Ecological Dynamics

Competition (2 / 2)

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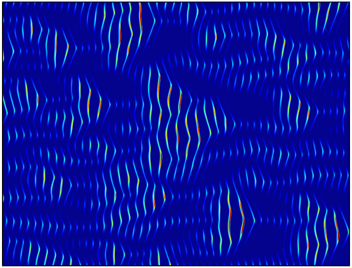


Discrete-time Lotka-Volterra model

We can write a discrete-time version of the 2-species Lotka-Volterra model as follows:

$$N_1\left(t+1\right) = N_1(t)\left(1 + R_1\left(\frac{K_1 - N_1(t) - \alpha_{12}N_2(t)}{K_1}\right)\right)$$
$$N_2\left(t+1\right) = N_2(t)\left(1 + R_2\left(\frac{K_2 - N_2(t) - \alpha_{21}N_1(t)}{K_2}\right)\right)$$

Where the interspecific competition coefficients $\alpha_{ij} \geq 0$ and the intraspecific competition coefficients $\alpha_{ii} = \alpha_{jj} = 1$.

Solving at equilibrium

This model has four possible equilibrium solutions: two monocultures such that $\hat{N}_i = K_i$ and $\hat{N}_j = 0$, one extinction such that $\hat{N}_i = \hat{N}_j = 0$, and the **interior equilibrium** where $\hat{N}_i > 0$ and $\hat{N}_j > 0$.

At the interior equilibrium, the growth rate of both species is zero so we have:

$$\frac{N_1(t+1)}{N_1(t)} = 1 + R_1\left(\frac{K_1 - N_1(t) - \alpha_{12}N_2(t)}{K_1}\right) = 1$$
$$\frac{N_2(t+1)}{N_2(t)} = 1 + R_2\left(\frac{K_2 - N_2(t) - \alpha_{21}N_1(t)}{K_2}\right) = 1$$

Solving at equilibrium

This can happen if the initial abundances $N_i(0) = 0$, the growth rates $R_i = 0$ or, more interestingly, if the term in the parentheses is zero (we now ditch the t):

$$\begin{aligned} K_1 - N_1 - \alpha_{12} N_2 &= 0 \\ K_2 - N_2 - \alpha_{21} N_1 &= 0 \end{aligned}$$

We can isolate the N_i terms in both equations:

$$\begin{aligned} N_1 &= K_1 - \alpha_{12} N_2 \\ N_2 &= K_2 - \alpha_{21} N_1 \end{aligned}$$

We now replace N_2 in the first equation with its expression from the second equation:

$$N_1 = K_1 - \alpha_{12} \left(K_2 - \alpha_{21} N_1 \right)$$

Solving at equilibrium

We now isolate N_1:

$$\boxed{\hat{N}_1 = \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12}\alpha_{21}}}$$

We proceed in the same way to get N_2:

$$\boxed{\hat{N}_2 = \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12}\alpha_{21}}}$$

We now need to determine when this equilibrium solution is **biologically feasible** (i.e., $\frac{\hat{N}_i}{\hat{N}_j} > 0$). This means that we must have:

$$\frac{\hat{N}_i}{\hat{N}_j} = \frac{K_1 - \alpha_{12} K_2}{K_2 - \alpha_{21} K_1} > 0$$

Solving at equilibrium

This leads to two separate conditions:

$$\frac{K_1}{K_2} > \alpha_{12}$$
$$\frac{K_2}{K_1} > \alpha_{21}$$

Combining these two conditions via multiplication yields:

$$1 > \alpha_{12}\alpha_{21}$$

The trick is to note that by definition, $\alpha_{11} = \alpha_{22} = 1$, so we can write:

$$\boxed{\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}}$$

This expression means that **intraspecific competition** must be greater than **interspecific competition** for coexistence to occur.

Stability analysis

We can use Taylor expansion for each growth equation $N_i\,(t+1) = f_i\,(N_i(t))$ in the model to determine whether perturbations $\epsilon_1(t)$ and $\epsilon_2(t)$ applied to species 1 and 2 respectively will grow over time:

$$N_1\,(t+1) + \epsilon_1\,(t+1) = f_1\left(\hat{N}_1(t) + \epsilon_1(t), \hat{N}_2(t) + \epsilon_2(t)\right)$$
$$N_2\,(t+1) + \epsilon_2\,(t+1) = f_2\left(\hat{N}_1(t) + \epsilon_1(t), \hat{N}_2(t) + \epsilon_2(t)\right)$$

Simplifying yields:

$$\epsilon_1\,(t+1) = \frac{\partial f_1}{\partial N_1}\epsilon_1(t) + \frac{\partial f_1}{\partial N_2}\epsilon_2(t)$$
$$\epsilon_2\,(t+1) = \frac{\partial f_2}{\partial N_1}\epsilon_1(t) + \frac{\partial f_2}{\partial N_2}\epsilon_2(t)$$

Stability analysis

This can be rewritten using matrix notation such that $\boldsymbol{\epsilon}(t+1) = \mathbf{J}\boldsymbol{\epsilon}(t)$:

$$\begin{bmatrix} \epsilon_1(t+1) \\ \epsilon_2(t+1) \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{bmatrix} \begin{bmatrix} \epsilon_1(t) \\ \epsilon_2(t) \end{bmatrix}$$

When will a set of perturbations ϵ_i applied to each species grow over time? To determine this, we have to compute the eigenvalues of the **Jacobian matrix**.

The perturbations will decay exponentially if the eigenvalues $-1 < \lambda < 1$ and grow exponentially otherwise.

Hence, an equilibrium will be stable if the absolute value of all eigenvalues is smaller than one.

Stability analysis of the Lotka-Volterra model

To assess the stability of the equilibria, we must first write the Jacobian matrix $\mathbf{J}$ by taking the partial derivatives of each population growth rate $\dot{N}_i$ with respect to each variable N_i:

$$\mathbf{J} = \begin{bmatrix} 1 + R_1 \left(\frac{K_1 - 2\hat{N}_1 - \alpha_{12}\hat{N}_2}{K_1} \right) & \frac{-R_1}{K_1} \left(\alpha_{12}\hat{N}_1 \right) \\ \frac{-R_2}{K_2} \left(\alpha_{21}\hat{N}_2 \right) & 1 + R_2 \left(\frac{K_2 - 2\hat{N}_2 - \alpha_{12}\hat{N}_1}{K_2} \right) \end{bmatrix}$$

We now assess the stability of the boundary (i.e., non-interior) equilibria. We begin with the extinction equilibrium $\left\{ \hat{N}_1 = 0, \hat{N}_2 = 0 \right\}$:

$$\mathbf{J}(0,0) = \begin{bmatrix} 1 + R_1 & 0 \\ 0 & 1 + R_2 \end{bmatrix}$$

Stability analysis of the Lotka-Volterra model

To determine the eigenvalues, we subtract $\lambda\mathbf{I}$ from $\mathbf{J}(0,0)$ and find the characteristic polynomial by computing the determinant:

$$0 = (1 + R_1 - \lambda_1)(1 + R_2 - \lambda_2)$$

There are two solutions to this equation: $\lambda_1 = 1 + R_1$ and $\lambda_2 = 1 + R_2$. This means that as long as the growth rates are greater than zero, both eigenvalues will be greater than 1 and the extinction equilibrium will be unstable.

We now determine the stability of the species 1 monoculture $\left\{\hat{N}_1 = K_1, \hat{N}_2 = 0\right\}$:

$$\mathbf{J}(K_1, 0) = \begin{bmatrix} 1 - R_1 & -R_1\alpha_{12} \\ 0 & 1 + R_2\left(1 - \frac{\alpha_{21}K_1}{K_2}\right) \end{bmatrix}$$

Stability analysis of the Lotka-Volterra model

The eigenvalues of $\mathbf{J}(K_1, 0)$ are:

$$0 = (1 - R_1 - \lambda_1)\left(1 + R_2\left(1 - \frac{\alpha_{21}K_1}{K_2}\right) - \lambda_2\right)$$

There are two solutions to this equation: $\lambda_1 = 1 - R_1$ and $\lambda_2 = 1 + R_2\left(1 - \frac{\alpha_{21}K_1}{K_2}\right)$.

The absolute value of the first eigenvalue is smaller than 1 only if $0 < R_1 < 2$. The absolute value of the second eigenvalue is smaller than 1 only if $K_2 < \alpha_{21}K_1$.

Hence, this equilibrium is stable only if the growth rate of species 1 is between 0 and 2, and the carrying capacity of species 1 multiplied by its competitive effect on species 2 is greater than the carrying capacity of species 2.

Stability analysis of the Lotka-Volterra model

We now determine the stability of the species 2 monoculture $\left\{\hat{N}_1 = 0, \hat{N}_2 = K_2\right\}$:

$$\mathbf{J}(0, K_2) = \begin{bmatrix} 1 + R_1\left(1 - \frac{\alpha_{12}K_2}{K_1}\right) & 0 \\ -R_2\alpha_{21} & 1 - R_2 \end{bmatrix}$$

The eigenvalues of $\mathbf{J}(0, K_2)$ are:

$$0 = \left(1 + R_1\left(1 - \frac{\alpha_{12}K_2}{K_1}\right) - \lambda_1\right)(1 - R_2 - \lambda_2)$$

There are two solutions to this equation: $\lambda_1 = 1 + R_1\left(1 - \frac{\alpha_{12}K_2}{K_1}\right)$ and $\lambda_2 = 1 - R_2$.

The absolute value of the first eigenvalue is smaller than 1 only if $K_1 < \alpha_{12}K_2 >$. The absolute value of the second eigenvalue is smaller than 1 only if $0 < R_2 < 2$.

Stability analysis of the Lotka-Volterra model

Hence, this equilibrium is stable only if the growth rate of species 2 is between 0 and 2, and the carrying capacity of species 2 multiplied its competitive effect on species 1 is greater than the carrying capacity of species 1.

We now determine the stability of the interior equilibrium $\left\{\hat{N}_1 = \frac{K_1 - \alpha_{12}K_2}{1-\alpha_{12}\alpha_{21}}, \hat{N}_2 = \frac{K_2 - \alpha_{21}K_1}{1-\alpha_{12}\alpha_{21}}\right\}$:

$$\mathbf{J}\left(\hat{N}_1, \hat{N}_2\right) = \begin{bmatrix} 1 - R_1 \frac{K_1 - \alpha_{12}K_2}{K_1(1-\alpha_{12}\alpha_{21})} & -\alpha_{12} \frac{K_1 - \alpha_{12}K_2}{K_1(1-\alpha_{12}\alpha_{21})} \\ -\alpha_{21} \frac{K_2 - \alpha_{21}K_1}{K_2(1-\alpha_{12}\alpha_{21})} & 1 - R_2 \frac{K_2 - \alpha_{21}K_1}{K_2(1-\alpha_{12}\alpha_{21})} \end{bmatrix}$$

Stability analysis of the Lotka-Volterra model

The eigenvalues of this Jacobian matrix are very complex. Although they can be computed, they cannot be easily interpreted ecologically. However, the sub-case where $R_1 = R_2 = R$ can be interpreted ecologically:

$$\lambda_1 = 1 - R$$
$$\lambda_2 = 1 - R\left(\frac{(K_1 - \alpha_{12}K_2)(K_2 - \alpha_{21}K_1)}{K_1K_2(1 - \alpha_{12}\alpha_{21})}\right)$$

The absolute value of the first eigenvalue will be smaller than one as long as $0 < R < 2$.

The second eigenvalue λ_2 can be rewritten in terms of $\hat{N}_1$ and $\hat{N}_2$ to facilitate its ecological interpretation:

$$\lambda_2 = 1 - R\left(\frac{\hat{N}_1\hat{N}_2(1 - \alpha_{12}\alpha_{21})}{K_1K_2}\right)$$

Stability analysis of the Lotka-Volterra model

The absolute value of the second value will be smaller than one as long as the term in parentheses is greater than 0. This will happen as long as $1 - \alpha_{12}\alpha_{21} > 0$ or when we remember that $\alpha_{11}\alpha_{22} = 1$:

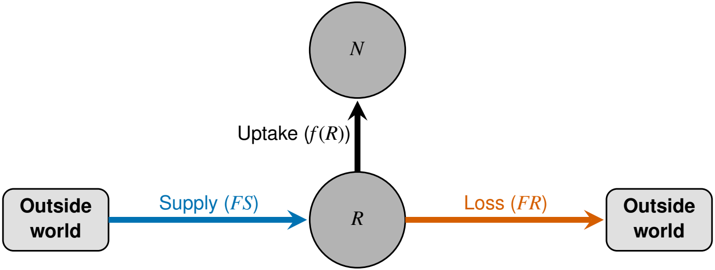
$$\boxed{\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}}$$

Hence, we recover the familiar condition for stable coexistence: intraspecific competition $\alpha_{11}\alpha_{22} = 1$ has to be greater than interspecific competition $\alpha_{12}\alpha_{21}$.

Mechanistic competition

Mechanistic competition theory was largely developed by Tilman (1977, 1980, 1982), who focused on consumer-resource dynamics in lakes.

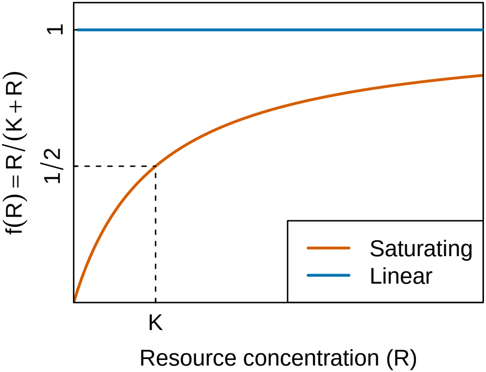
These models consist of a consumer N and a resource R:



How would you construct a continuous-time model based on the diagram above?

Mechanistic competition

Mechanistic consumer-resource models assume that resource uptake is saturating and follows a Michaelis-Menten or Monod function $f(R)$:



Here, K represents the half-saturation constant (i.e., the concentration of the resource R at which half of it is taken-up).

A mechanistic model of consumer-resource dynamics

The dynamics of a system with a single resource R and consumer N can be modeled as follows:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left(\mu\frac{R}{K+R} - M\right)$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = F(S-R) - N\left(\frac{\mu}{Y}\frac{R}{K+R}\right)$$

Where μ and M represents respectively the maximum growth rate and the mortality rate of the consumer, F is the flow or supply of the resource, S is the maximum concentration of the resource, Y is the consumer yield (i.e., the number of consumers produced per unit of resource R).

Solving the model at equilibrium

Since we are dealing coupled nonlinear differential equations, we have to solve the system at equilibrium by setting $\frac{\mathrm{d}N}{\mathrm{d}t} = 0$ and $\frac{\mathrm{d}R}{\mathrm{d}t} = 0$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left(\mu\frac{R}{K+R} - M\right) = 0$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = F\left(S - R\right) - N\left(\frac{\mu}{Y}\frac{R}{K+R}\right) = 0$$

Solving the model at equilibrium

We can now solve for the equilibrium concentration of resource $\hat{R}$ and the equilibrium abundance of consumer $\hat{N}$:

$$\boxed{\hat{R} = \frac{KM}{\mu - M}}$$

$$\boxed{\hat{N} = \frac{F\left(S - \frac{KM}{\mu - M}\right)}{\frac{\mu}{Y} \cdot \frac{\frac{KM}{\mu - M}}{K + \frac{KM}{\mu - M}}}}$$

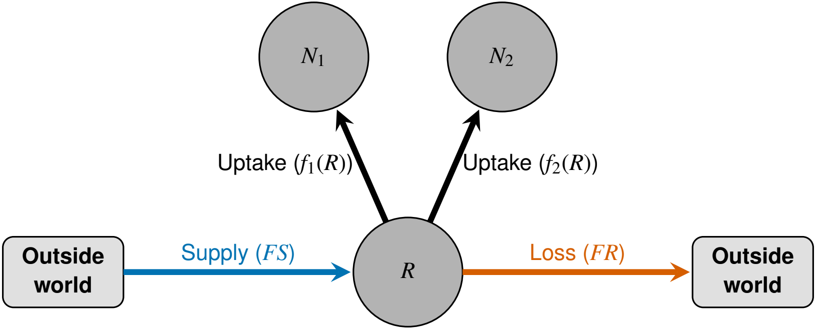
For this equilibrium to be **biologically feasible**, we must have $\hat{R} > 0$ and $\hat{R} > 0$:

$$\mu > M$$

$$S > \frac{KM}{\mu - M}$$

A model of mechanistic competition

Naturally, we can extend this model to include competition between two consumer species N_1 and N_2:



A model of mechanistic competition

The dynamics of two consumers N_1 and N_2 competing for a common resource R can be modeled as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = N_1\left(\mu_1 \frac{R}{K_1 + R} - M_1\right)$$
$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = N_2\left(\mu_2 \frac{R}{K_2 + R} - M_2\right)$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = F\left(S - R\right) - N_1\left(\frac{\mu_1}{Y_1} \frac{R}{K_1 + R}\right) - N_2\left(\frac{\mu_2}{Y_2} \frac{R}{K_2 + R}\right)$$

Where each consumer species i has its own half-saturation constant K_i, mortality rate M_i, maximum growth rate μ_i, and yield Y_i.

Solving the model at equilibrium

We can solve the model at equilibrium by setting $\frac{\mathrm{d}N_i}{\mathrm{d}t} = 0$ and $\frac{\mathrm{d}R}{\mathrm{d}t} = 0$:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = N_1 \left(\mu_1 \frac{R}{K_1 + R} - M_1 \right) = 0$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = N_2 \left(\mu_2 \frac{R}{K_2 + R} - M_2 \right) = 0$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = F\,(S - R) - N_1 \left(\frac{\mu_1}{Y_1} \frac{R}{K_1 + R} \right) - N_2 \left(\frac{\mu_2}{Y_2} \frac{R}{K_2 + R} \right) = 0$$

The equilibrium is only biologically feasible if $\hat{N}_i > 0$ and $\hat{R}_i > 0$. $\hat{N}_1 > 0$ if:

$$R_1^* = \frac{K_1 M_1}{\mu_1 - M_1}$$

Solving the model at equilibrium

Similarly, $\hat{N}_2 > 0$ if:

$$R_2^* = \frac{K_2 M_2}{\mu_2 - M_2}$$

Both consumers can coexist if and only if $R_1^* = R_2^*$. Otherwise, only the species with the lowest R^* value will persist by drawing-down the resource R below the critical concentration required by all other consumers.

This is known as the R^* rule.

Solving the model at equilibrium

We can extend the model to P consumers competing for a resource R:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\mu_i \frac{R}{K_i + R} - M_i\right)$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = F\left(S - R\right) - \sum_{i=1}^{P} N_i\left(\frac{\mu_i}{Y_i}\frac{R}{K_i + R}\right)$$

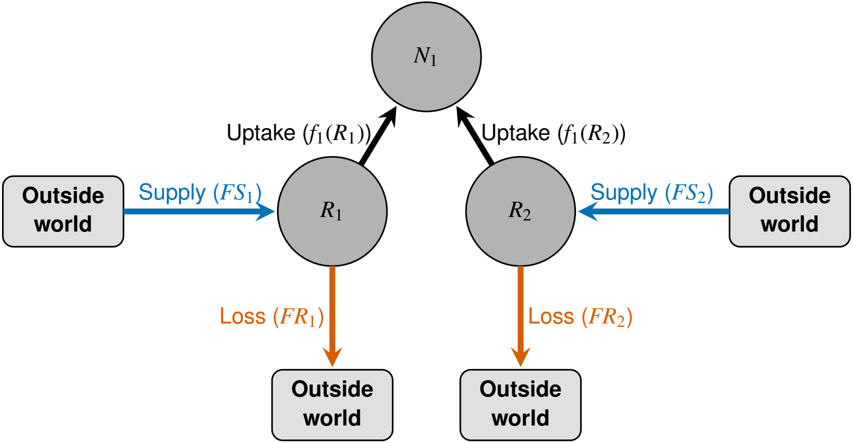
This yields the following R_i^* for each consumer i:

$$R_i^* = \frac{K_i M_i}{\mu_i - M_i}$$

Two consumers i and j can coexist if and only if $R_i^* = R_j^*$. **This is known as the competitive exclusion principle: P consumers cannot coexist stably on fewer than P resources.**

Diagram of a one-consumer, two-resources model

To understand how coexistence can occur between multiple consumer competing for multiple resources, we begin with a simple one-consumer, two-resources model:



A one-consumer, two-resources model

The dynamics of a single consumer N_1 and two resources R_1 and R_2 can be modeled as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = N_1\left(\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) - M_1\right)$$

$$\frac{\mathrm{d}R_1}{\mathrm{d}t} = F\left(S_1 - R_1\right) - Q_{11}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right)N_1$$

$$\frac{\mathrm{d}R_2}{\mathrm{d}t} = F\left(S_2 - R_2\right) - Q_{12}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right)N_1$$

Here, Q_{1i} represents the number of resources i required to produce a single consumer N_1 (i.e., the inverse of yield Y_{1i}).

Note that consumer growth will be determined by the concentration of the limiting resource (either R_1 or R_2) according to **Liebig's law of the minimum**.

Solving the model at equilibrium

By setting the growth rate to zero, it is possible to show that the equilibrium concentration of each resource will be:

$$R^*_{11} = \frac{M_1 K_{11}}{\mu_1 - M_1}$$
$$R^*_{12} = \frac{M_1 K_{12}}{\mu_1 - M_1}$$

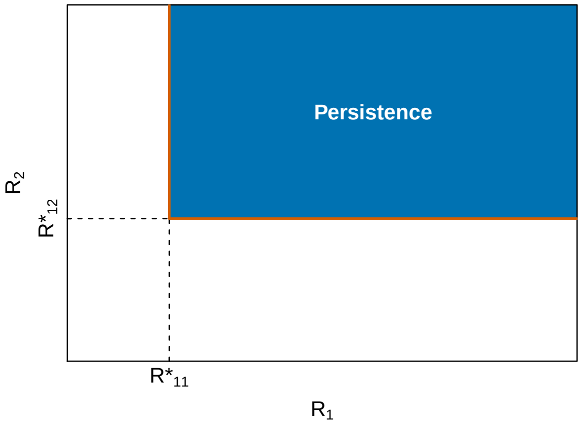
This means that the only difference between these R^* values will be dictated by the consumer's half-saturation constant K_{1i}.

The consumer's ability to persist will be defined by the following equation:

$$M_1 = \mu_1 \cdot \min\left(\frac{R_1}{K_{11} + R_1}, \frac{R_2}{K_{12} + R_2}\right)$$

This equation defines a broad region of parameter space delineated by two perpendicular lines that define the consumer's ZNGI.

ZNGI for one-consumer, two-resources model



The consumer can persist within the blue rectangle delineated by the red ZNGI, which are based on the R^* values for each resource.

Graphical analysis of the equilibrium

To determine the equilibrium abundance of the consumer, we can define how it will draw down the resources in the (R_1, R_2) parameter space via the consumption vector $\mathbf{Q}$ by taking the ratio of the negative terms in the resource equations:

$$\frac{Q_{11}}{Q_{12}} = \frac{Q_{11}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) N_1}{Q_{12}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) N_1}$$

This means that the consumer will always draw down resources in direction $\mathbf{Q} = \begin{pmatrix} -Q_{11} \\ -Q_{12} \end{pmatrix}$.

Graphical analysis of the equilibrium

Given a supply point (S_1, S_2), we can also determine how resources will be replenished by taking the ratio of the first term of the resource equations to obtain the supply vector:

$$\frac{S_1 - R_1}{S_2 - R_2} = \frac{F\,(S_1 - R_1)}{F\,(S_2 - R_2)}$$

At equilibrium, the consumption and supply vectors must be equal in size and point in opposite directions in order to cancel out and lead to zero net growth.

Hence, if the equilibrium concentration of resource 1 is $\hat{R}_1$, the equilibrium abundance of consumer 1 will be:

$$\hat{N}_1 = \frac{F\left(S_1 - \hat{R}_1\right)}{Q_{11}\mu_1\hat{R}_1} = \frac{F\left(S_1 - \hat{R}_1\right)}{Q_{11}M_1} = \frac{F\,(S_1 - M_1/\mu_1)}{Q_{11}M_1}$$

Graphical analysis of the equilibrium

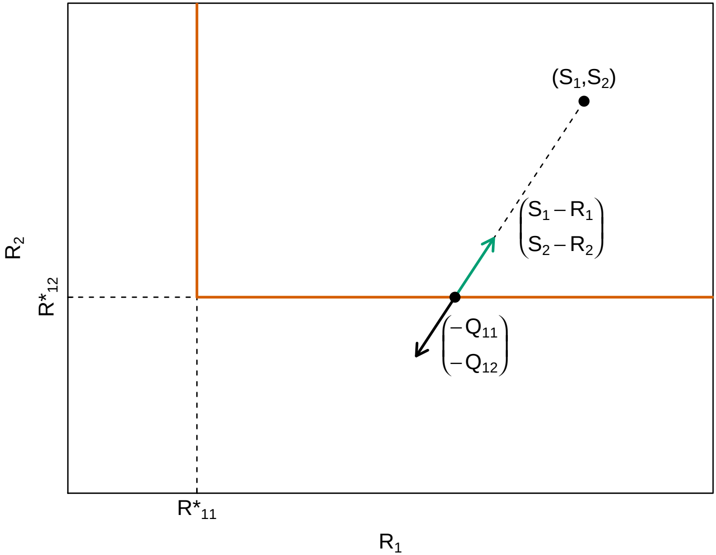
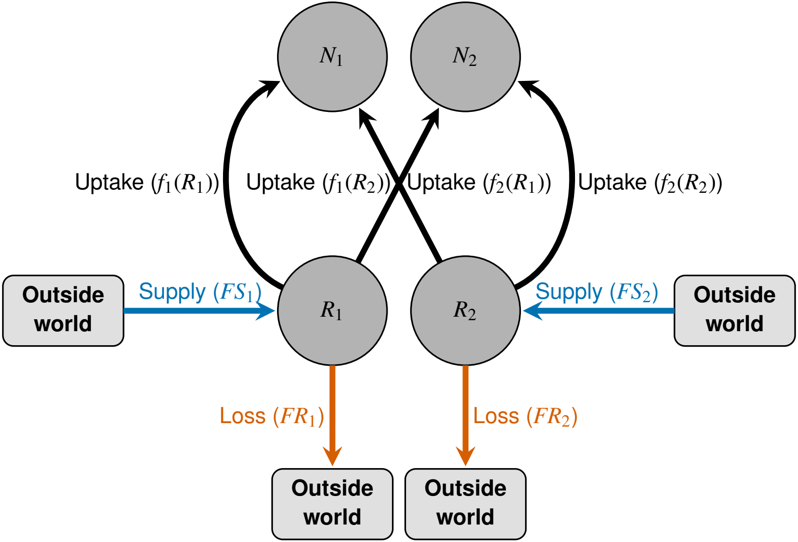


Diagram of a two-consumers, two-resources model



The two-consumers, two-resources model

$$
\begin{aligned}
\frac{\mathrm{d}N_1}{\mathrm{d}t} &= N_1\left(\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) - M_1\right) \\
\frac{\mathrm{d}N_2}{\mathrm{d}t} &= N_2\left(\mu_2 \cdot \min\left(\frac{R_1}{K_{21}+R_1}, \frac{R_2}{K_{22}+R_2}\right) - M_2\right) \\
\frac{\mathrm{d}R_1}{\mathrm{d}t} &= F\left(S_1 - R_1\right) - Q_{11}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) N_1 \\
&\qquad\qquad\qquad - Q_{21}\mu_2 \cdot \min\left(\frac{R_1}{K_{21}+R_1}, \frac{R_2}{K_{22}+R2}\right) N_2 \\
\frac{\mathrm{d}R_2}{\mathrm{d}t} &= F\left(S_2 - R_2\right) - Q_{12}\mu_1 \cdot \min\left(\frac{R_1}{K_{11}+R_1}, \frac{R_2}{K_{12}+R_2}\right) N_1 \\
&\qquad\qquad\qquad - Q_{22}\mu_2 \cdot \min\left(\frac{R_1}{K_{21}+R_1}, \frac{R_2}{K_{22}+R_2}\right) N_2
\end{aligned}
$$

Consumer ZNGI

This model has two sets of ZNGI. For species N_1:

$$M_1 = \mu_1 \cdot \min\left(\frac{R_1}{K_{11} + R_1}, \frac{R_2}{K_{12} + R_2}\right)$$

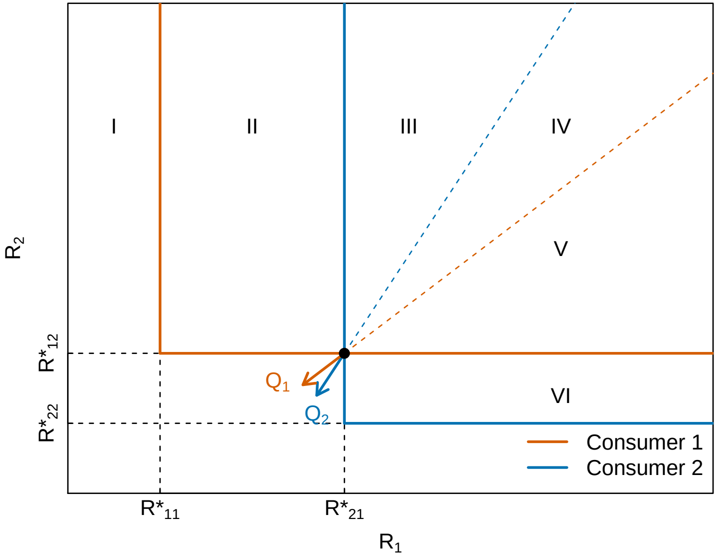
For species N_2:

$$M_2 = \mu_2 \cdot \min\left(\frac{R_1}{K_{21} + R_1}, \frac{R_2}{K_{22} + R_2}\right)$$

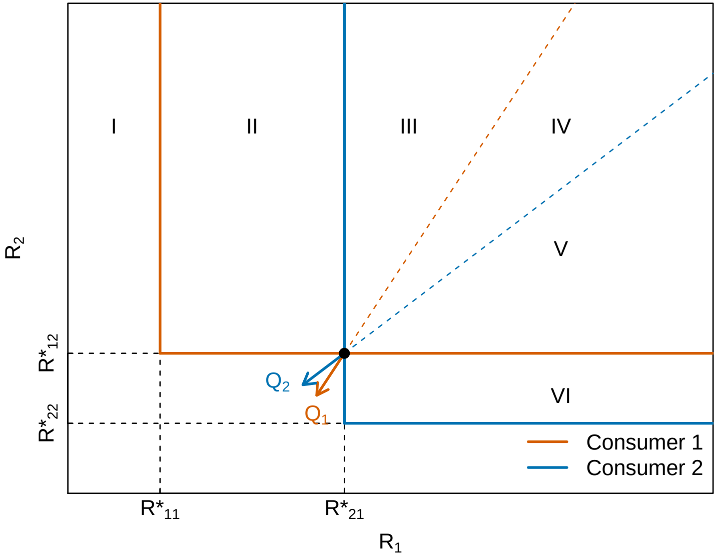
These equations define a broad region of parameter space delineated by perpendicular lines that define each consumer's ZNGI.

Coexistence is only possible when the ZNGI of the consumers intersect and when the supply point is in the correct quadrant of the (R_1, R_2) parameter space.

Equilibrium outcomes of the model



Equilibrium outcomes of the model



Competition and coexistence

- The p consumers, one-resource model shows that coexistence can only occur when there are p resources.
- The 2-consumers, 2-resources model shows that coexistence can only occur if each species consumes proportionally more of its limiting resource.
- Overall, this means that p consumers can only coexist on p resources if each species preferentially consumes the resource that most limits its own growth.
- This is very much akin to the coexistence condition for the Lotka-Volterra model: species must limit themselves (intraspecific competition) more than each other (interspecific competition).

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