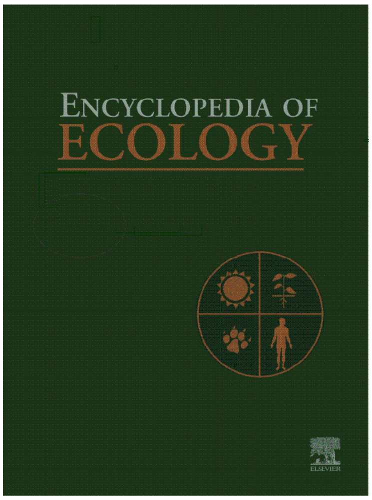

K C Burns and P J Lester. Competition and Coexistence in Model Populations. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Population Dynamics. Vol. [1] of Encyclopedia of Ecology, 5 vols. pp. [701-707] Oxford: Elsevier.

Competition and Coexistence in Model Populations

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Introduction

'Competition' refers to a negative interaction between organisms. When one organism physically restricts another organism's access to resources, it is referred to as 'interference competition'. Interference competition is common in animals such as songbirds, which maintain exclusive spatial territories with the aid of vocalizations. Although it is more difficult to envision, interference competition also occurs between plants. Many plants secrete chemicals into the soil via their root systems in a process called 'allelopathy'. These chemicals negatively impact the root systems of neighboring plants, which helps promote a plant's exclusive access to soil nutrients and water. A second, distinctly different type of competition is called 'exploitative competition'. Exploitative competition occurs between organisms that consume the same resources, when resource consumption by one organism lowers its availability for other organisms. Examples of exploitative competition include shading by neighboring plants, or when nectar consumption by one pollinator lowers nectar availability for other pollinators. Both interference and exploitative competition can occur within (intraspecific) and between (interspecific) species. Both forms of competition can operate simultaneously in natural populations (**Figure 1a**). When one competitor is more effective than another, competition is said to be 'asymmetric'. For example, taller plant species are often better competitors for light than shorter species. Conversely, 'symmetric' competition occurs between similarly matched competitors (**Figure 1b**).

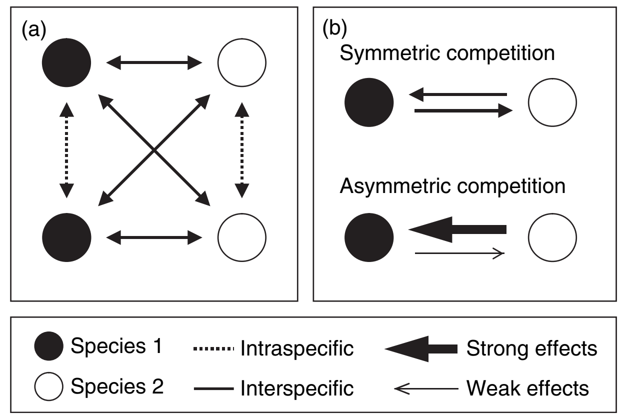

Figure 1 Schematic illustrating different types of competitive interactions. (a) Illustrates intraspecific (dashed line) and interspecific (solid line) competition between two species, which are represented by black and white circles. (b) Illustrates symmetric (above) and asymmetric (below) competition. Arrow size indicates interaction strength. Redrawn from Keddy PA (1995) *Competition*. London: Chapman and Hall.

The Lotka–Volterra Equations

In the early twentieth century, Alfred Lotka and Vito Volterra simultaneously derived a model that described how competition affects population growth. Their goal was to explore how competition might affect population dynamics, not necessarily to make specific predictions to be tested with field data. The 'Lotka–Volterra' model, which it is now known, begins by equating changes in the size of a population through time (dN_1/dt) to the product of its intrinsic rate of increase (r_1) and current population size (N_1):

$$\frac{dN_1}{dt} = r_1 N_1 \qquad [1]$$

The 'intrinsic rate of increase' (r) is the per capita population growth rate that could potentially be realized by a species. In other words, it represents the potential for a species to increase in abundance. For example, mice can rapidly fill a landscape, and have greater intrinsic rates of increase than elephants, which proliferate more slowly. Equation [1] represents exponential growth, meaning growth accelerates through time without bound and is therefore unrealistic. The subscript 1 assigns each variable to a specific species. Different subscripts will be introduced when the effect of interspecific competition is added to the model.

As populations grow, intraspecific competition intensifies, which places limits on population growth. To incorporate the effects of crowding, a third term called the carrying capacity (K) is incorporated into the model. The carrying capacity is specifically defined as the

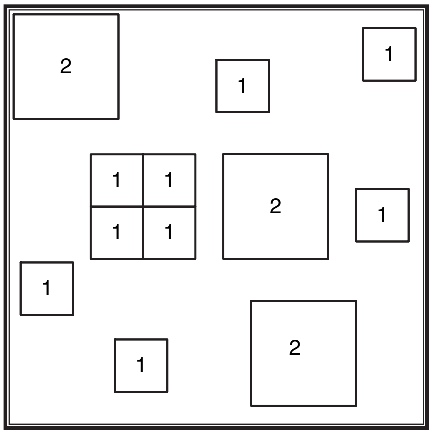

Figure 2 Schematic illustrating carrying capacities and competition coefficients. The large box refers to the carrying capacity of two species, illustrated as different numbered tiles. Populations of both species are below carrying capacity because more tiles can fit within the larger box. Tiles representing species 2 are four times larger than species 1. Therefore, individuals of species 2 have four times the per capita resource consumption rate as species 1, indicating the competition coefficient of species 2 on species 1 (α_{12}) is equal to 4. Redrawn from Krebs CJ (2001) *Ecology: The Experimental Analysis of Distribution and Abundance*. San Francisco: Benjamin Cummings.

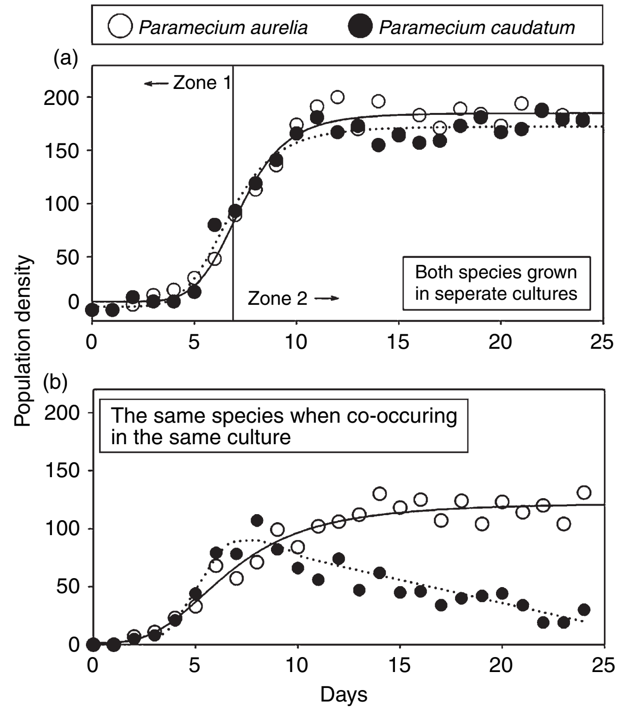

Figure 3 Growth of two *Paramecium* species when growing alone (a) or together (b). Both species show similar logistic growth patterns when grown separately, but *P. aurelia* outcompetes *P. caudatum* when grown together. In (a), zone 1 shows changes in population size similar to exponential growth, while zone 2 illustrates the effects of intraspecific competition on population dynamics. Redrawn from Gause GF (1934) *The Struggle for Existence*. Baltimore: Williams & Wilkins.

maximum population size a given locale can support. Imagine a species' carrying capacity as a square box, which contains tiles representing individuals. When the box is filled completely by tiles, it represents a population at carrying capacity. When there are too many tiles to fit in the box, it represents an unstable population, which is larger than its carrying capacity. In this situation, the population will decline, or by analogy, tiles are taken away. If there is empty space within the box, more tiles can be added, representing population growth. Figure 2 illustrates the carrying capacity of two species, which are represented by different-sized boxes. Although the size of box (or the total amount of resources) is the same for both species, species 1 has a larger carrying capacity, because more of its tiles can fit inside the box.

Carrying capacity is incorporated in the model by including a new term $[(K-N)/K]$ into eqn [1]:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1}\right) \qquad [2]$$

This term places a limit on exponential growth, and the resulting equation represents 'logistic growth', which is illustrated by the two *Paramecium* species shown in Figure 3a. When their population sizes are low ($K >> N$), the new term in eqn [2] approximates 1, so the population behaves basically as in eqn [1] (zone 1, Figure 3a). However, as the population grows, this new term becomes smaller and smaller, placing stronger and stronger limits on population growth (zone 2, Figure 3a). If the population overshoots its carrying capacity ($K < N$), it becomes negative and the population declines. When the population size equals its carrying capacity ($K = N$) the equation equals zero, representing a stable or equilibrium population size.

So how might competition between species influence population dynamics? To incorporate interspecific competition into the logistic equation, a fourth and final variable, called the 'competition coefficient' (α), is included. It represents the per capita, competitive effect of one species on another and converts individuals of one species into an equivalent number of individuals of another species. Figure 2, which describes the concept of a carrying capacity, also illustrates competition coefficients. Tiles representing species 2 are four times larger than species 1 indicating that individuals of species 2 require four times more resources. Therefore, the competition coefficient representing the effect of species 2 on species 1 (α_{12}) is 4.00, while that of species 1 on species 2 (α_{21}) is 0.25. The coefficients representing intraspecific competition (i.e., α_{11} and α_{22}) are assumed to equal 1. To incorporate interspecific competition into the logistic equation, the competition coefficients are multiplied by population sizes, and then subtracted from the carrying capacity. When the abundance of species 1 is multiplied by the competition coefficient corresponding to its per capita effects on species 2 (i.e., $N_1 \alpha_{21}$), it represents the total competitive effect of species 1 on species 2. Similarly, the competitive effect of species 2 on species 1 is $N_2 \alpha_{12}$. Taken altogether

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - \alpha_{11} N_1 - \alpha_{12} N_2}{K_1} \right) \qquad [3]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - \alpha_{22} N_2 - \alpha_{21} N_1}{K_2} \right) \qquad [4]$$

The conditions under which both populations are stable are identified by setting both equations equal to zero and solving for the abundance of both species at equilibrium. Equilibrium conditions are then plotted in 'state space', which illustrates the population size of both species. The abundance of one species is plotted on the x-axis, while the other is shown on the y-axis (**Figure 4**). Let us consider species 1 first. After setting eqn [3] equal to zero and rearranging for species 1 when species 2 is absent, we get $N_1 = K_1$. This point can be plotted in state space where $x = K_1$ and $y = 0$. Similarly, eqn [3] at equilibrium can be rearranged to obtain the abundance of species 2 when species 1 is absent, which is $N_2 = K_1/\alpha_{12}$. This point can also be plotted in state space where $x = 0$ and $y = K_1/\alpha_{12}$. If we assume that the relationship between these two points is linear, we can plot a straight line in state space that represents the equilibrium population growth rate of species 1. This is called an 'isocline' and it represents combinations of abundances of both species where population growth of species 1 is stable (i.e., $dN/dt = 0$). The isocline for species 1 is plotted in **Figure 4a**. The same procedure can be followed for species 2, which is shown in **Figure 4b**.

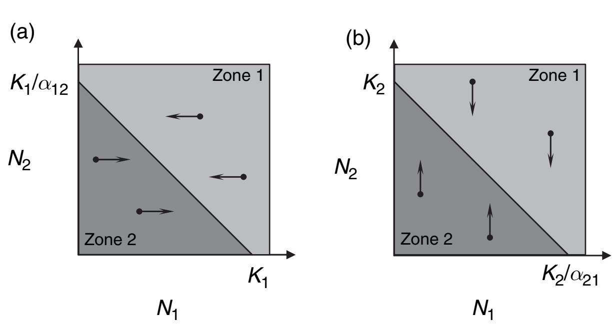

Figure 4 Zero-growth isoclines of two competing species under the Lotka–Volterra model. (a) Shows the isocline for species 1 and (b) Shows the isocline for species 2. In (a) points above the isocline (zone 1) represent population sizes above equilibrium. These points will move horizontally toward the origin, until they reach the isocline representing population equilibrium, indicating population decline. Points in zone 2 move in the opposite direction, which illustrates population growth. Similar conditions occur in (b), which illustrates species 2, so trajectories are vertical.

Four hypothetical population sizes are shown as points in **Figures 4a** and **4b**. Arrows illustrate predictions of how population size will change. In **Figure 4a**, any point in zone 1 will move horizontally toward the origin until it reaches the isocline, where it will stop and the population size of species 1 will remain stable. Points in zone 2 will move horizontally away from the origin, or increase in size, until it reaches the isocline where it will remain stable. Similar circumstances occur with species 2 (**Figure 4b**); however, points move vertically because species 2 is plotted on the y-axis.

Notice that the state space graphs for species 1 and species 2 have the same axes. Therefore, we can plot both species' isoclines on the same graph, and compare their population dynamics simultaneously. Several hypothetical outcomes can be observed for species dynamics by plotting both isoclines together in state space. One outcome is that the isoclines will be more or less parallel, with one species having greater intercept values. This situation represents asymmetric interspecific competition or that one species is competitively dominant over the other. In **Figure 5a**, the isocline for species 1 lies above the isocline for species 2. Under these circumstances ($K_1/\alpha_{12} > K_2$ and $K_1 > K_2/\alpha_{21}$), species 1 is competitively dominant. At small populations of both species, both will increase in size, which is represented by the point and arrow closest to the origin. When both species have large population sizes, both will decline. However, the relative abundances represented by points between the isoclines move diagonally, away from the origin towards the point on the x-axis representing equilibrium population size of species 1 (K_1), which is represented by a gray circle. The analogous situation is shown is **Figure 5b**. Here, species 2 is a stronger competitor than species 1, and the isocline for species 2 lies above species 1 ($K_2 > K_1/\alpha_{12}$, and $K_2/\alpha_{21} > K_1$), and species 2 excludes species 1. The competitive dynamics of two *Paramecium* species provides a good example of this situation (**Figure 3b**). Although both have similar dynamics when grown separately, when grown together *P. aurelia* outcompetes *P. caudatum*, driving it to local extinction.

Another possible outcome is that the isoclines differ in slope and intersect somewhere in state space, as in **Figure 5c**. Here, the isocline for species 1 has a steeper slope, greater y-intercept, and lower x-intercept than species 2. Under these conditions ($K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} > K_1$), intraspecific competition is stronger than interspecific competition. Both can stably coexist under these circumstances and their population sizes converge on a single point at the intersection of the two species' isoclines. Desert grainivores provide a good example of this situation in the wild. Many species of ants and rodents eat seeds as their primary food source in of North American deserts. While both types of competitors stably coexist under normal circumstances, when one type of seed-eater is removed from large field enclosures the other increases in abundance.

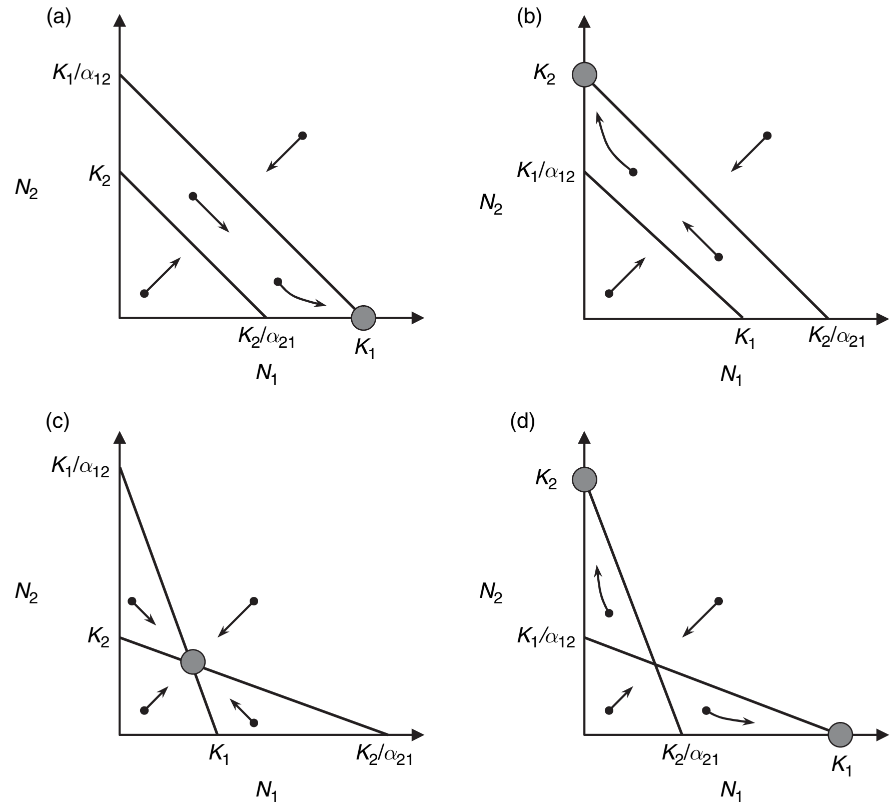

Figure 5 Four potential outcomes of the Lotka–Volterra model. Isoclines for two species are plotted against their respective population sizes. Gray points represent equilibrium population sizes. In (a) species 1 outcompetes species 2 and population sizes will follow the trajectory of arrows until it reaches K_1 on the *x*-axis. (b) Illustrates competitive exclusion by species 2. (c) Illustrates coexistence, with populations reaching an equilibrium at the intersection of both species' isoclines. (d) Represents two possible outcomes, competitive exclusion by species 2 (gray point, *y*-axis) and exclusion by species 1 (gray point, *x*-axis).

A second outcome of intersecting isoclines is that the positions of each species are switched (**Figure 5d**). In this instance ($K_2 > K_1/\alpha_{12}$ and $K_1 > K_2/\alpha_{21}$) interspecific competition is greater than intraspecific competition. This situation is unstable and populations come to equilibrium on either the *x*- or *y*-axis, effectively with the local extinction of one species (**Figure 5d**). Small islands off the coast of New Guinea house a variety of bird species. Yet similar species (i.e., similar in size, diet, and habitat use) often fail to co-occur with each another. Islands house either one or the other putative competitors, which is what would be expected if interspecific competition was stronger than intraspecific competition.

Tilman's Resource-Based Model

The Lotka–Volterra model explores how competition influences the abundance of two competing species. Changes in the abundance of one species are modeled as a function of its competitor's abundance, but the specific competitive mechanism is not explicitly stated or explored. Therefore, the model does not clarify how competition influences population dynamics. This has led some authors to label these equations as 'phenomenological' and to advocate the use of a different theoretical perspective, one that specifically focuses on resources.

Competition occurs over resources, which can be defined as any attribute required for an organism's survival or reproduction. For our purposes, we will use Tilman's specific definition of a resource as "any substance or factor which is consumed by an organism and which can lead to increased growth rates as its availability in the environment increases." Food and space are commonly considered as resources. An approach that focused explicitly on resources was originally developed by Robert H. MacArthur. David Tilman greatly expanded MacArthur's ideas into a model whose basic tenets can be illustrated graphically.

Tilman's resource-based model has three components: (1) 'resource requirements', (2) 'resource consumption', and (3) 'resource supply'. The requirement component is easy to conceptualize. All organisms require certain resources for growth and reproduction. For instance, light and nitrogen are important resources for plants. As individuals consume resources, resource availability to other individuals is reduced. This process is the consumption component. Most resources are replenished as they are being consumed. For example, as nitrogen is absorbed by plants it is simultaneously being replenished by soil microbes and mycorrhizae. This replenishment is the supply component.

Figure 6 illustrates the basic principles of Tilman's model. This figure is similar to a state space graph, and shows the zero-growth isocline for a single species. However, unlike the Lotka–Volterra model illustrated in Figures 4 and 5, the two axes represent the availability of two essential resources, which are labeled A and B, instead of population sizes. Another major difference is that the isocline is bent at a right angle. The isocline is nonlinear because both resources are essential and are needed in a particular quantity for a species to exist. At any point along this isocline, which represents a combination of resources, the population is stable (i.e., $dN/dt=0$). Points above the line indicate resource levels that would result in population growth. Points labeled with * represent the minimum level of resources needed for population persistence. When resources drop below A_1^* or B_1^*, the population is predicted to become locally extinct.

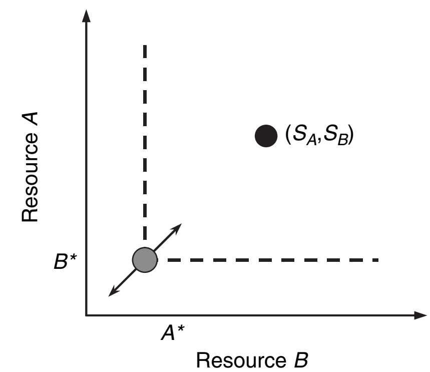

Figure 6 Basic principles of Tilman's resource-based model. The dashed line represents the resource-dependent isocline. A^* and B^* represent minimum levels of essential resources required for population persistence, and the black point (S_A, S_B) represents the supply point of both resources. The gray point, and all other points on the isocline, represents equilibrium conditions where resource consumption (arrow pointing toward the origin) is balanced by resource supply (arrow away from the origin). Redrawn from Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. New Jersey: Princeton University Press.

Figure 7 shows the resource-dependent, zero-growth isoclines of two hypothetical competitors, which is analogous to Figure 5. In Figure 7a, the curve for species

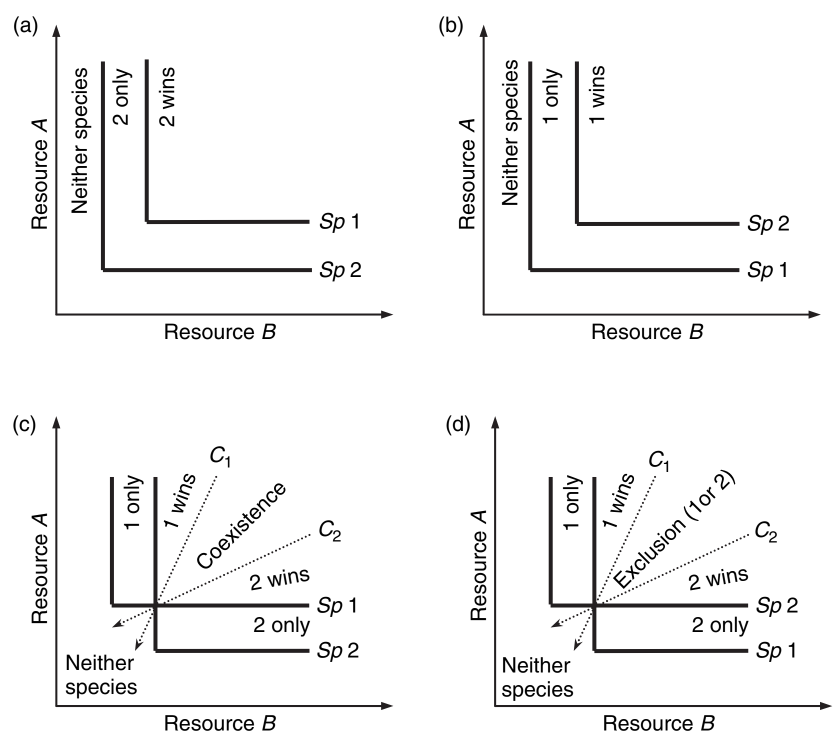

Figure 7 Four possible outcomes of Tilman's resource-based model. In (a) species 2 requires less of both resources to exist, and is therefore competitively dominant and exists alone. In (b) the situation is reversed and species 2 is competitively dominant. The isoclines cross in (c) and (d), indicating each species requires less of one particular resource. Under these circumstances, the outcome of competition is determined by the position of the consumption curves (C_1 and C_2) and resource supply points. In (c) if the supply point lies between the consumption curves, both species can coexist. In (d) the positions of the isoclines are reversed and the two species cannot coexist. Redrawn from Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. New Jersey: Princeton University Press.

1 lies above species 2, indicating that species 1 requires greater amounts of both resources than species 2 (i.e., $A_1^* > A_2^*$ and $B_1^* > B_2^*$). Under these circumstances, species 2 is competitively superior because it can persist on less of both resources. Therefore, consumption by species 2 will lower resource levels below that needed by species 1 to survive, which will be excluded. Conversely, Figure 7b shows the opposite situation ($A_1^* < A_2^*$ and $B_1^* < B_2^*$), where species 1 excludes species 2.

Figures 7c and 7d represent situations where isoclines intersect. Under these circumstances, one competitor requires less of one resource, but more of the other. It also introduces a second type of curve, called a 'resource consumption vector'. Each species has a separate consumption vector, labeled C_1 and C_2, which illustrate their impact on both resources. Differences in the slope of consumption vectors indicate rates of consumption of each resource. On these graphs a steep curve indicates faster consumption of resource A per unit resource B. Conversely, a more gently sloping curve indicates that resource B is consumed more rapidly. When a species rapidly consumes the resource that it requires in greater quantities, coexistence is possible and is illustrated in Figure 7c. It shows that species 1 requires more of resource A ($A_1{}^* > A_2{}^*$), and consumes resource A more rapidly (the slope of its consumption vector is greater than 1). Similar to the Lotka–Volterra situation illustrated in Figure 5c, this scenario indicates that intraspecific competition is greater than interspecific competition and that coexistence is possible. When the positions of the isoclines are switched (or the positions of the consumption vectors are switched) interspecific competition is greater and coexistence is not possible.

The third component, or 'resource supply point', is needed to determine which of these outcomes will actually occur. The resource supply point indicates the availability of resources if they were not being consumed by either species. Supply points can be anywhere on the graph, and the outcome of competition depends on its position. If the supply point occurs between the axes and the closest isocline, resources are consumed faster than they are renewed and both species will go locally extinct. If the supply point is located anywhere else on the graph, several outcomes are possible, which are labeled in different regions of Figures 7c and 7d.

Tilman's experiments on algae provide a useful example of the model's predictions. Tilman cultured two species of diatom under different concentrations of silicate and phosphate. Although three trials generated outcomes that were somewhat different from that predicted, the model provided a good overall fit to the effect of resource competition on population dynamics. Both species coexisted when resource supply rates occurred

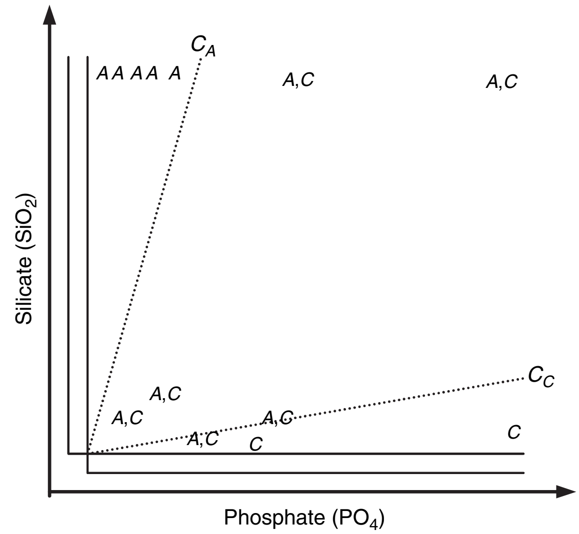

Figure 8 A laboratory test of Tilman's resource-based model with two diatom species, *Asterionella* (A) and *Cyclotella* (C). Zero-growth isoclines relative to two essential recourses, silicate and phosphate, are shown along with consumption vectors. The outcomes of 13 trials are labeled with the letters representing competitive outcomes. *A* refers to competitive exclusion by species *Asterionella*, *C* to exclusion by *Cyclotella*, and *A,C* refers to their coexistence. Redrawn from Tilman D (1980) Resources: A graphical-mechanistic approach to competition and predation. *American Naturalist* 116: 362–393.

between consumption curves (Figure 8). Competitive exclusion also occurred under predicted resource concentrations and supply rates.

See also: Cycling and Cycling Indices; Death; Metapopulation Models; Parasites; Predation; Recruitment; Resilience; Stability; Temperature Regulation.

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Competition and Competition Models

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Definitions

Competition is defined as an interaction between two or more individuals of the same population or two or more populations in which each negatively affects the other in access to a limited resource(s) (food, water, nesting sites, shelter, mates, etc.). Mutualism is defined as an interaction between populations that is favorable to both. Two main types of competition are identified: intraspecific competition and interspecific competition.

Intraspecific Competition

Intraspecific competition is a competition between individuals from the same species (cospecifics). The effect of competition on each individual within the species depends on the type of competition that takes place. 'Contest-competition' may be passive or active and may result in different outcomes. A species that competes for a limited resource where all individuals consume equal amounts until the resource is depleted, may result in all individuals of that population dying of starvation. On the other hand, and the more common outcome is, when one individual competes and wins over the resource, and by exploiting that resource it continues to survive. Two basic types have been identified for intraspecific competition:

1. *Interference (adapted) intraspecific competition.* This occurs in species that establish hierarchies through aggressive behavior where one or more individuals within the population hold a dominant status over the others. Through direct interaction these individuals will limit or prevent access of more subordinate individuals to a resource. This type of competition may also occur when individuals within a species establish territories and limit the access of others to a resource. In this type of competition only those individuals who are dominant or hold territories will increase their reproduction success. It is sometimes called 'contest competition' indicating displays and contents between individuals for access to a resource (usually mates).
2. *Exploitation (contest) intraspecific competition.* This occurs between individuals of the same population exploiting the same resources and reducing or depleting its availability to others. This competition is indirect interactions between individuals such as deleting of a food source.

Intraspecific competition is affected not only by the type of competition but also by the type of resource. A territory, which is not depletable, will affect the survivorship of future generations. Competition over consumables, such as food, may result in decreased availability for future generations and such resources may need time to recover.

Intraspecific competition is density dependent and may cause density-dependent mortality. At low densities no intraspecific competition exists and competition for resources does not play a role in survivorship. As densities increase, a threshold is reached where density begins to influence mortality through resource availability. When plotted as a graph in terms of population growth rate, the result is either a J-shaped growth or an S-shaped/sigmoidal curve, both referred to as logistic growth.

Logistic growth models

A population growth pattern is represented by:

$$\Delta N/\Delta t = rN \qquad [1]$$

where N is the size of the population with a limit imposed on it by limited resources, t is time, and r is growth rate. Figure 1 shows that in this scenario (J-shaped growth)