

Competition, predation and mutualism

Erol Akçay
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Competition

One of the most fundamental facts about nature is that sometimes there is not enough for everyone to have everything they need. We saw an example of this in a single-population world where as the number of existing individuals of a single population increases, the resources available to each of them to breed further (or survive) decreases, and thus, the per-capita growth rate (and eventually the total growth rate) of the population decreases. This we called density dependence, but we could have chosen to call it intra-species competition with as much validity. Much of ecological research is based on the extension of this idea to populations of multiple species coexisting in the same place, and this is what this lecture is going to be about.

Consider the logistic growth equation for some species (denoted by 1) that should by now be very familiar:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right) \quad (1)$$

Now, imagine a new species comes into the geographical region that consumes some of the same resources. Perhaps the easiest resource to imagine is space for a sessile organism (e.g., a plant or a barnacle): Suppose individuals of species 1 occupy 1 cm² and species 2 occupy 2 cm². Supposing a total available area of X (measured in cm²), the carrying capacity of species 1 is $K_1 = X$ and for species 2 is $K_2 = X/2$. Now a single individual of species 2 occupies twice as much space as an individual of species 1, so we need to amend the dynamics of N_1 in the following way:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - 2N_2}{K_1} \right) \quad (2)$$

Likewise, for the dynamics of N_2 we can write:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - 0.5N_1}{K_2} \right), \quad (3)$$

since an individual of species 1 takes up half as much space as one of species 2. More generally, one can quantify the per-capita effect of species 2 on 1 with a parameter α and of 1 on 2 with β to arrive at ¹

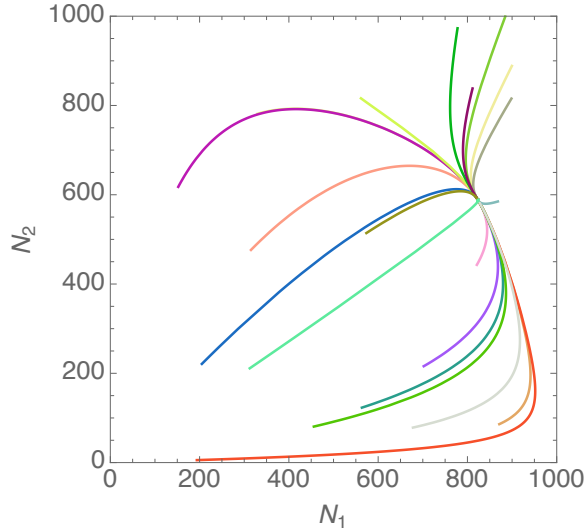
$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \quad (4)$$

¹ Note that the competition coefficients α and β are effectively scaled to measure the effect of one species on the other, *relative* to the target species's effect on itself. Also, in the space-competition example, $\alpha = 1/\beta$ necessarily, but that's in general not a necessary requirement. Both species might have higher or lower effect on each other than on themselves.

Likewise, for the dynamics of N_2 we can write:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right), \quad (5)$$

One useful way to visualize what happens in this model is to look at the “phase plane”, i.e., a 2 dimensional plot that depicts N_1 and N_2 at each time point, and tracks the dynamics of them.



Lotka-Volterra competition dynamics in the phase space, for 20 populations initiated at random points (each depicted in a different color). The parameters for this graph are $K_1 = K_2 = 1000$, $\alpha = 0.3$, $\beta = 0.5$, and $r_1 = r_2 = 1$. Regardless of the initial condition, the population reaches a stable equilibrium at $N_1 \approx 824$ and $N_2 \approx 588$.

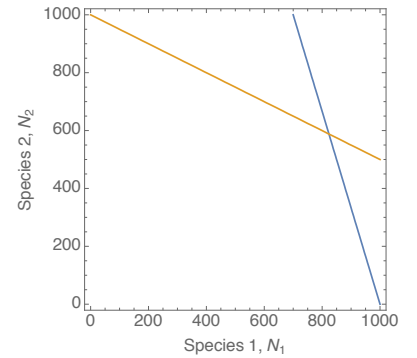
How do we go about analyzing the dynamics? First we can look at the equilibrium. There are four: three boundary (one or both species being zero) and one internal. The internal equilibrium can be found by solving equations (4) and (5) for non-zero N_1 and N_2 , which means that the parentheses in each equation has to vanish. So we have for the internal equilibrium abundances N_1^* and N_2^* :

$$N_1^* = \frac{K_1 - \alpha K_2}{1 - \alpha\beta} \quad (6)$$

$$N_2^* = \frac{K_2 - \beta K_1}{1 - \alpha\beta}. \quad (7)$$

The internal equilibrium exists if these quantities are non-negative. In particular, if both $K_1 > \alpha K_2$ and $K_2 > \beta K_1$, it has to be that $\alpha\beta < 1$ for an internal equilibrium to exist.

But the existence of an internal equilibrium is not a guarantee for coexistence. The equilibrium also has to be stable, i.e., when the system starts out not at equilibrium, it should tend to converge to it. The easiest way to determine the stability of the equilibrium is graphical. We can easily plot the combination of population sizes that yield a positive growth rate for species 1 (or 2). In particular, if somehow we kept N_2 constant, the population dynamics of N_1



The isoclines for two species engaged in Lotka-Volterra competition. The blue line is the isocline for species 1, the orange for species 2. Parameters are: $r_1 = r_2 = 1$, $K_1 = K_2 = 1000$, $\alpha = 0.3$, $\beta = 0.5$. To the left of the blue line, species 1 will increase (i.e., the system's trajectory would point to the right; to the right of it, N_1 will decrease. Likewise, above the orange isocline, Species 2 will decrease, and below it it will increase.

would look just like a logistic growth, but with a reduced carrying capacity of $K_1 - \alpha N_2$. So, if $N_1 > K_1 - \alpha N_2$, species 1 would experience negative growth rate, and positive otherwise. So, the line $N_1 = K_1 - \alpha N_2$ defines the boundary for where species 1 grows and where it shrinks in population size. Likewise, $N_2 = K_2 - \beta N_1$ gives the same boundary for species 2. These boundaries are called isoclines. The isocline for species 1 intersects the horizontal axis at K_1 and the vertical axis at K_1/α^2 , and the isocline for species 2 intersects the vertical axis at K_2 and horizontal one at K_2/β .

² good exercise to verify.

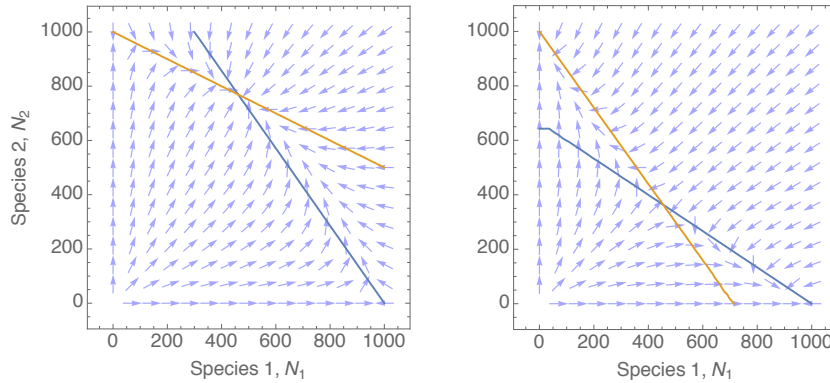
For coexistence, both species must be able to invade a single-species community at equilibrium. In other words, the growth rate of species 1 when $N_1 \approx 0$ and $N_2 \approx K_2$ should be positive, and vice versa. Graphically, this corresponds to the isocline of species 1 intersecting the vertical axis above that of species 2, or:

$$K_1/\alpha > K_2 \quad \Rightarrow \quad \frac{K_1}{K_2} > \alpha \quad (8)$$

Likewise for species 2, the condition is for its isocline to intersect the horizontal axis to the right of species 1's isocline, which yields

$$\frac{K_2}{K_1} > \beta. \quad (9)$$

If both conditions are satisfied, then both species can invade when they are initially absent, and we have stable coexistence. If one is satisfied and the other not, we have competitive exclusion of one of the species. If both are not satisfied, then there is an internal equilibrium that is unstable and one of the species will eventually be competitively excluded, but which one depends on the initial conditions. The figures below illustrate the cases with an internal equilibrium.



The phase diagram of Lotka-Volterra competition models for a case yielding stable (RHS panel) and unstable (LHS panel) coexistence. The blue line gives the isocline of species 1 (i.e., the combination of N_1 and N_2 that yields zero growth rate for species 1); the orange line of species 2. The light blue arrows depict the direction of the joint trajectory of two populations in different regions. In both panels, the carrying capacities are $K_1 = K_2 = 1000$ and $r_1 = r_2 = 1$. In the RHS panel, $\alpha = 0.7$, $\beta = 0.5$ and in the LHS panel $\alpha = 1.5$, $\beta = 1.4$.

Linear stability analysis of two-dimensional systems

The above analysis relies on graphical depiction of flows, and works in many two-dimensional systems. But sometimes the graphical depiction can be confusing (e.g., when there are cycles) and in any case, it will be very hard to implement it in three dimensions, and impossible for more. Thus, having a method to analytically determine the stability of an equilibrium would be desirable.

Such a method exists of course, and it relies on doing precisely what we did for a one-dimensional dynamical system: approximating the dynamics of the non-linear system near an equilibrium by a linear system. Suppose a non-linear dynamics of two variables x and y given by the following equations:³

$$\frac{dx}{dt} = f_x(x, y) \quad (10)$$

$$\frac{dy}{dt} = f_y(x, y) \quad (11)$$

where f_x and f_y are some functions of x and y . Suppose the system has an equilibrium at $x = x^*$ and $y = y^*$, i.e., $f_x(x^*, y^*) = f_y(x^*, y^*) = 0$. Now, assuming f_x and f_y are differentiable at the point $(x^*, y^*)^4$, we can Taylor-expand them, so that for x, y near x^* and y^* , we have

$$f_x(x, y) \approx f_x(x^*, y^*) + \frac{\partial f_x}{\partial x} \delta_x + \frac{\partial f_x}{\partial y} \delta_y \quad (12)$$

$$f_y(x, y) \approx f_y(x^*, y^*) + \frac{\partial f_y}{\partial x} \delta_x + \frac{\partial f_y}{\partial y} \delta_y, \quad (13)$$

where $\delta_x \equiv (x - x^*)$ and $\delta_y \equiv (y - y^*)$ (i.e., the deviations from the equilibrium), and all the partial derivatives are evaluated at the equilibrium point, $x = x^*$ and $y = y^*$. We can switch to matrix notation to express the dynamics of the deviations from the equilibrium in a compact form:

$$\frac{d}{dt} \begin{pmatrix} \delta_x \\ \delta_y \end{pmatrix} = \begin{pmatrix} \frac{\partial f_x}{\partial x} & \frac{\partial f_x}{\partial y} \\ \frac{\partial f_y}{\partial x} & \frac{\partial f_y}{\partial y} \end{pmatrix} \begin{pmatrix} \delta_x \\ \delta_y \end{pmatrix}. \quad (14)$$

The matrix of partial derivatives in the above equation is called the *Jacobian* of the system, so we'll denote by \mathbf{J} .⁵ Remember that the partial derivatives are evaluated at the equilibrium point, so they are just numbers. By now we know that linear dynamical systems (i.e., with constant coefficients in front of the functions and their derivatives) are especially easy to analyze, and their solutions are usually of an exponential type, so let us propose one like the following:

$$\begin{pmatrix} \delta_x \\ \delta_y \end{pmatrix} = e^{\lambda_1 t} C_1 \vec{v}_1 + e^{\lambda_2 t} C_2 \vec{v}_2 \quad (15)$$

where λ_i and \vec{v}_i are two constant numbers and vectors respectively, and C_1 and C_2 are constants determined by the initial conditions. Substituting this solution into our equation above, we find:

$$\lambda_1 C_1 e^{\lambda_1 t} \vec{v}_1 + \lambda_2 C_2 e^{\lambda_2 t} \vec{v}_2 = C_1 e^{\lambda_1 t} \mathbf{J} \vec{v}_1 + C_2 e^{\lambda_2 t} \mathbf{J} \vec{v}_2. \quad (16)$$

³ Strogatz (2001) is a classic and accessible introduction to non-linear dynamical systems, where all of these derivations can be found in much greater detail, with examples.

⁴ One should note here that differentiability of a multivariate function is a stronger condition than the existence of the derivatives at that point; it also requires that the derivatives are continuous.

⁵ After the German mathematician Carl Gustav Jacob Jacobi.

Collecting the terms with C_1 and C_2 together we can see that

$$\mathbf{J}\vec{v}_1 = \lambda_1\vec{v}_1 \quad \text{and} \quad \mathbf{J}\vec{v}_2 = \lambda_2\vec{v}_2, \quad (17)$$

In other words, the vectors \vec{v}_i and constants λ_i are the eigenvectors and eigenvalues of the Jacobian matrix \mathbf{J} . Thus, we can calculate the λ s from the characteristic equation:

$$\det(\mathbf{J} - \lambda\mathbf{I}) = 0 \quad (18)$$

Our original question, whether δ_x and δ_y will grow or not is therefore determined by the eigenvalues of \mathbf{J} . The eigenvalues can in general be complex; the imaginary part of the eigenvalue will contribute to oscillatory behavior⁶, but it is the real parts of λ_i that will determine if δ_x and δ_y will grow or shrink: if the real parts are both negative, then the difference will shrink, and the dynamics will asymptotically converge to the equilibrium; the equilibrium can be classified as stable. If at least one of them is positive, the difference between the initial value of the dynamics and the equilibrium will eventually grow.

A necessary and sufficient condition for the real parts of both eigenvalues to be negative is for the trace and the determinant⁷ of the Jacobian to be negative and positive, respectively. To see why, write out the determinant in the characteristic equation:

$$\det(\mathbf{J} - \lambda\mathbf{I}) = \lambda^2 - (j_{11} + j_{22})\lambda + (j_{11}j_{22} - j_{12}j_{21}) = \lambda^2 + \text{Tr}(\mathbf{J})\lambda + \det(\mathbf{J}) \quad (19)$$

The solutions to this equation are:

$$\lambda_{1,2} = \frac{\text{Tr}(\mathbf{J}) \pm \sqrt{\text{Tr}(\mathbf{J})^2 - 4\det(\mathbf{J})}}{2} \quad (20)$$

You can verify that as long as $\text{Tr}(\mathbf{J}) < 0$ and $\det(\mathbf{J}) > 0$, the real part of these solutions will be negative. If the term in the square root is negative, then the eigenvalues will be complex, and the dynamics will be oscillatory (spiraling in or out depending on the real part of the eigenvalue.)

Predation

Lotka-Volterra Predator-Prey dynamics

The ecological theory of predation also starts with Lotka and Volterra⁸. As they did for competition, they also came up (independently) with the simplest set of equations that describe a prey-predator system. These equations are:

$$\frac{dV}{dt} = (r - aP)V \quad (21)$$

$$\frac{dP}{dt} = (bV - d)P. \quad (22)$$

⁶ Since $e^{it} = \cos(t) + i\sin(t)$

⁷ The trace of a matrix is defined as the sum of the diagonal elements, i.e.,

$$\text{Tr} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = a + d$$

and the determinant (for the 2x2 case) is the product of the diagonal minus the product of the anti-diagonal:

$$\det \begin{pmatrix} a & b \\ c & d \end{pmatrix} = ad - bc$$

⁸ See Berryman (1992) for a history of the development of predation theory in Ecology.

Again, we can start analyzing them with solving for equilibria, which is very easy in the current case:

$$V^* = d/b \quad P^* = r/a. \quad (23)$$

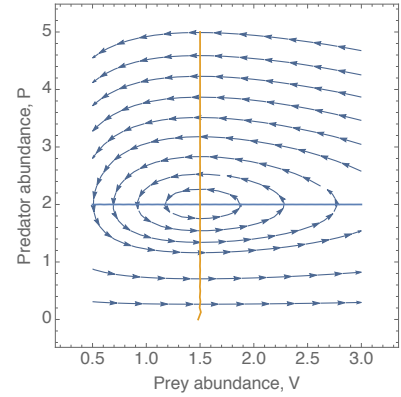
The first observation is somewhat strangely, the equilibrium prey abundance is given by the ratio of the birth and death rates of the predator, and the equilibrium predator abundance is only dependent on the growth and death rate of the prey. More generally, regardless of the prey population size, there is a unique predator abundance that makes the prey's growth rate zero. Likewise, there is a unique prey abundance that makes predator growth rate zero, regardless of predator abundance. This is illustrated in the phase diagram, where the isoclines for the prey and predator are vertical and horizontal, respectively. The arrows in the phase diagram depict the trajectory of the two populations starting out at different initial values. As the figure makes clear, the system has cyclic dynamics: no matter where the population starts (as long as it is with strictly positive prey and predator values), the time-trajectory of the population will be a cycle that returns to the original point after some amount of time.

One way to show the cycling property of Lotka-Volterra predator dynamics is to observe that the quantity $C = P^r e^{-aP} V^d e^{-bV}$ is a constant of motion, that is C does not change at all when the system moves according to the Lotka-Volterra predator-prey dynamics⁹. The points of constant C delineate closed trajectories (as can be seen in the figure below), leading to cycling. The cycling trajectories are neutrally stable, meaning that if some external disturbance shifts the system to a different trajectory (with a different value of C), the populations do not recover their initial cycle, rather they remain at the new trajectory.

The indefinite cycling of the Lotka-Volterra dynamics might potentially explain famous cases like the apparently stable cycling in the snowshoe hare-lynx dynamics. But the neutral stability of the cycle suggests that these systems would not be stable in the very-long term, since external shocks (e.g., a climate event that kills off many prey) can drive the system to trajectories that spend a lot of time near one of the axes (i.e. very low population sizes of either the prey or predator), meaning that these populations are prone to extinction. The neutrally stable cycles also end up being a structurally unstable feature of the model, as any number of modifications (even if they are slight) completely do away with that feature. Below, we discuss some of these modifications.

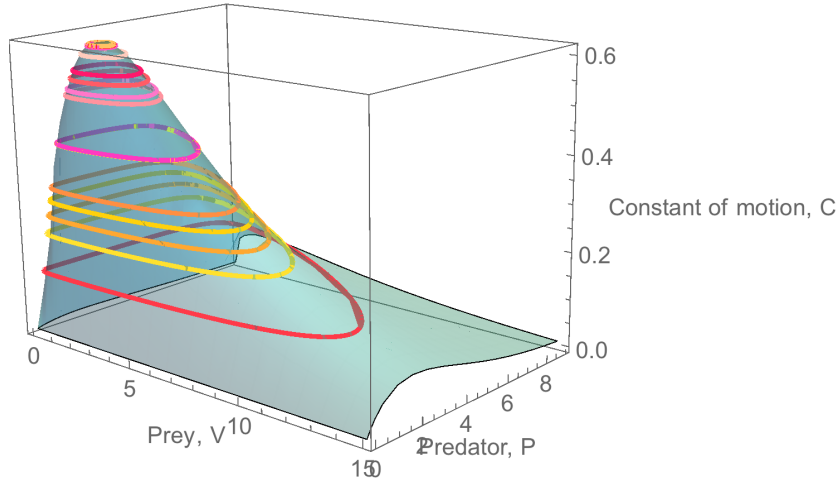
Density dependence of the prey

Strangely, neither Lotka nor Volterra incorporated density dependence into their canonical prey-predator equations (even though their competition theory is based on logistic growth). But we know that even if a species is eaten by another, and therefore never reaches its carrying capacity, it might still experience density dependence. So, let us incorporate prey density dependence while



The phase diagram of the classic Lotka-Volterra prey-predator dynamics. The blue line is the isocline for the prey, the orange line for the predator. The arrows depict the trajectory of the system for various initial conditions.

⁹ A good exercise is to verify this by taking the derivative $\frac{dC}{dt}$.



Trajectories of the LV-Predator prey dynamics with different initial conditions (rings with assorted colors), drawn on the surface depicting the value of the constant of movement C . The figure shows that the trajectories follow points of constant C .

keeping the predator equation unchanged.

$$\frac{dV}{dt} = \left(r \frac{K - V}{K} - aP\right)V \quad (24)$$

$$\frac{dP}{dt} = (bV - d)P. \quad (25)$$

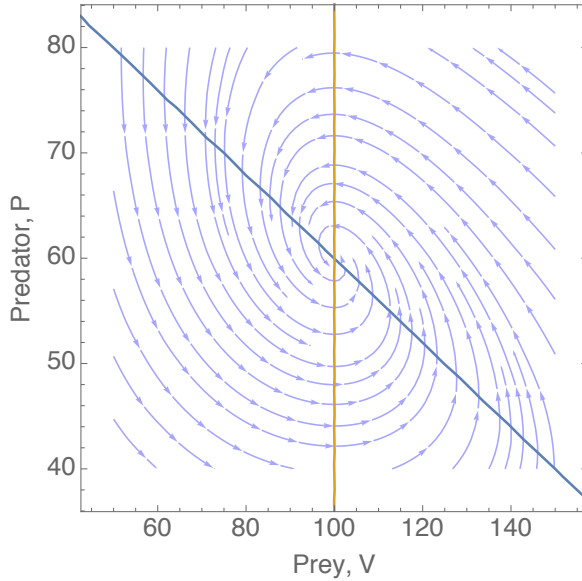
Since we haven't changed the predator equation, its isocline is still a vertical line at $V = d/b$. However, now the prey's isocline is a downward sloping line given by $P = r(K - V)/(Ka)$. The intersection of these lines is $P^* = r(bK - d)/(abK)$ and $V^* = d/b$. Visually checking the stability of the dynamics confirms that the equilibrium is always stable (with damped oscillations taking place of the neutrally stable cycles of the non-density dependent case).

Using the linearization method, we find the Jacobian evaluated at the equilibrium to be:

$$J = \begin{pmatrix} -\frac{dr}{bK} & -\frac{ad}{b} \\ \frac{(bk-d)r}{aK} & 0 \end{pmatrix} \quad (26)$$

Whose determinant is $\det(J) = adP^*$ and $\text{Tr}(J) = -\frac{dr}{bK}$. The determinant is positive whenever P^* is positive, and the trace is always negative, meaning that the equilibrium is indeed stable.¹⁰ So, density dependence of the prey stabilizes the L-V dynamics.

¹⁰ Depending on r , the approach to the equilibrium could be of the spiral or node type.



The isoclines and trajectories of the prey-predator dynamics with prey density dependence. The orange line is the predator's isocline, the blue line the prey's. The arrows depict the trajectory of the system. Parameters are: $a = 0.01$, $b = 0.005$, $d = 0.5$, $r = 1$, $K = 250$.

Functional responses: predator satiation

Another modification to the L-V dynamics gets rid of the (admittedly unrealistic) assumption that the per-capita prey consumption rate of predators increases linearly with prey numbers. This is reflected in the second term of the prey's equation, which is linear in V . This might be a reasonable approximation for low to moderate densities of prey, but for very high densities of prey, predator individuals will likely start to get satiated (either literally, i.e., eating to their physiological limit, or time-budget wise, due to the handling time for each prey)¹¹

The relation between the number of prey and the per-capita consumption by the predators is called the functional response. In principle, the functional response might have many different forms¹², only three of the most commonly considered are labeled: types 1, 2 and 3. Type 1 is the linear form in the original L-V model; Type 2 is a concave function corresponding to predator saturation, and Type 3 is a sigmoidal function that is initially accelerating, then becomes saturating. Type 3 functional responses can obtain when predators need a certain density of a given prey to either become proficient in catching them, or switch to the focal prey over other prey types.

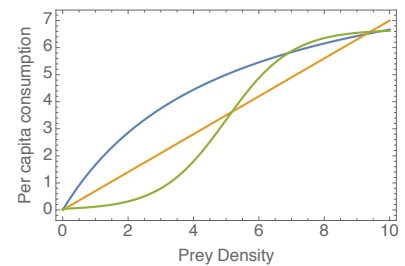
Let's suppose the functional response is of Type 2, given by the Holling's disk equation:¹³

$$f_2(V) = \frac{mV}{h + V},$$

where m is the maximum attack rate, and h is the prey density required to reach half this attack rate, i.e., a shape parameter that describes how quickly predators

¹¹ The classical representation of this phenomenon is called "Holling's disk equation", so named b/c it was derived in part by C.S. Holling using experiments where blindfolded students picked up paper disks from a table.

¹² including non-monotonic forms where predation rate decreases with increasing prey density, e.g. due to social defense mechanisms.



Different types of functional responses. The orange curve is type 1 functional response (linear), blue is type 2 (saturating), and green is Type 3 (sigmoidal).

¹³ Obviously, this is also identical to Michaelis-Menten kinematics.

get satiated. The modified prey-predator dynamics are now:

$$\frac{dV}{dt} = rV - f_2(V)P \quad (27)$$

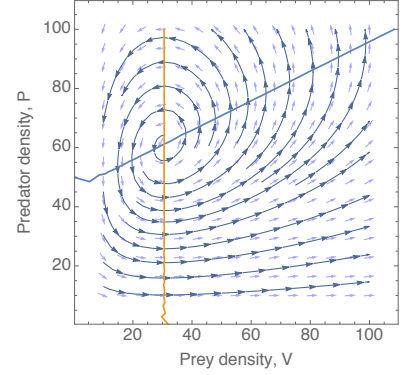
$$\frac{dP}{dt} = (bf_2(V) - d)P. \quad (28)$$

The isoclines are two lines given by: $V = dh/(bm - d)$ and $P = r(h + v)/m$, and their intersection, the equilibrium point, is at $P^* = bhr/(bm - d)$. However, a plot of the vector field (in the figure to the right) shows that the equilibrium point is unstable: populations starting near it will trace an expanding spiral, eventually blowing up. This can be checked with the linearization analysis near the equilibrium, which yields the Jacobian:

$$J = \begin{pmatrix} \frac{dr}{bm} & -\frac{d}{b} \\ r(b - \frac{d}{m}) & 0 \end{pmatrix}, \quad (29)$$

which has a positive trace.

The intuition behind this result is simple: the satiation of the predators means that they eventually will not be able to keep up with increased prey, because there is no instantaneous increase in predator consumption rate at high enough prey densities. Thus, the population regulation of prey (since we assumed no density dependence) fails. Eventually, predators will catch up in population size to the prey, and reduce the latter's density, but the next time the cycle repeats itself will be farther away from the equilibrium.



Interlude: proving the relation between stability and slope of Prey's isocline

At this point, you might have noticed a graphical way of distinguishing the stability of the prey-predator model. In all of the models we considered so far, the isocline of the predator is a vertical line, while the isocline of the prey has been changing from a horizontal line, to a decreasing to an increasing one. The first yields neutrally stable cycles, the second stable, the third unstable. So, it seems like a decreasing prey isocline near an equilibrium is a necessary and sufficient condition for stability. One can in fact prove that using the Jacobian method: you will notice that both Jacobian matrices so far had entries with the following signs:

$$\begin{pmatrix} \pm & - \\ + & 0 \end{pmatrix}, \quad (30)$$

The stability of an equilibrium requires $\det(J) > 0$ and $\text{Tr}(J) < 0$. The former is always satisfied, while the latter is only a function of the upper left element. Now, that element is defined as $\frac{\partial}{\partial V} \frac{dV}{dt} = \frac{\partial}{\partial V} (rV - f_2(V)P)$, evaluated at the equilibrium. On the other hand, the prey's isocline is given by $(rV - f_2(V)P) = 0$. Differentiating this with respect to V (taking P as a function of V), we get $\frac{\partial}{\partial V} (rV - f_2(V)P) - f_2(V)P'(V) = 0$. In other words,

$P'(V) = \left(\frac{\partial}{\partial V}(rV - f_2(V)P) \right) / f_2(V)$. Since $f_2(V)$ is positive, that means the slope of the prey's isocline has the same sign as the upper left element of the Jacobian. If the slope is positive, the system is unstable, if it is negative, stable (and neutral if it is zero). Note that this works only because of the form of the predator equation, which yields a vertical line for the predator's isocline (and thus makes the lower right entry zero).

Prey density dependence + Type 2 functional response

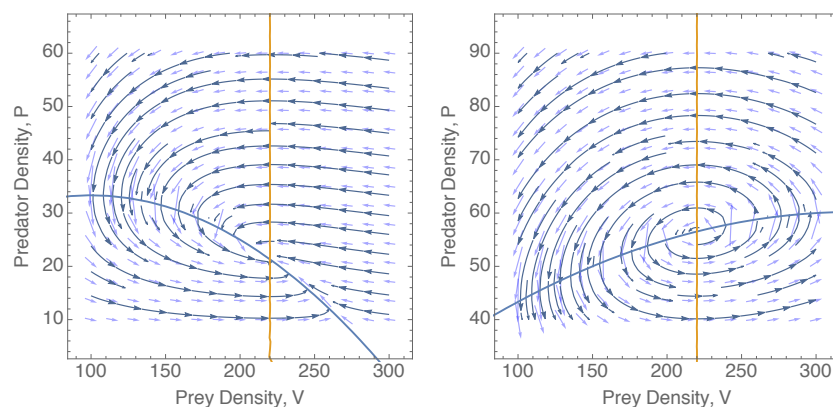
Now we put the two modifications together. The dynamics are now given by:

$$\frac{dV}{dt} = r \left(\frac{K - V}{K} \right) - f_2(V)P \quad (31)$$

$$\frac{dP}{dt} = (bf_2(V) - d)P. \quad (32)$$

The isocline for the predator is still a vertical line but now the prey's is a parabola, which gives rise to interesting dynamics.¹⁴

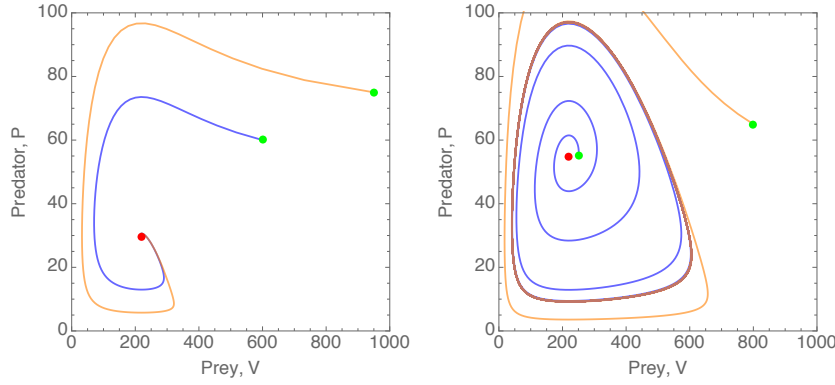
¹⁴ Verify that the isocline is quadratic.



The isoclines and sample flows on the state space for two values of the carrying capacity of the prey. $K = 300$ in the LHS panel and $K = 750$ in the RHS panel. The prey isocline is downward sloping at the equilibrium on the LHS panel, while upward sloping on the RHS. Correspondingly, the equilibrium is stable in the RHS case and unstable in the LHS case. Other parameters are: $m = 4$, $h = 100$, $r = 1$, $b = 0.4$, $d = 1.1$.

As the figure above shows, the dynamics of this system are stable for low carrying capacity of the prey, but become unstable as the carrying capacity increases. This has been called the **paradox of enrichment** by Michael Rosenzweig (1971): by adding resources to the system (to increase the carrying capacity of the prey) we can destabilize it, and potentially cause one or both species to go extinct.

What happens when the system switches from being stable to being unstable? As the figure below shows, as the equilibrium point becomes unstable, the system gains another stable attractor: a limit cycle around that point. This is called a Hopf bifurcation, and happens when the real part of the pair of complex conjugate eigenvalues (i.e., ones that differ only in the sign of the imaginary part) goes from negative to positive. Usually the result is the appearance of a limit cycle, as in our case.



Trajectories before and after the Hopf bifurcation. Green dots depict initial conditions for each trajectory and red dot the location of the equilibrium point. On the LHS panel, $K = 350$; RHS, $K = 700$. Each trajectory on the LHS converges to the stable equilibrium point, while they all converge to the stable limit cycle (regardless of whether they start inside or outside of it) on the RHS plot. Other parameters are $m = 4$, $h = 100$, $r = 1$, $b = 0.4$, $d = 1.1$.

Mutualism

Mutualisms have long been the neglected interactions in the cannon of two-species population dynamics. This is perhaps due to the fact that in the context of the standard L-V models, mutualistic dynamics, with both species helping each other's growth, tend to unstable with significant mutualistic benefits, as we will see now

Mutualism in the Lotka-Volterra competition model

We can use the most basic L-V competition model to represent a mutualism, by simply making the interspecies interaction coefficients be positive instead of negative, reflecting the fact that increased abundance of one species will increase the growth rate of the other in a mutualism.

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 + \alpha N_2}{K_1} \right) \quad (33)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 + \beta N_1}{K_2} \right), \quad (34)$$

with $\alpha, \beta > 0$. The equilibria can be found setting the RHS of the above equation equal to 0 and solving, or simply realizing that they are going to be the same equilibrium as in the competition case, but with the sign of both α and β reversed, i.e.:

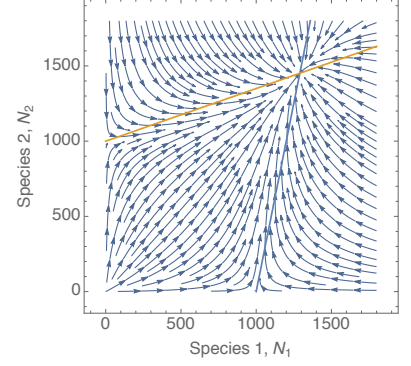
$$N_1^* = \frac{K_1 + \alpha K_2}{1 - \alpha\beta} \quad (35)$$

$$N_2^* = \frac{K_2 + \beta K_1}{1 - \alpha\beta}. \quad (36)$$

As expected, both species are predicted to be above their carrying capacities now. Plotting the trajectories in the phase place with the isoclines, we see that

the latter are both upwards sloping, and yield a stable equilibrium when they intersect.

The problem is, that the two isoclines may not intersect. In particular, the slope of the isoclines are given by $1/\alpha$ and β , for species 1 and 2, respectively. Since species 2's starts higher on the vertical axis, the two isoclines will only intersect when $1/\alpha > \beta$, or $1 > \alpha\beta$. This can also be seen as the condition for the equilibrium abundances to be positive (if the condition is not satisfied, the lines diverge in the positive quadrant, and intersect in the negative one). Hence, for mutualistic L-V dynamics to be stable, the strength of the mutualism cannot be too high. This may have been one of the reasons people regarded mutualisms as a relatively unimportant (compared to competition and predation) type of interaction, thinking unless it is weak, it's not stable.



Lotka-Volterra dynamics for mutualisms in the phase plane. Blue line is species 1's isocline; orange species 2's. The intersection point is stable.

Mutualisms with diminishing returns to scale

The preceding conclusion, of course, is overgeneralizing from a simple toy model. In particular, as we have seen with predation, linear effects of one species on another tends to create unrealistic situations when applied globally (as opposed to near an equilibrium point). In particular, the L-V model for mutualism implies that for each individual from a partner species that is added to the population, an individual from a focal species experiences the same increase in growth rate, regardless of how many individuals there are already. In reality, the benefits from increased partner abundance are likely to diminish, as individuals will have a finite need for those benefits (e.g., finite number of flowers to be pollinated, or pollen to be carried away), or capacity to interact with finite number of individuals (e.g., finite root area to be colonized by mycorrhizae). This suggest, we might employ something like a Type-2 functional response to make the L-V model more realistic.

We modify the Lotka-Volterra dynamics above, using the now-familiar Michaelis-Menten functional response:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 + m_1 N_2 / (h_1 + N_2)}{K_1} \right) \quad (37)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 + m_2 N_1 / (h_2 + N_1)}{K_2} \right), \quad (38)$$

Now the isoclines are no longer straight lines, but are curved inwards and always intersect, regardless of the initial (i.e., at low partner species abundances) strength of the mutualism. This can be seen from the fact that the Michaelis-Menten function reaches an asymptote at m_i as the partner species abundance N_j ($j \neq i$) goes to infinity. That means for very large population sizes of, say, N_1 , the isocline for species 2 will be a horizontal line. Likewise, for very large population sizes of N_2 , species 1's isocline becomes vertical. Since both isoclines are continuous, that implies they have to intersect somewhere.

This offers a way to reconcile the simple observation that mutualisms in nature are very important, and provide a lot of benefits to the species involved (indeed, might be obligatory for reproduction to happen at all) with the stability properties of the Lotka-Volterra system.

Coexistence in mutualistic systems

Mutualisms can not only alter the abundance of particular species, but change competitive relations between them in unexpected ways. Here is an example model, from Bever (2002), which considers competition between two plant species whose growth rates depend in part on their interactions with the soil community (mycorrhizae, rhizosphere bacteria, etc.). For simplicity, Bever assumes there are two partner species (e.g., mycorrhizae) in the soil and that their abundances add up to 1. This allows us to represent the soil community as a one-dimensional variable, S (between 0 and 1), which gives the frequency of mycorrhizal species 1. The two mycorrhizal species can have differential effects on the plant. In particular, let us denote mycorrhizal species 1 has an effect α_1 on plant species 1's growth rate, and α_2 on plant species 2, while the mycorrhizal species 2 has effect β_1 and β_2 on plant species 1 and 2, respectively¹⁵. Finally, the composition of the plant community affects the different mycorrhizae; without loss of generality, assume that mycorrhizal species 1 benefits from increased abundance of plant species 1. The full dynamics of the two-plant species and the soil community is given by:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - c_1 N_2}{K_1} + \alpha_1 S + \beta_1 (1 - S) \right) \quad (39)$$

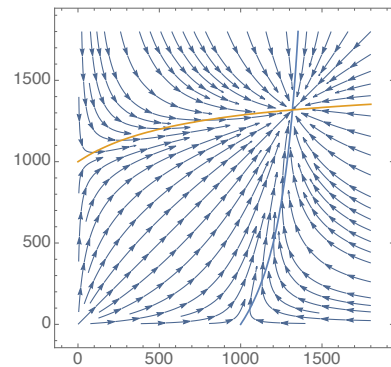
$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - c_2 N_1}{K_2} + \alpha_2 S + \beta_2 (1 - S) \right) \quad (40)$$

$$\frac{dS}{dt} = S(1 - S) \left(\frac{N_1}{N_1 + N_2} - \nu \frac{N_2}{N_1 + N_2} \right). \quad (41)$$

Here, c_i are positive (interspecific competition coefficients), α_i and β_i can be positive or negative (corresponding to the mycorrhizae being mutualistic or parasitic), and ν is positive (such that plant species 2 favors mycorrhizal species 2).

This model has a lot of parameters, and can generate lots of different patterns. Let us look at an interesting subset¹⁶: first let's assume the soil community has no differential impact on either species, i.e., set all α s and β s equal to the same constant. Obviously we get classic Lotka-Volterra competition among the two plant species, and suppose that species 1 competitively excludes species 2, as depicted in the figure on the margin.

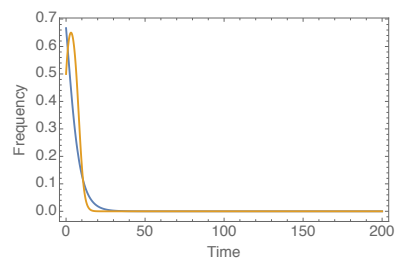
Now, "turn on" the soil community feedback; in particular, assume that mycorrhizal species 1 (which benefits from plant species 1) benefits plant species 2 most, and vice versa. Then, we might get fundamentally different dynamics, as depicted in the second figure to the right. Coexistence becomes possible, since



The isoclines and trajectories for mutualism dynamics with type-two functional response. As usual, blue curve is the isocline for species 1, orange curve for species two. The equilibrium always exists, and is stable.

¹⁵ Note that the notation is a bit different than the classical L-V competition, where the α and β would have referred to between-plant species competition, which is denoted by c_1 and c_2 here.

¹⁶ see the paper for more.



Dynamics of competition without differential feedback from the soil community. The blue curve depicts the trajectory of the plant species composition (frequency of species 1; $N_1/(N_1 + N_2)$); the orange curve the soil community composition. Species 2 quickly outcompetes species 1, and the soil community therefore quickly converges to zero as well. Parameters are: $\alpha_i = \beta_i = 0.1$, $c_1 = 0.7$, $c_2 = 1.2$, $K_1 = K_2 = 100$, $r_1 = 0.9$, $r_2 = 1.1$, and $\nu = 0.8$.

as the frequency of one plant goes up in the community, it favors one of the mycorrhizal species, which (by our assumption) favors the competitor plant. In this way, each species gets a growth advantage when rare, and a stable equilibrium obtains.

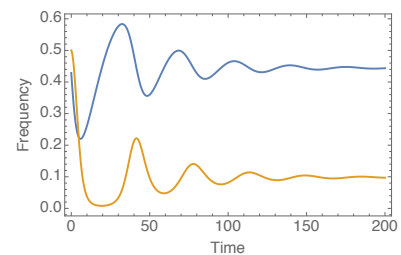
One can obtain the condition for stable coexistence analytically, by looking at invasion growth rate as in the L-V dynamics; i.e., the growth rate of a plant when its abundance is almost zero. The added twist is that when a plant species is initially excluded (or very low frequency) in a community, the soil community will also reflect that. Suppose $N_1 \approx 0$, which implies that $S \approx 0$ and $N_2 = K_2(1 + \beta_2)$. Then, the per-capita growth rate of plant species 1 is given by $r_1((K_1 - c_1 K_2(1 + \beta_2))/K_1 + \beta_1)$. This is going to be positive when:

$$\frac{K_1}{K_2} > c_1 \frac{1 + \beta_2}{1 + \beta_1} \quad (42)$$

Comparing this with the corresponding condition without soil feedback (8), we find that the differential effects make it easier for plant 1 to invade if it benefits from mycorrhizal species 2 more than plant species 2 benefits. In this way, feedbacks from soil mutualists can facilitate competitive coexistence.

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Dynamics of competition with differential feedback from the soil community, showing stable coexistence due to the soil feedback. Parameters are as in previous figure, except that $\alpha_2 = \beta_1 = 0.5$, meaning that each plant gets higher benefit (5-fold) from the mycorrhizal species favored by the other plant.