants and resource contents for each resource j and species i are given below, using the compact 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, and different rows represent different resources. Whereas our figures show coexistence for the first few thousand days, species continued to coexist in the simulations for more than 250,000 days.

Figures 1a, b use species 1–3 of Fig. 1d.

In Fig. 1c, $S_1 = 6$, $S_2 = 10$, $S_3 = 14$, and K and C are given by:

$$K = \begin{pmatrix} 1.00 & 0.90 & 0.30 & 1.04 & 0.34 & 0.77 \\ 0.30 & 1.00 & 0.90 & 0.71 & 1.02 & 0.76 \\ 0.90 & 0.30 & 1.00 & 0.46 & 0.34 & 1.07 \end{pmatrix}$$

$$C = \begin{pmatrix} 0.04 & 0.07 & 0.04 & 0.10 & 0.03 & 0.02 \\ 0.08 & 0.08 & 0.10 & 0.10 & 0.05 & 0.17 \\ 0.14 & 0.10 & 0.10 & 0.16 & 0.06 & 0.14 \end{pmatrix}$$

Species 1–3 start at $t = 0$, species 4 at $t = 1,000$, species 5 at $t = 2,000$, species 6 at $t = 5,000$.

In Fig. 1d, $S_1 = 10$, $S_2 = 10$, $S_3 = 10$ and K and C are given by:

$$K = \begin{pmatrix} 1 & 0.75 & 0.25 & 0.7 & 0.2 & 0.65 & 0.68 & 0.38 & 0.46 \\ 0.25 & 1 & 0.75 & 0.2 & 1.01 & 0.55 & 0.83 & 1.10 & 0.85 \\ 0.75 & 0.25 & 1 & 1.10 & 0.7 & 0.95 & 0.6 & 0.5 & 0.77 \end{pmatrix}$$

$$C = \begin{pmatrix} 0.10 & 0.20 & 0.15 & 0.05 & 0.01 & 0.40 & 0.30 & 0.20 & 0.25 \\ 0.15 & 0.10 & 0.20 & 0.15 & 0.30 & 0.35 & 0.25 & 0.02 & 0.35 \\ 0.20 & 0.15 & 0.10 & 0.25 & 0.05 & 0.20 & 0.40 & 0.15 & 0.10 \end{pmatrix}$$

Species 1–3 start at $t = 0$, species 4 at $t = 250$, species 5 at $t = 500$, species 6 at $t = 750$, species 7 at $t = 1,000$, species 8 at $t = 1,250$, species 9 at $t = 1,500$.

Figs 2 and 3 use species 1–5 of Fig. 4.

In Fig. 4, $S_1 = 6$, $S_2 = 10$, $S_3 = 14$, $S_4 = 4$, $S_5 = 9$, and K and C are given by:

$$K = \begin{pmatrix} 0.39 & 0.34 & 0.30 & 0.24 & 0.23 & 0.41 & 0.20 & 0.45 & 0.14 & 0.15 & 0.38 & 0.28 \\ 0.22 & 0.39 & 0.34 & 0.30 & 0.27 & 0.16 & 0.15 & 0.05 & 0.38 & 0.29 & 0.37 & 0.31 \\ 0.27 & 0.22 & 0.39 & 0.34 & 0.30 & 0.07 & 0.11 & 0.05 & 0.38 & 0.41 & 0.24 & 0.25 \\ 0.30 & 0.24 & 0.22 & 0.39 & 0.34 & 0.28 & 0.12 & 0.13 & 0.27 & 0.33 & 0.04 & 0.41 \\ 0.34 & 0.30 & 0.22 & 0.20 & 0.39 & 0.40 & 0.50 & 0.26 & 0.12 & 0.29 & 0.09 & 0.16 \end{pmatrix}$$

$$C = \begin{pmatrix} 0.04 & 0.04 & 0.07 & 0.04 & 0.04 & 0.22 & 0.10 & 0.08 & 0.02 & 0.17 & 0.25 & 0.03 \\ 0.08 & 0.08 & 0.08 & 0.10 & 0.08 & 0.14 & 0.22 & 0.04 & 0.18 & 0.06 & 0.20 & 0.04 \\ 0.10 & 0.10 & 0.10 & 0.10 & 0.14 & 0.22 & 0.24 & 0.12 & 0.03 & 0.24 & 0.17 & 0.01 \\ 0.05 & 0.03 & 0.03 & 0.03 & 0.03 & 0.09 & 0.07 & 0.06 & 0.03 & 0.03 & 0.11 & 0.05 \\ 0.07 & 0.09 & 0.07 & 0.07 & 0.07 & 0.05 & 0.24 & 0.05 & 0.08 & 0.10 & 0.02 & 0.04 \end{pmatrix}$$

Species 1–5 start at $t = 0$, species 6–8 at $t = 1,000$, species 9 and 10 at $t = 3,000$, species 11 and 12 at $t = 5,000$.

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