Stability of Chemostat-Type Equations and Biodiversity

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Biodiversity has long 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 in lakes and oceans, the limiting nutrient resources for phytoplankton are known to be less than three kinds: phosphorus or nitrogen[7]. In such ecosystems, however, dozens of phytoplankton species coexist[2,7].

We discuss a model based on the simplest case of well-known resource competition models[6,8-11] that has been tested and verified extensively using competition experiments with phytoplankton species[9,12-18]. Consider n species and one resource. Let N_i denote the population abundance of species i, and let R denote the availability of the resource. The dynamics of the species depend on the availability of the resource and the crowding effect caused by their own population density. The resource availability depends on the rate of resource supply and the amount of a

resource consumed by the species. This gives the following model:

$$\frac{dN_i}{dt} = N_i \left(c_i(N_1, \cdots, N_n)\mu_i(R) - d_i \right) \quad i = 1, 2, \cdots n$$

$$\frac{dR}{dt} = D(S - R) - \sum_{i=1}^{n} \gamma_i \mu_i(R) N_i \tag{1}$$

Here, $c_i(N_1, \cdots, N_n)$ reflects the crowding effect on the specific growth or reproduction of species i; $\mu_i(R)$ is the specific growth rate of species i as a function of the resource availability; d_i is the specific death rate of species i; D is the system's turnover rate; S is the supply concentration of the resource; and γ_i is the content of the resource in species i. We assume that the specific growth rates follow the Monod equation[19], and are determined by $\mu_i(R) = (r_i R)/(K_i + R)$, where r_i is the maximum specific growth rate of species i and K_i is the half-saturation constant for the resource of species i. For natural phytoplankton communities, crowding may have a negative effect on their own growth or reproduction. It is natural to assume that c_i is a decreasing function in all arguments.

What happens if the crowding effect on the specific growth of species i, respectively, is limited to the case where $c_i(N_1, \cdots, N_n) = f_i(N_i)$ with $f_i(0) = 1$? Let

$$\lambda_i = \frac{K_i d_i}{r_i - d_i} > 0$$

and assume $\lambda_1 \leq \lambda_2 \leq \cdots \leq \lambda_n$ without loss of generality. We have the following:

Theorem 1. *(1) has a unique stable interior equilibrium if and only if $\lambda_n < S$ and $R_{i-1}^* > \lambda_i$ ($i = 2, 3, \cdots, n$) hold, where R_{i-1}^* represents the R component of the coordinates of an interior equilibrium for a subsystem $(R, N_1, \cdots, N_{i-1})$*

The proof needs an algebraic method for the existence and uniqueness of an interior equilibrium, and uses the V-L stability theory for its stability[24]. $\frac{K_i d_i}{S(r_i - d_i)}$ is the break-even concentration of species i[25]. We here call it as the *crude* break-even concentration of species i. λ_i is then called the *net* break-even concentration of species i, which is its crude break-even concentration multiplied by the supply concentration of the resource. The case $n = 2$, that is, the case where two species and one resource are considered, implies permanence as well as stability at a unique interior equilibrium by constructing a Liapunov function.

It is known that competition models with the crowding effect (or intraspecific interference) on the growth of species enable the stable coexistence of many species for homogeneous resources that reproduce by themselves[26-34]. What is new here is that we found the mathematically ensured stable coexistence situation of an unlimited number of species in a competition model even for a single nutrient resource (or one abiotic resource). The model is based on the simplest case with the crowding effect at the specific reproduction level. In general, the limiting nutrient resource to phytoplankton species in lakes and oceans is phosphorus or nitrogen[7]; at most two limiting resources. Moreover, the non-equilibrium dynamics cannot lead the robust coexistence of species even if oscillations and chaos in species abundances allow the coexistence of many more species than limiting resources[12]. Without the robust coexistence of species, it may be hardly possible that natural phytoplankton communities have survived against some environmental fluctuations. Our results state that the robust coexistence occurs whenever each species has self-inhibitory (in its reproduction) well-balanced to the resource. We conclude that the biodiversity of plankton communities not only need be explained by external factors[12,14,21-23] and come from the competition process itself on three or more nutrients[12], but also could be based on the crowding effect to their own growth at the specific reproduction level. Once a plankton community has the well-balanced crowding effect to its own population growth, the number of coexisting phytoplankton species can greatly exceed the number of limiting resources, even for a single limiting resource and even in a constant and well-mixed environment.

References

1. Wilson, E. O. *The Diversity of Life* (Belknap, Cambridge, Massachusetts, 1992).

2. Hutchinson, G. E. The paradox of the plankton. *Am. Nat.* **95**, 137-145 (1961).

3. Hardin, G. The competitive exclusion principle. *Science* **131**, 1292-1298 (1960).

4. Phillips, O. M. The equilibrium and stability of simple marine biological systems. I. Primary nutrient consumers. *Am. Nat.* **107** 73-93 (1973).

5. Armstrong, R. A. & McGehee, R. Competitive exclusion. *Am. Nat.* **115**, 151-170

(1980).

6. Grover, J. P. *Resource Competition* (Chapman and Hall, London, 1997).

7. Odum, E. P. *Fundamentals of Ecology* (W. B. Saunders Company, Philadelphia, Pa. 19105, 1971).

8. Leon, J. A. & Tumpson, D. B. Competition between two species for two complementary or substitutable resources. *J. Theor. Biol.* **50**, 185-201 (1975).

9. Tilman, D. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**, 338-348 (1977).

10. Hsu, S. B., Cheng, K. S. & Hubbell, S. P. Exploitative competition of microorganisms for two complementary nutrients in continuous cultures. *SIAM J. Appl. Math.* **41**, 422-444 (1981).

11. Huisman, J. & Weissing, F. J. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology* **75**, 507-520 (1994).

12. Huisman, J. & Weissing, F. J. Biodiversity of plankton by species oscillations and chaos. *Nature* **402**, 407-410 (1999).

13. Holm, N. P. & Armstrong, D. E. Role of nutrient limitation and competition in controlling the populations of *Asterionella formosa* and *Microcytis aeruginosa* in semicontinuous culture. *Limnol. Oceanogr.* **26**, 622-634 (1981).

14. Sommer, U. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnol. Oceanogr.* **30** 335-346 (1985).

15. Sommer, U. Nitrate- and silicate-competition among Antarctic phytoplankton. *Mar. Biol.* **91** 345-351 (1986).

16. Van Donk, E. & Kilham, S. S. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. *J. Phycol.* **26**, 40-50 (1990).

17. Rothhaupt, K. O. Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. *Ecology* **77**, 716-724 (1996).

18. Huisman, J., Jonker, R. R., Zonneveld, C. & Weissing, F. J. Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology*

80, 211-222 (1999).

19. Monod, J. La technique de culture, théorie et applications. *Ann. Inst. Pasteur (Paris)* **79** 390-410 (1950).

20. Von Liebig, J. *Die organische Chemie in ihrer Anwendung auf Agrikultur und Physiolosie* (Friedrich Vieweg, Braunschweig, 1840).

21. Richerson, P. J. Armstrong, R. & Goldman, C. R. Contemporaneous disequilibrium: a new hypothesis to explain the paradox of the plankton. *Proc. Natl Acad. Sci. USA* **67**, 1710-1724 (1970).

22. Levins, R. Coexistence in a variable environment. *Am. Nat.* **114**, 765-783 (1979).

23. Padisák, J., Reynolds, C. S. & Sommer, U. (eds) The intermediate disturbance hypothesis in phytoplankton ecology. *Hydrobiologia* **249** 1-199 (1993).

24. Hofbauer, J. & Sigmund, K. *The theory of evolution and dynamical systems* (Cambridge university press, Cambridge, 1988).

25. Smith, H. L. & Waltman, P. *The theory of the chemostat: Dynamics of Microbial Competition* (Cambridge university press, 1995).

26. Kuang, Y., Fagan, W. F., & Loladze, I. Biodiversity, habitat area, resource growth rate and interference competition. *Bull. Math. Biol.* **62**, 497-518 (2003).

27. Case, T. J. & Gilpin M. E. Interference competition and niche theory. *Proc. Natl. Acad. Sci. USA* **71**, 3073-3077 (1974).

28. Goh, B. S. Global stability in many species systems. *Am. Nat.* **111**, 135-143 (1977).

29. Case, T. J., & Casten R. G. Global stability and multiple domains of attraction in ecological systems. *Am. Nat.* **113**, 705-714 (1979).

30. Abrams, P. A. Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80-96 (1984).

31. Abrams, P. A. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theor. Popul. Biol.* **29**, 107-160 (1986).

32. Abrams, P. A. Alternative models of character displacement and niche shift 2: displacement when there is competition for a single resource. *Am. Nat.* **130**, 271-282 (1987).

33. Abrams, P. A. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer resource system. *Am. Nat.* **152**, 114-128 (1998).

34. Abrams, P. A. The effect of density-independent mortality on the coexistence of exploitative competitors for renewing resources. *Am. Nat.* **158**, 459-470 (2001).