Resource competition

Key concepts

- Competitive exclusion principle

- Niche partitioning

- Paradox of the plankton

- R^* theory

- Zero net growth isocline

- Conditions for coexistnce

The phytoplankton of Lake Michigan

Diatoms such as *Asterionella formosa* and *Synedra ulna* are the main source of carbon to large, mid-latitude, mesotrophic lakes. Both species require dissolved Silicon in the form of silicate (SiO_2) for the formation of frustrules, the hard, porous cell walls exhibited by this group of algae. Indeed, silicate is one of two nutrients that are typically limiting to diatom growth. (The other is Phosphorus, in aqueous solution typically in the form of phosphate, PO_4^{3-}.)

In Lake Michigan, *A. formosa* is the dominant species. However, *Synedra ulna* may also be found, predominantly nearshore areas. Otherwise these species are very similar in their resource requirements. If *A. formosa* thrives in open water, what then explains why *S. ulna* fails to do so? Conversely, why does *S. ulna* replace *A. formosa* in nearshore areas? Answers to these questions are provided by the theory of competition for a single resource.

Figure 1: The pennate diatom (*Asterionella formosa*).

Competitive exclusion principle

The principle of competitive exclusion is a cornerstone of species interaction theory. One version of the theory was expressed by naturalist
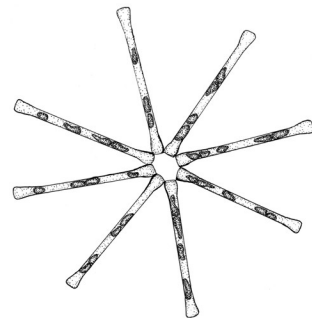
Joseph Grinnell in 1904 as a means to explain the restricted distribution of sub-species of chestnut-backed chicakadee (*Parus rufescens*) in Western North America:

> Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other; the one longest exposed to local conditions, and hence best fitted, though ever so slightly, will survive, to the exclusion of any less favored would-be "invader". However, should some new contingency arise, placing the native species at a disadvantage, such as the introduction of new plants, then there might be a fair chance for a neighboring species to gain a foothold, even ultimately crowding out the native form.[1]

This early reference to the competitive exclusion principle already identifies some of its key features, namely:

- Both resources ("food habits") and other environmental conditions ("introduction of new plants") may be important to species' persistence

- The outcome of competition is likely to be exclusion of one species

- The determination of the species to be excluded is based on differences in fitness, and

- Even small differences in fitness may be sufficient to result in competitive exclusion

These observations are the basis for both Grinnell's early geographic *niche theory*[2] and the modern one introduced by Hutchinson[3]. A more precise description of the principle was articulated by Hardin[4]: If

- two noninterbreeding populations occupy the same ecological niche,

- are *sympatric* (occupy the same geographic territory),

- and, population A is fitter than population B,

then A will eventually displace B, which will become extinct.

Paradox of the plankton

The competitive exclusion principle presents a scientific conundrum. On one hand, ecological and evolutionary theory and a large quantity of experimental evidence supports the competitive exclusion principle. On the other hand, many communities, particularly producive ones like tropical forests, coral reefs, and salt marshes exhibit an extraordinary diversity of life forms coexisting. How do all these species coexist? A speculative answer, referred to as *niche partitioning* is

[1] J Grinnell. The origin and distribution of the chestnut-backed chickadee. *The Auk*, 21(3):364–382, 1904

[2] J. Grinnell. The Niche-Relationships of the California Thrasher. *The Auk*, 34:427–433, 1917

[3] G.E. Hutchinson. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22:415–427, 1957

[4] G Hardin. The competitive exclusion principle. *Science*, 131(3409):1292–1297, 1960

that species specialize, very finely differentiating among available resources, adapting to their very specialized use, and partitioning accordingly, perhaps more finely than may be apparent to even a very observant naturalist. Possibly this explanation might hold for structurally complex habitats (such as tropical forests, coral reefs, and and salt marshes). By contrast, if niche partitioning is the main cause of species coexistence, then competitive exclusion should apply in very homogeneous environments, which should therefore exhibit very low levels of species diversity. In a famous article[5], G. Evelyn Hutchinson observed that the ocean is in fact an extremely homogeneous environment, exhibiting very few gradients with the chief one being light (correlated with depth). Yet, four different sets of diatom data showed around 40 species to be coexisting, which he called the *paradox of the plankton.*

[5] G Evelyn Hutchinson. The paradox of the plankton. *The American Naturalist*, 95(882):137–145, 1961

Equilibrium theory of competition for a single resource

Before addressing such broad coexistence, it is instructive to understand the competitive exclusion principle in greater detail. We will begin by studying two species competing for a single resource. The theory of this special case was developed in the 1970s and 1980s by Tilman and colleagues.[6] For illustration, we assume that the effects of resource limitation are expressed in depressed reproduction while mortality remains constant. Thus, for instance, as the concentration of silica declines, the production of new diatoms is reduced. For unicellular organisms such as diatoms, reproduction (birth rate) as a function of resource concentration may be expressed using the Monod equation,

$$b(R) = r\frac{R}{k + R} \tag{1}$$

where r is the intrinsic rate of of increase (maximum population growth rate), k is a the "half saturation constant", and R is the concentration or quantity of resource available. Since mortality (denoted m) is independent of resource concentration, we have an equation for the per capita population growth rate expressed exclusively in terms of the resource concentration R:

$$\frac{1}{n}\frac{dn}{dt} = b(R) - m = r\frac{R}{k + R} - m. \tag{2}$$

Plots of equation 1 for two hypothetical species a and b are shown in Figure 2. Mortality is a horizontal line in this plane.

How do we determine under what conditions species a and b grow, decline, or remain at the same size? We know that a population is at equilibrium when the per capita population growth rate is 0. By

[6] David Tilman. Resource Competition between Plankton Algae: An Experimental and Theoretical Approach. *Ecology*, 58(2):338–348, 1977; David Tilman, Mark Mattson, and Sara Langer. Competition and nutrient kinetics along a temperature gradient: An experimental test of a mechanistic approach to niche theory. *Limonology And Oceanography*, 26(6): 1020–1033, 1981; and D. Tilman, S.K. Kilham, and P. Kilham. Phytoplankton Community Ecology: The Role of Limiting Nutrients. *Annual Review of Ecology and Systematics*, 13:349–372, 1982
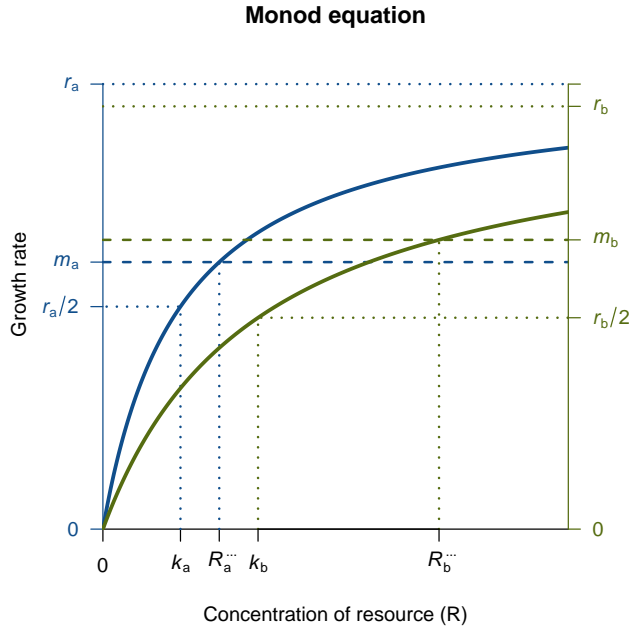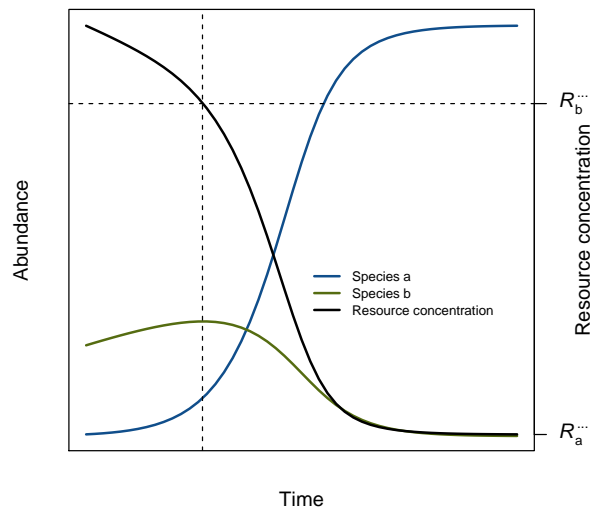
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Monod equation

Figure 2: Monod function for the reproduction rate of two species (solid lines) plotted against mortality (dashed lines). R^* values and other key quantities are indicated along the axes.

rearranging equation 2 we see that this occurs when the resource-dependent birth rate is equal to mortality, which is the intersection of the species birth rate in Figure 2 with its (constant) mortality curve. This point is designated R^*. Populations in environments enriched in resource compared with this point (the the right of the species-specific R^* in Figure 2) will increase in size; populations depleted in resourcs compared with R^* will decline. If we consider a population initially very enriched in resources, say to the right of R_b^* in Figure 2, then all species may be able to grow. However as the populations of species a and b sequester resources from the environment, its concentration will be reduced moving the system from right to left along the x-axis. When the concentration of resources in the environment reaches R_b^*, species b will be at equilibrium, with the birth and death rates perfectly balanced. Under this condition species a will continue to grow, however, and continue to sequester resources. As a consequence, the system will continue to move from right to left. As soon as $R < R_b^*$, mortality in species b will exceed reproduction and the population will begin to decline. It is clear from Figure 2 that as this occurs, since species a is still able to sequester resources and grow, conditions will only deteriorate further for species b. In fact, species a will continue sequestering and depleting R until it reaches its own equilibrium at R_a^*. At this point species b (if it still persists in the ecosystem) is declining dramatically and cannot recover. From this graph, therefore, we can see that when two species compete for a common limiting

resource, the species with the smaller R^* will exclude the other. This theory, which was developed by David Tilman[7], is known colloquially as "R-star theory".

[7] David Tilman. Resource Competition between Plankton Algae: An Experimental and Theoretical Approach. *Ecology*, 58(2):338–348, 1977

Figure 3: Dynamics of two species competing for a common resource. Reduction of resource concentration leads to the exclusion of the species with the greatest R^*, which begins to decline as soon as resource concentration is reduced below this point.

What do the dynamics of such a system look like? Figure 3 shows the characteristic pattern when both species are introduced in small numbers to a resource rich environment. Initially both species increase due to the abundance of resources. However, once resources are reduced below the greater R^* (species b), that species begins to decline in abundance. Initially the decline is slow, but it quickly accelerates. Meanwhile the species with the lower R^* (species a) continues to increase until resources are reduced to the level of its R^* at which the species and its resources come into equilibrium. In the case where the dominant species (species a) is at equilibrium with the resource, then species b is unable to invade. In the case where species b is resident at equilibrium with the resource and species a is introduced, species b begins to decline and species a comes to replace it (Figure 4).

In a series of studies focusing on the diatom plankton of Lake Michigan, Tilman and colleagues[8] established that the principle of competitive exclusion applies quite generally to the dominant species in this ecosystem.

[8] David Tilman. Tests of resource competition theory using four species of Lake Michigan algae. *Ecology*, 62(3):802–815, 1981
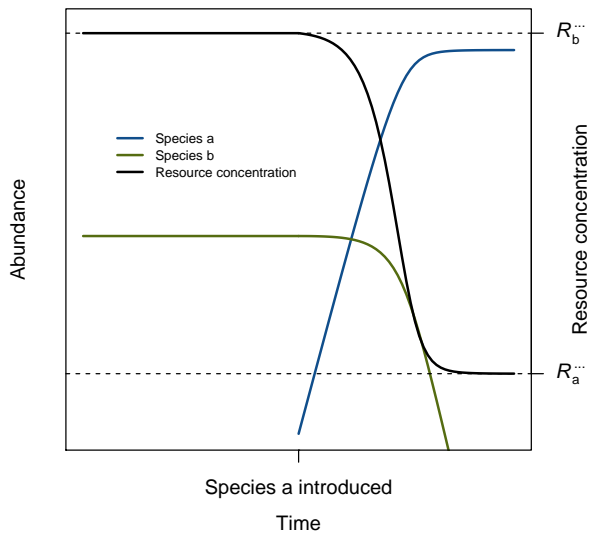
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Figure 4: A resident species (*b*) may be displaced by an invader with a smaller R^* value.

Temperature-dependent resource competition

Now we understand why the coexistence of forty species of plankton is a paradox. The first step in resolving the paradox is to consider other properties of the environment. Besides resources, external conditions, particularly temperature and light, are important for the growth of algae, including diatoms. In a series of detailed trials, Tilman and colleagues determined that R^* was a temperature-dependent property. Particularly, at low temperatures *A. formosa* exhibited a much smaller half saturation constant (k) meaning that it would grow to its maximum density quickly, compared with *S. ulna*, which would be excluded. By contrast, at high tempertatures, *S. ulna* would grow quite rapidly (with both high intrinsic rate of increase and high half saturation constant), excluding *A. formosa*. Of course, this transition doesn't happen rapidly with respect to a gradient in temperature. Therefore Tilman and colleagues introduced the concept of a *zero net growth isocline* (or *ZNGI* as it is often referred to), the curve that connects the R^* values for a species over a range of temperatures. The ZNGIs of *A. formosa* and *S. ulna* intersect, which is why *A. formosa* can be dominant under one set of conditions and *S. ulna* can be dominant under another set of conditions (Figure 5).
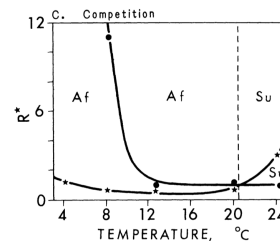

Figure 5: Zero net growth isoclines of *A. formosa* and *S. ulna*. Positions above the ZNGI for each species permits its persistence in isolation. When both species are cultured together the competitive exclusion principle holds that silicate will be reduced to the the concentration that corresponds to the lower of the two R^* values. Thus, *A. formosa* excludes *S. ulna* at low temperatures and *S. ulna* excludes *A. formosa* at high temperatures. At the value indicated by the vertical dashed line the two species have equal R^* values and are predicted to coexist. In fact, the ZNGIs are so close over a range from about 12 degrees C to about 20 degrees C that it is not possible to predict with confidence which species is competitively dominant and extinction due to competitive exclusion will take a very long time to occur.

Complementarity in resource use

Of course, although species are ultimately limited by one resouce, what resource this is may depend on other circumstances. For diatoms in mesotrophic lakes, that other resource is often phosphate. To generalize from the R^* theory for competition for one limiting resource to two limiting resources, we first require a determination of the R^* value for each resource in the presence of an effectively unlimited supply of the other. These values then allow us to draw two ZNGIs – one a horizontal line and one a vertical line – in a plane defined by the concentrations of the two resources (Figure 6).
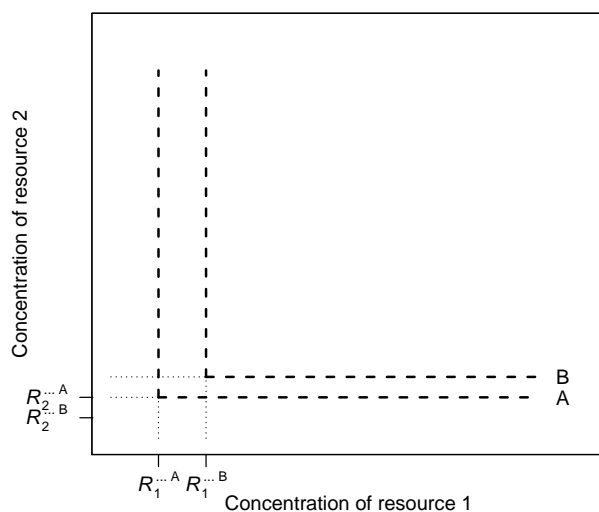

Figure 6: Species A excludes species B because the ZNGI for species B is completedly contained within the ZNGI for species A. If the ZNGIs are reversed than the outcome is reversed.

The effect of a second species can be investigated by plotting the ZNGIs of another species on the same axes. There are three possibilities for how these curves can intersect:

- The ZNGI for species A can be entirely enclosed within the ZNGI for species B

- The ZNGI for species B can be entirely enclosed within the ZNGI for species A

- the ZNGIs can intersect

The outcome of the first two cases is illustrated in Figure 6. If the ZNGIs intesect the situation is more complicated. Here there are two possible outcomes and which one obtains depends on an additional

property, which is how the species' exploit the two resources. One situation is illustrated in Figure 7. The equilibrium in this example is indicated by a point. This is an equilibrium because both species have zero net growth at this point. Also depicted in this figure are two sets of vectors, one for species A and one for species B. These are the *consumption vectors*. The horizontal and vertical vectors indicate the relative amounts by which Resource 1 and Resource 2 are reduced when they are sequestered by each species for growth. The diagonal vector is the sum of these two vectors and represents the corresponding change of the system overall.
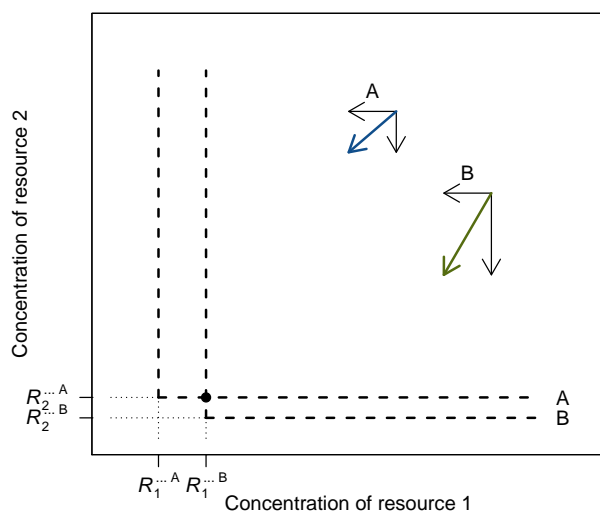
Figure 7: Species A excludes species B because the ZNGI for species B is completedly contained within the ZNGI for species A. If the ZNGIs are reversed than the outcome is reversed.

To determine the outcome of competition, lines are drawn from equilibrium point at an angle equal to the consumption vector for each species (Figure 8). The ZNGIs and the consumption vectors together define six regions of the figure. Clearly, if either Resource 1 or Resource 2 is so dilute that the system is in Region I then neither species persists. By contrast, if the system is in Region II then species A will persist, but species B will not; if the system is in Region VI then species B will persist, but species A will not. If the system is in Region III then consumption will eventually move it to Region II (crossing the ZNGI for species B), leading to persistence only of species A. If the system is in Region V then consumption will move it to Region VI (crossing the ZNGI for species A) and only species B will persist.

Finally we are left to determine the outcome of a sytem in Region

IV. In this situation the system moves toward the equilibrium point and there are two possible outcomes. Either the equilibrium is stable, in which case the two species coexist, or the equilibrium is unstable, in which case one species excludes the other (and the only way to determine which one is dominant is by a careful numerical study of the initial condition). For the equilibrium to be stable, we require the consumption vector with the shallower slope (in this case species A) to be the species with the lower horizontal ZNGI. In our case, the lower horizontal ZNGI for is for species B. Therefore, in this diagram the equilibrium is unstable. We can develop some intuition for why this is the case. Here, species B consumes relatively more of Resource 2 than species A and also tolerates a lower concentration of Resource 2 (it has a lower R^*). We might say that species B consumes more of the resource that limits the growth of species A, and vice versa, which is destabilizing. If the consumption vectors were reversed, then species A would be the greedier consumer of its more limiting resource. This is consistent with a more general principle in ecology: *Coexistence is promoted when the strenth of intraspecific competition is greater than the strength of interspecific competition.*
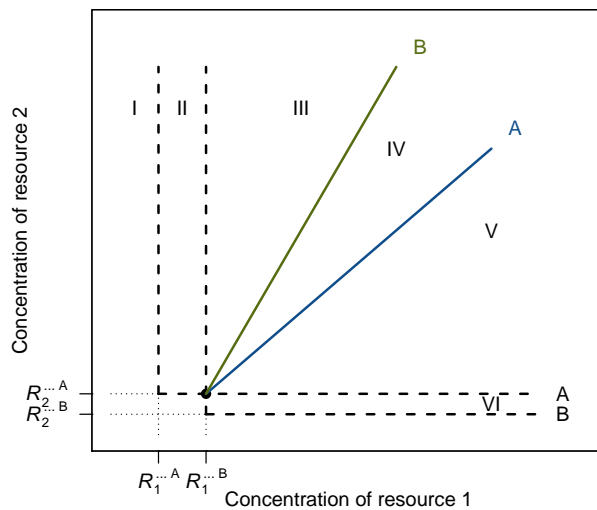

Figure 8: Species A excludes species B because the ZNGI for species B is completedly contained within the ZNGI for species A. If the ZNGIs are reversed than the outcome is reversed.

Test yourself

- What is the competitive exclusion principle?

- What is the R^* of a species and how do you estimate it?

- What conditions promote species coexistence?

Homework

1. Derive an expression for R^* in terms of r, k, and m.

2. *A. formosa* and *S. ulna* were grown in pure culture in the laboratory by Tilman et al. at 24 degrees C. Figures 9 and 10 show the decline in Si as these cultures increased from low abundance. Estimate the R^*s of these species.

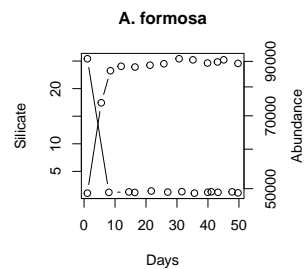3. From these estimates, which species do you predict would be excluded in a mixed culture.

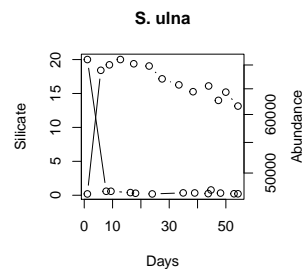Figure 9: Experimental dynamics of (*Asterionella formosa*).

Figure 10: Experimental dynamics of (*Synedra ulna*).

Bibliography

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