

## Stability Analysis of Species Interactions

The dynamics (changes over time) of abundances of interacting species can be modeled by sets of coupled equations. The specifics of these equations will differ depending on whether the interactions are competitive, exploitative (predator-prey, plant-herbivore, etc.), mutualistic, etc. The process of determining the equilibria, and their local stability, however is the same regardless of the nature of the interactions.

### Model

If there are  $k$  interacting species, their dynamics will be described by  $k$  equations giving their rates of change (for continuous time) or abundances in the next time step (for discrete time), as functions of the current abundances of all the species.

#### *Continuous time*

$$\frac{dN_1}{dt} = f_1(N_1, N_2, \dots, N_k)$$

$$\frac{dN_2}{dt} = f_2(N_1, N_2, \dots, N_k)$$

...

$$\frac{dN_k}{dt} = f_k(N_1, N_2, \dots, N_k)$$

Here  $N_i$  is the abundance of species  $i$ , and  $f_i$  is the absolute rate of increase of species  $i$ , a function of the abundances of all the species (note that  $f_i$  is not the per capita rate).

#### *Discrete time*

Discrete-time models can be expressed in the form of projections of abundances at time  $t+1$  from the abundances at time  $t$ , or as equations describing the change in abundance from time  $t$  to time  $t+1$ . The projection form would be:

$$N_{1,t+1} = g_1(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

$$N_{2,t+1} = g_2(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

...

$$N_{k,t+1} = g_k(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

The change form is:

$$\Delta N_1 = N_{1,t+1} - N_{1,t} = G_1(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

$$\Delta N_2 = N_{2,t+1} - N_{2,t} = G_2(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

...

$$\Delta N_k = N_{k,t+1} - N_{k,t} = G_k(N_{1,t}, N_{2,t}, \dots, N_{k,t})$$

In these models  $N_{i,t}$  is the abundance of species  $i$  at time  $t$ ;  $g_i$  is the absolute finite rate of increase of species  $i$ , a function of the abundances of all the species; and  $G_i$  is the absolute change in the abundance of species  $i$ , again a function of the abundances of all the species.

## Equilibria

Equilibria of these models are the sets of abundances  $(N_1^*, N_2^*, \dots, N_k^*)$  at which

$$f_1(N_1^*, N_2^*, \dots, N_k^*) = 0$$

$$f_2(N_1^*, N_2^*, \dots, N_k^*) = 0$$

...

$$f_k(N_1^*, N_2^*, \dots, N_k^*) = 0$$

for the continuous-time model, or

$$G_1(N_1^*, N_2^*, \dots, N_k^*) = 0$$

$$G_2(N_1^*, N_2^*, \dots, N_k^*) = 0$$

...

$$G_k(N_1^*, N_2^*, \dots, N_k^*) = 0$$

for the discrete-time model.

Finding the equilibria is a task of algebra, straightforward in principle but often difficult, or at least tedious, in practice.

There will always be the trivial equilibrium in which all species are absent, i.e.  $N_i = 0$  for all  $i$ .

There often also will be equilibria in which some species are absent ( $N_i = 0$ ) and others are present ( $N_i > 0$ ). We usually are most interested, though, in the equilibrium (or perhaps multiple equilibria) at which all species are present (all  $N_i > 0$ ).

## Stability analysis

### *Definitions*

**local** stability: whether the system will return to the equilibrium after **small** perturbations away from it.

**global** stability: whether the system will return to the equilibrium from anywhere (other than another, unstable, equilibrium), i.e. after a perturbation of any size.

stable **cycle**: cycles (e.g. two-point oscillations) also can be locally or globally stable, in that the system will return to the cycle after a perturbation, and the cycle will exactly repeat itself.

Most stability analyses are of the local stability of single equilibrium points; this is what will be presented in the following.

### *The basic idea*

The question in local stability analysis is, as noted above, whether the system will return to the equilibrium after a small perturbation away from it. The analysis therefore consists of

1. converting the model into one modeling the change over time — growth or decline — of a small deviation from the equilibrium,
2. getting a linear model approximating the model in step 1, using a Taylor-series expansion; this will constitute a matrix projection model for the deviation vector,
3. determining the leading eigenvalue of the matrix from step 2, to determine whether the deviation will increase or decrease over time.

### *Details — continuous-time model*

Model the deviations:

I will use the notation  $n_i$  for the deviation of the abundance of species  $i$  from its equilibrium abundance  $N_i^*$ , i.e.  $n_i = N_i - N_i^*$  (which of course also means  $N_i = n_i + N_i^*$ ). A model for the dynamics of these deviations can be gotten from the original model. First, since the equilibrium value  $N_i^*$  is a constant, at any time the change in the deviation is equal to the change in the abundance  $N_i$ :

$$\frac{dn_i}{dt} = \frac{d}{dt}(N_i - N_i^*) = \frac{dN_i}{dt}$$

So then

$$\begin{aligned}\frac{dn_i}{dt} &= f_i(N_1, N_2, \dots, N_k) \\ &= f_i[(n_1 + N_1^*), (n_2 + N_2^*), \dots, (n_k + N_k^*)]\end{aligned}$$

Get a linear approximation near the equilibrium:

The Taylor's expansion for a function of several variables, say  $H(y_1, y_2, \dots, y_k)$ , around some point  $(y_1^*, y_2^*, \dots, y_k^*)$ , is

$$\begin{aligned}H(\underline{y}) &\approx H(\underline{y}^*) \\ &+ \frac{1}{1!} \left[ (y_1 - y_1^*) \frac{\partial H(\underline{y})}{\partial y_1} \Big|_{\underline{y}^*} + (y_2 - y_2^*) \frac{\partial H(\underline{y})}{\partial y_2} \Big|_{\underline{y}^*} + \dots + (y_k - y_k^*) \frac{\partial H(\underline{y})}{\partial y_k} \Big|_{\underline{y}^*} \right] \\ &+ \frac{1}{2!} \left[ (y_1 - y_1^*)^2 \frac{\partial^2 H(\underline{y})}{\partial y_1^2} \Big|_{\underline{y}^*} + (y_2 - y_2^*)^2 \frac{\partial^2 H(\underline{y})}{\partial y_2^2} \Big|_{\underline{y}^*} + \dots + (y_k - y_k^*)^2 \frac{\partial^2 H(\underline{y})}{\partial y_k^2} \Big|_{\underline{y}^*} \right] \\ &+ \dots\end{aligned}$$

where for conciseness I have adopted the vector notation  $\underline{y} = (y_1, y_2, \dots, y_k)$ , and where  $\frac{\partial H(\underline{y})}{\partial y_i} \Big|_{\underline{y}^*}$  means the partial derivative is to be evaluated at the equilibrium point  $\underline{y}^*$ .

The first-order Taylor-series approximation for the model for the change in the deviation is

$$\begin{aligned}\frac{dn_i}{dt} &\approx f_i(N^*) \\ &+ \frac{1}{1!} \left[ (N_1 - N_1^*) \frac{\partial f_i(N)}{\partial N_1} \Big|_{N^*} + (N_2 - N_2^*) \frac{\partial f_i(N)}{\partial N_2} \Big|_{N^*} + \dots + (N_k - N_k^*) \frac{\partial f_i(N)}{\partial N_k} \Big|_{N^*} \right]\end{aligned}$$

Since by definition of the equilibrium,  $f_i(N^*) = 0$ , (and  $1! = 1$ ) this model becomes

$$\frac{dn_i}{dt} \approx n_1 \frac{\partial f_i(N)}{\partial N_1} \Big|_{N^*} + n_2 \frac{\partial f_i(N)}{\partial N_2} \Big|_{N^*} + \dots + n_k \frac{\partial f_i(N)}{\partial N_k} \Big|_{N^*}$$

The system of these equations for the  $k$  species can be expressed in terms of the vector of deviations and a projection matrix as

$$\begin{bmatrix} \frac{dn_1}{dt} \\ \frac{dn_2}{dt} \\ \dots \\ \frac{dn_k}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} & \dots & \frac{\partial f_1}{\partial N_k} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} & \dots & \frac{\partial f_2}{\partial N_k} \\ \dots & \dots & \dots & \dots \\ \frac{\partial f_k}{\partial N_1} & \frac{\partial f_k}{\partial N_2} & \dots & \frac{\partial f_k}{\partial N_k} \end{bmatrix}_{N^*} \begin{bmatrix} n_1 \\ n_2 \\ \dots \\ n_k \end{bmatrix}$$

where for conciseness I have omitted the arguments ( $N_1, N_2, \dots, N_k$ ) of the functions  $f_i$ , and indicated for the entire matrix, rather than each partial derivative, that the partial derivatives are evaluated at the equilibrium.

Using vector notation for the set of deviations, the preceding can be expressed as

$$\frac{d}{dt}\underline{n} = \underline{J}\underline{n}$$

where  $\underline{J}$  is the matrix of partial derivatives (evaluated at the equilibrium).

In general mathematical terminology the matrix  $\underline{J}$  is called the ‘‘Jacobian’’ matrix of the original system of equations; in ecological usage it is often termed the ‘‘community’’ matrix. Its elements  $j_{ij}$  (i.e. the term in the  $i$ th row and  $j$ th column of  $\underline{J}$ ) are the per capita effect of species  $j$  on the rate of increase of species  $i$ , with all other species at their equilibrium abundances:

$$\left. \frac{\partial}{\partial N_j} f_i(N) \right|_{N^*}$$

Determine stability from the eigenvalues of  $\underline{J}$ :

The equation  $\frac{d}{dt}\underline{n} = \underline{J}\underline{n}$  has exactly the same form as the equation for exponential population growth  $dN/dt = rN$ , except that now it involves a vector of population sizes in place of  $N$  and a matrix  $\underline{J}$  in place of the growth rate  $r$ . The solution to the differential equation for exponential growth  $N(t) = N_0 e^{rt}$  suggests a solution for the system of equations in the form of  $\underline{n}(t) = \underline{n}_0 e^{Jt}$  except that we can’t exponentiate the matrix  $\underline{J}$ . We can, though, substitute the eigenvalues of  $\underline{J}$ , i.e. numbers  $\lambda$  such that  $\underline{J}\hat{n} = \lambda\hat{n}$  (with  $\hat{n}$  being the corresponding eigenvector). Then

$$\underline{n}(t) = c_1 \hat{n}_1 e^{\lambda_1 t} + c_2 \hat{n}_2 e^{\lambda_2 t} + \dots + c_k \hat{n}_k e^{\lambda_k t}$$

where the  $c_i$  are constants determined by the initial  $n_0$ .

From this result we see that the deviations  $\underline{n}$  will shrink if all the  $\lambda$ s are real and negative (so each  $e^{\lambda_i t}$  goes to 0 as  $t$  increases).

Eigenvalues, however, can be complex numbers (this happens if, for instance, the quadratic equation for an eigenvalue involves the square root of a negative value). In this case,  $\lambda = a + bi$  (where  $i$  is the square root of  $-1$ ), so the term  $e^{\lambda t} = e^{(a+bi)t} = e^{at} + e^{bti}$ . It turns out that  $e^{bti} = \cos(bt) + i\sin(bt)$  which is the equation for a circle of radius 1, centered around the origin. The **imaginary part** of the eigenvalue therefore represents **undamped oscillation** that neither expands or contracts. The full behavior of the complex eigenvalue therefore represents an oscillation that shrinks if the real part  $a$  is negative, or expands if  $a$  is positive.

The **criterion for stability** — for the vector of deviations,  $\underline{n}$ , shrinking — is that **the real part of every eigenvector of  $J$  must be negative**. If any eigenvalue has a positive real part the deviations will increase — the system will move away from the equilibrium. In the rare case that all the real parts of the eigenvalues are exactly 0, neutral stability occurs: after a small perturbation the system will oscillate around the equilibrium, neither returning to it or moving away from it.

### *Modifications for discrete time*

Using the change formulation of the discrete-time model, defining the deviations from equilibrium just as for the continuous-time model, and using the first-order Taylor-series approximation, gives:

$$\Delta n_i \approx n_{1,t} \left. \frac{\partial}{\partial N_1} G_i(N) \right|_{N^*} + n_{2,t} \left. \frac{\partial}{\partial N_2} G_i(N) \right|_{N^*} + \dots + n_{k,t} \left. \frac{\partial}{\partial N_k} G_i(N) \right|_{N^*}$$

The Jacobian matrix of this linearized system therefore is

$$J = \begin{bmatrix} \frac{\partial G_1}{\partial N_1} & \frac{\partial G_1}{\partial N_2} & \dots & \frac{\partial G_1}{\partial N_k} \\ \frac{\partial G_2}{\partial N_1} & \frac{\partial G_2}{\partial N_2} & \dots & \frac{\partial G_2}{\partial N_k} \\ \dots & \dots & \dots & \dots \\ \frac{\partial G_k}{\partial N_1} & \frac{\partial G_k}{\partial N_2} & \dots & \frac{\partial G_k}{\partial N_k} \end{bmatrix}_{N^*}$$

and the model is

$$\Delta \underline{n} = \mathbf{J} \underline{n}.$$

Since  $\Delta n_i = n_{i,t+1} - n_{i,t}$ , the linearized model can be put in projection form as

$$\underline{n}_{t+1} = \Delta \underline{n} + \underline{n}_t = \mathbf{J} \underline{n}_t + \underline{n}_t = (\mathbf{J} + \mathbf{I}) \underline{n}_t$$

or, letting  $\mathbf{J}' = (\mathbf{J} + \mathbf{I})$ ,

$$\underline{n}_{t+1} = \mathbf{J}' \underline{n}_t.$$

The solution to this sort of matrix projection model is (from Chapter 3 of Case)

$$\underline{n}_t = c_1 \hat{n}_1 \lambda_1^t + c_2 \hat{n}_2 \lambda_2^t + \dots + c_k \hat{n}_k \lambda_k^t$$

where the  $\hat{n}_i$  are the eigenvectors of  $\mathbf{J}'$ , the  $\lambda_i$  are the corresponding eigenvalues, and the  $c_i$  are constants determined by the initial values of  $\underline{n}_0$ . This result closely resembles that given above for the continuous-time model, but with the crucial difference that in this discrete-time model the eigenvalues ( $\lambda$ s) are raised to the power  $t$  while in the continuous-time model they were exponentiated before being raised to the power  $t$  (i.e. the term was  $e^{\lambda t}$ ).

From this model we see that for the deviations  $n_i$  to shrink to 0 — i.e. for stability — **all the eigenvalues of  $\mathbf{J}'$  must have absolute values less than 1.**

Since  $G_i(\underline{N}_t) = g_i(\underline{N}_t) - N_{i,t}$ ,  $\mathbf{J}$  also can be written as

$$\mathbf{J} = \begin{bmatrix} \frac{\partial g_1}{\partial N_1} - 1 & \frac{\partial g_1}{\partial N_2} & \dots & \frac{\partial g_1}{\partial N_k} \\ \frac{\partial g_2}{\partial N_1} & \frac{\partial g_2}{\partial N_2} - 1 & \dots & \frac{\partial g_2}{\partial N_k} \\ \dots & \dots & \dots & \dots \\ \frac{\partial g_k}{\partial N_1} & \frac{\partial g_k}{\partial N_2} & \dots & \frac{\partial g_k}{\partial N_k} - 1 \end{bmatrix}$$

so that  $\mathbf{J}' = (\mathbf{J} + \mathbf{I})$  equals

$$J' = \begin{bmatrix} \frac{\partial g_1}{\partial N_1} & \frac{\partial g_1}{\partial N_2} & \cdots & \frac{\partial g_1}{\partial N_k} \\ \frac{\partial g_2}{\partial N_1} & \frac{\partial g_2}{\partial N_2} & \cdots & \frac{\partial g_2}{\partial N_k} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial g_k}{\partial N_1} & \frac{\partial g_k}{\partial N_2} & \cdots & \frac{\partial g_k}{\partial N_k} \end{bmatrix}$$

Also, the eigenvalues of  $J$  equal 1 less than the eigenvalues of  $J'$  (see derivation on next page).

The stability condition therefore can be expressed in terms of the eigenvalues of the Jacobian  $J'$  of the projection form of the model, i.e. using the functions  $g_i$ , as

**all eigenvalues of  $J'$  must have absolute value less than 1**

or in terms of the eigenvalues of the Jacobian  $J$  of the change form of the model, i.e. using the functions  $G_i$ , as

**all eigenvalues of  $J$  must lie inside the circle centered at  $-1$  with radius 1.**

The eigenvalues of  $\mathbf{J}$  are the solutions  $\lambda$  to

$$\det \begin{bmatrix} \frac{\partial G_1}{\partial N_1} - \lambda & \frac{\partial G_1}{\partial N_2} & \cdots & \frac{\partial G_1}{\partial N_k} \\ \frac{\partial G_2}{\partial N_1} & \frac{\partial G_2}{\partial N_2} - \lambda & \cdots & \frac{\partial G_2}{\partial N_k} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial G_k}{\partial N_1} & \frac{\partial G_k}{\partial N_2} & \cdots & \frac{\partial G_k}{\partial N_k} - \lambda \end{bmatrix} = 0$$

which is equivalent to

$$\det \begin{bmatrix} \frac{\partial g_1}{\partial N_1} - 1 - \lambda & \frac{\partial g_1}{\partial N_2} & \cdots & \frac{\partial g_1}{\partial N_k} \\ \frac{\partial g_2}{\partial N_1} & \frac{\partial g_2}{\partial N_2} - 1 - \lambda & \cdots & \frac{\partial g_2}{\partial N_k} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial g_k}{\partial N_1} & \frac{\partial g_k}{\partial N_2} & \cdots & \frac{\partial g_k}{\partial N_k} - 1 - \lambda \end{bmatrix} = 0$$

or

$$\det \begin{bmatrix} \frac{\partial g_1}{\partial N_1} - \lambda' & \frac{\partial g_1}{\partial N_2} & \cdots & \frac{\partial g_1}{\partial N_k} \\ \frac{\partial g_2}{\partial N_1} & \frac{\partial g_2}{\partial N_2} - \lambda' & \cdots & \frac{\partial g_2}{\partial N_k} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial g_k}{\partial N_1} & \frac{\partial g_k}{\partial N_2} & \cdots & \frac{\partial g_k}{\partial N_k} - \lambda' \end{bmatrix} = 0$$

where  $\lambda' = \lambda + 1$  are the eigenvalues of the matrix of partial derivatives of the  $g_i$  functions, i.e. of  $\mathbf{J}'$ .

Thus the eigenvalues of  $\mathbf{J}$ , the  $\lambda$ , equal 1 less than the eigenvalues of  $\mathbf{J}'$ , the  $\lambda'$ .

## Special case: two species

The Jacobian matrix can be represented as

$$J = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

where

$$a = \frac{\partial f_1}{\partial N_1} \quad b = \frac{\partial f_1}{\partial N_2}$$
$$c = \frac{\partial f_2}{\partial N_1} \quad d = \frac{\partial f_2}{\partial N_2}$$

for the continuous-time model, or the equivalent with partial derivatives of the  $g_i$  for the discrete-time model.

The four elements of the Jacobian are easily interpreted. The diagonal terms,  $a$  and  $d$ , are the self-density dependence in species 1 and in species 2, respectively: the effect of each species on its own growth rate. The off-diagonal terms,  $b$  and  $c$ , are the interaction: the effect of one species on the growth rate of the other.

The eigenvalues of this 2x2 matrix are found by solving

$$\det \begin{bmatrix} a - \lambda & b \\ c & d - \lambda \end{bmatrix} = 0$$

which gives the quadratic equation (the “characteristic equation”)

$$(a - \lambda)(d - \lambda) - bc = \lambda^2 - (a + d)\lambda + (ad - bc) = 0$$

The middle coefficient,  $(a + d)$ , is the “**trace**” of the matrix  $J$ : the sum of its diagonal elements. This represents the sum of intra-specific density dependence. The third coefficient,  $(ad - bc)$  is the **determinant** of  $J$ . This represents a sort of contrast between the intra-specific density dependence ( $a \times d$ ) and the interaction ( $b \times c$ ).

Two facts about the eigenvalues of a 2x2 matrix greatly facilitate determining the stability of the model:

- the trace is equal to the sum of the eigenvalues
- the determinant is equal to the product of the eigenvalues.

### *Dynamics — continuous-time model*

For the continuous-time model, **stability requires that both eigenvalues be negative** (in their real parts, if complex). Using the preceding facts about the eigenvalues, this means that

- **the trace ( $a + d$ ) must be negative**

**and**

- **the determinant ( $ad - bc$ ) must be positive.**

If both these conditions are met, the characteristic equation becomes

$$\lambda^2 + (\text{something positive})\lambda + (\text{something else positive}) = 0$$

or

$$(\lambda + \text{positive term})(\lambda + \text{another positive term}) = 0$$

The  $\lambda$ s are the values which make one or the other of the  $(\lambda + \text{positive term})$  parts equal 0. They therefore must both be negative.

### Kinds of dynamics:

If **both** eigenvalues are **real** and **negative**, the system returns to the equilibrium without oscillating; this is called a “stable knot” or “stable node.”

If the eigenvalues are **complex** with **negative** real parts, the system has damped oscillations, i.e. it returns to the equilibrium but cycles while doing so; this is called a “stable focus.” (Since complex roots come in pairs, if one eigenvalue is complex the other must be also, and with the same real part.)

If **both** eigenvalues are **real** and **positive**, the system moves away from the equilibrium without oscillating; this is called an “unstable knot” or “unstable node.”

If the eigenvalues are **complex** with **positive** real parts, the system has increasing oscillations, i.e. cycles which get larger, moving it away from the equilibrium; this is called an “unstable focus.”

Finally, if the eigenvalues are **real** with **one positive** and **one negative**, the system moves towards the equilibrium in one direction but away from it in the perpendicular direction, with the latter eventually dominating; this is called an “unstable saddle.”

Criteria:

conditions		eigenvalues	dynamics
$ad - bc < 0$ [det < 0]		real, positive & negative	unstable saddle
$0 < (ad - bc)$ [det > 0]	$(a+d)^2 > 4(ad - bc)$ or $(a-d)^2 > 4bc$	$a + d > 0$ [trace > 0]	unstable knot
		$a + d < 0$ [trace < 0]	<b>stable</b> knot
	$(a+d)^2 < 4(ad - bc)$ or $(a-d)^2 < 4bc$	$a + d > 0$ [trace > 0]	complex, real parts positive
		$a + d < 0$ [trace < 0]	complex, real parts negative

*Dynamics — discrete-time model*

For the discrete-time model, stability requires that the **absolute values of the eigenvalues** be **less than 1**.

If  $(a+d)^2 - 4(ad - bc) < 0$ , the eigenvalues will be complex. Stability then requires that the **determinant  $(ad - bc)$  be less than 1**.

If both these conditions hold, the dynamics will be a **stable** focus: the system will undergo damped oscillations converging on the equilibrium. If the eigenvalues are complex but the determinant is greater than 1, the dynamics will be an unstable focus, with oscillations diverging away from the equilibrium.

If  $(a+d)^2 - 4(ad - bc) > 0$ , the eigenvalues will be real. In this situation there is no simple general rule for whether the absolute values will be less than 1 (giving stability). Such rules may exist, however, for specific kinds of models — e.g. predator-prey — in which the signs of at least some of the four elements of the Jacobian are determined.