

Supplementary material to:

Chapter 8: Equilibria and Stability Analyses – Non-Linear Models with Multiple Variables

From:

A Biologist's Guide to Mathematical Modeling in Ecology and Evolution

S. P. Otto and T. Day (2005)

Princeton University Press

Supplementary Material 8.1: Graphing the characteristic polynomial to determine stability

Here we describe a method that can be used to determine the stability of an equilibrium without explicitly calculating the eigenvalues. The method involves a graphical analysis of the characteristic polynomial of the Jacobian matrix.

Let's first consider a discrete-time model with an $n \times n$ Jacobian matrix, $\mathbf{J}$. As described in Primer 2, the characteristic polynomial of this matrix is defined as $\text{Det}(\mathbf{J} - \lambda \mathbf{I})$ and is an n^{th} degree polynomial. To simplify the graphical analysis, let's multiply the characteristic polynomial by $(-1)^n$, so that the term containing λ^n always has a positive coefficient. Let's call the resulting polynomial, P , where $P = (-1)^n \text{Det}(\mathbf{J} - \lambda \mathbf{I})$. The eigenvalues of the model, λ , are the roots of the equation $P = 0$.

To make this procedure more concrete, let's consider the 2×2 matrix, $\mathbf{J} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, of a discrete-time model. Its characteristic polynomial is:

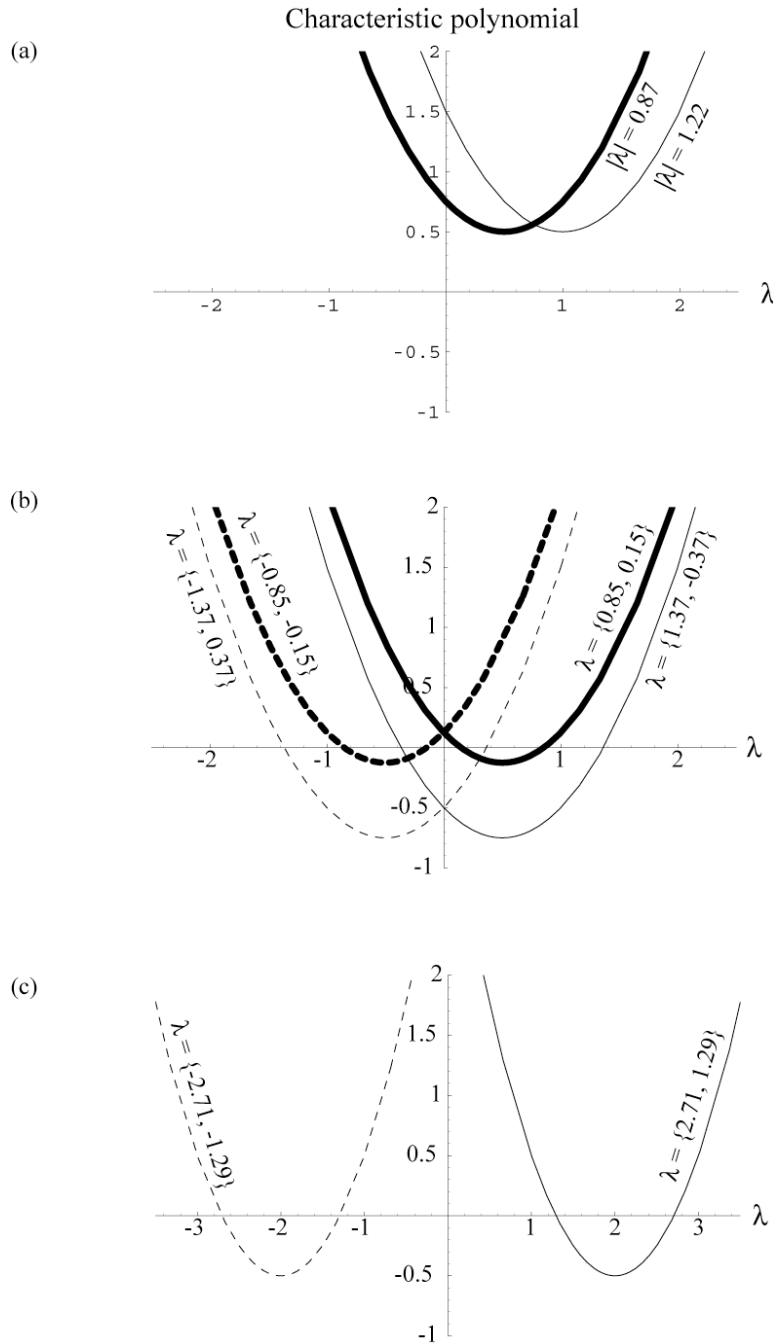
$$P = (-1)^2 \text{Det} \begin{pmatrix} a - \lambda & b \\ c & d - \lambda \end{pmatrix} = \lambda^2 - (a + d)\lambda + (ad - bc) \quad (\text{S8.1.1})$$

We could always use the quadratic formula (A1.10) to solve for λ , but the solution might involve the square-root of a function that is cumbersome to interpret. Progress can be made, however, by plotting the shape of (S8.1.1) with respect to λ . Because (S8.1.1) is quadratic, and because the

coefficient of the λ^2 term is positive (it is one in this case), it is a parabola opening upwards (see Figure S8.1.1). The parabola will cross the horizontal axis as long as the roots of equation (S8.1.1) are real rather than complex (see Figure S8.1.1). For the rest of this box, we'll assume that it can be proven that the roots are real (e.g., by using the Perron-Frobenius theorem, Appendix 3, or by analysis of the square-root term in the quadratic formula).

The crux of the graphical analysis is that an equilibrium is stable in a discrete-time model if the parabola crosses the horizontal axis only at points that lie between -1 and 1 . Only then will the absolute values of the eigenvalues be less than one (Recipe 8.4). This is true for the parabolas shown by thick curves in Figure S8.1.1b. It wouldn't help us much if we had to plot every combination of parameters to determine where the characteristic polynomial crosses the horizontal axis, but fortunately, it is often possible to determine roughly where P must cross the horizontal axis by considering the behavior of P at $\lambda = 1$ and $\lambda = -1$.

Figure S8.1.1: Graphs of the characteristic polynomial. Parabolas illustrating the shape of the characteristic polynomial, (8.3.1), in a two-variable discrete-time model. (a) Examples with complex roots. (b) Examples with real roots. (c) Examples with real roots both of which fall outside of $\{-1, 1\}$. The thick curves indicate that the equilibrium under examination is stable, because the absolute values of the eigenvalues (written alongside each curve) all fall between 0 and 1.



To begin, let's consider what must be true for the roots of a quadratic characteristic polynomial to fall between -1 and 1 . Because P is an upwards-facing parabola, a negative value of P at $\lambda = 1$ implies that at least one eigenvalue is greater than one, because the characteristic polynomial rises as λ increases and must eventually cross the horizontal axis at some root greater than one. Consequently, a negative value of P at $\lambda = 1$ always implies that the equilibrium is unstable (as in the parabola furthest to the right in Figure S8.1.1b). For an equilibrium to be stable, we therefore require that P is positive at $\lambda = 1$ (see bold curves in Figure S8.1.1b). The same is true at $\lambda = -1$; P must be positive or else there will be an eigenvalue less than -1 (as in the parabola furthest to the left in Figure 8.3.1b). Even if P is positive at both $\lambda = 1$ and $\lambda = -1$, however, we cannot necessarily conclude that the equilibrium is stable because there could be two roots above $+1$ or two roots below -1 (Figure S8.1.1c). As long as the slope is negative at $\lambda = -1$ and positive at $\lambda = +1$, however, then these possibilities can also be ruled out. The requirements for stability are summarized in Recipe S8.1.1:

Recipe S8.1.1: Determining stability from a quadratic characteristic polynomial in a discrete-time model

An equilibrium in a discrete-time model with a 2×2 stability matrix and real roots is stable if and only if the characteristic polynomial, P , satisfies all of the following four conditions:

Condition 1: P is positive at $\lambda = 1$, requiring that $1 - (a + d) + (ad - bc) > 0$.

Condition 2: P is positive at $\lambda = -1$, requiring that $1 + (a + d) + (ad - bc) > 0$.

Condition 3: $\frac{dP}{d\lambda}$ is positive at $\lambda = 1$, requiring that $2 - (a + d) > 0$.

Condition 4: $\frac{dP}{d\lambda}$ is negative at $\lambda = -1$, requiring that $-2 - (a + d) < 0$.

If any of these conditions fail to be met, then the equilibrium is unstable.

Example: The Lotka-Volterra model of competition

In Chapter 3, we introduced the Lotka-Volterra model of competition. The model extends the logistic growth model by allowing more than one species to compete for resources. Letting r_i and K_i be the intrinsic growth rate and carrying capacity of species i , and letting the competition coefficient, α_{ij} , measure the *per capita* effect of species j on species i , the discrete-time recursion equations for the Lotka-Volterra model with two species are:

$$n_1(t+1) = n_1(t) + r_1 n_1(t) \left(1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right) \quad (\text{S8.1.2a})$$

$$n_2(t+1) = n_2(t) + r_2 n_2(t) \left(1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right). \quad (\text{S8.1.2b})$$

System (S8.1.2) has four equilibria. Here, we will focus only on the equilibrium with both species present (Problem 8.10):

$$\hat{n}_1 = \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}} \quad (\text{S8.1.3a})$$

$$\hat{n}_2 = \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}} \quad (\text{S8.1.3b})$$

For this equilibrium to be biologically valid (i.e., for the number of both species to be positive) requires either:

$$\text{Weak Competition: } 1 - \alpha_{12} \alpha_{21} > 0, K_1 > \alpha_{12} K_2 \text{ and } K_2 > \alpha_{21} K_1 \quad (\text{S8.1.4a})$$

or $\text{Strong Competition: } 1 - \alpha_{12} \alpha_{21} < 0, K_1 < \alpha_{12} K_2 \text{ and } K_2 < \alpha_{21} K_1 \quad (\text{S8.1.4b})$

The stability matrix of (S8.1.2) evaluated at the equilibrium (S8.1.3) is:

$$\mathbf{J} = \begin{pmatrix} 1 + r_1 - 2r_1 \frac{\hat{n}_1}{K_1} - r_1 \frac{\alpha_{12} \hat{n}_2}{K_1} & -r_1 \frac{\alpha_{12} \hat{n}_1}{K_1} \\ -r_2 \frac{\alpha_{21} \hat{n}_2}{K_2} & 1 + r_2 - 2r_2 \frac{\hat{n}_2}{K_2} - r_2 \frac{\alpha_{21} \hat{n}_1}{K_2} \end{pmatrix}. \quad (\text{S8.1.5a})$$

Plugging in for the equilibrium and simplifying,

$$\mathbf{J} = \begin{pmatrix} 1 - r_1^* & -\alpha_{12} r_1^* \\ -\alpha_{21} r_2^* & 1 - r_2^* \end{pmatrix}. \quad (\text{S8.1.5b})$$

where $r_1^* = r_1 \frac{K_1 - \alpha_{12} K_2}{K_1(1 - \alpha_{12} \alpha_{12})} = r_1 \frac{\hat{n}_1}{K_1}$ and $r_2^* = r_2 \frac{K_2 - \alpha_{21} K_1}{K_2(1 - \alpha_{12} \alpha_{12})} = r_2 \frac{\hat{n}_2}{K_2}$. The characteristic polynomial of $\mathbf{J}$ is:

$$P = \lambda^2 - (2 - r_1^* - r_2^*)\lambda + (1 - r_1^*)(1 - r_2^*) - \alpha_{12} \alpha_{21} r_1^* r_2^*. \quad (\text{S8.1.6})$$

According to the quadratic formula, the roots of (S8.1.6) are real if $(r_1^* - r_2^*)^2 + 4\alpha_{12} \alpha_{21} r_1^* r_2^*$ is positive. We will assume that the competition coefficients are both positive, meaning that the relationship between the two species is truly competitive, and that both species have positive intrinsic growth rates and positive carrying capacities. Thus, $r_i^* = r_i \frac{\hat{n}_i}{K_i}$ must be positive at an equilibrium with positive numbers of both species, and the roots will necessarily be real.

To determine whether two species can co-exist if they interact competitively, let's work through the conditions of Recipe S8.1.1.

Condition 1: For P to be positive at $\lambda = 1$, the following must be positive:

$$1 - (2 - r_1^* - r_2^*) + (1 - r_1^*)(1 - r_2^*) - \alpha_{12} \alpha_{21} r_1^* r_2^* = r_1^* r_2^* (1 - \alpha_{12} \alpha_{21}).$$

Because we have assumed that r_i^* is positive, Condition 1 tells us that competition must be weak, $1 - \alpha_{12} \alpha_{21} > 0$, for the equilibrium to be stable.

Condition 2: For P to be positive at $\lambda = -1$, the following must be positive:

$$1 + (2 - r_1^* - r_2^*) + (1 - r_1^*)(1 - r_2^*) - \alpha_{12} \alpha_{21} r_1^* r_2^* = 4 - 2r_1^* - 2r_2^* + r_1^* r_2^* (1 - \alpha_{12} \alpha_{21}).$$

Condition 2 tells us that the growth rates must be small enough for the equilibrium to be stable, which we'll write as $\frac{r_1^* + r_2^*}{2} < 1 + \frac{r_1^* r_2^* (1 - \alpha_{12} \alpha_{21})}{4}$. (We chose this form because of a similar restriction that arises from Condition 4.)

Condition 3: For $\frac{dP}{d\lambda}$ to be positive at $\lambda = 1$, the following must be positive:

$$2 - (2 - r_1^* - r_2^*) = r_1^* + r_2^*.$$

Condition 3 is true under our assumption that r_i^* is positive.

Condition 4: For $\frac{dP}{d\lambda}$ to be negative at $\lambda = -1$, the following must be negative:

$$-2 - (2 - r_1^* - r_2^*) = -4 + r_1^* + r_2^*.$$

Again, condition 4 tells us that the growth rates must be small enough for the equilibrium to be stable, $\frac{r_1^* + r_2^*}{2} < 2$.

Putting together all of the above conditions, the equilibrium with both species present is stable only if all of the following restrictions are met:

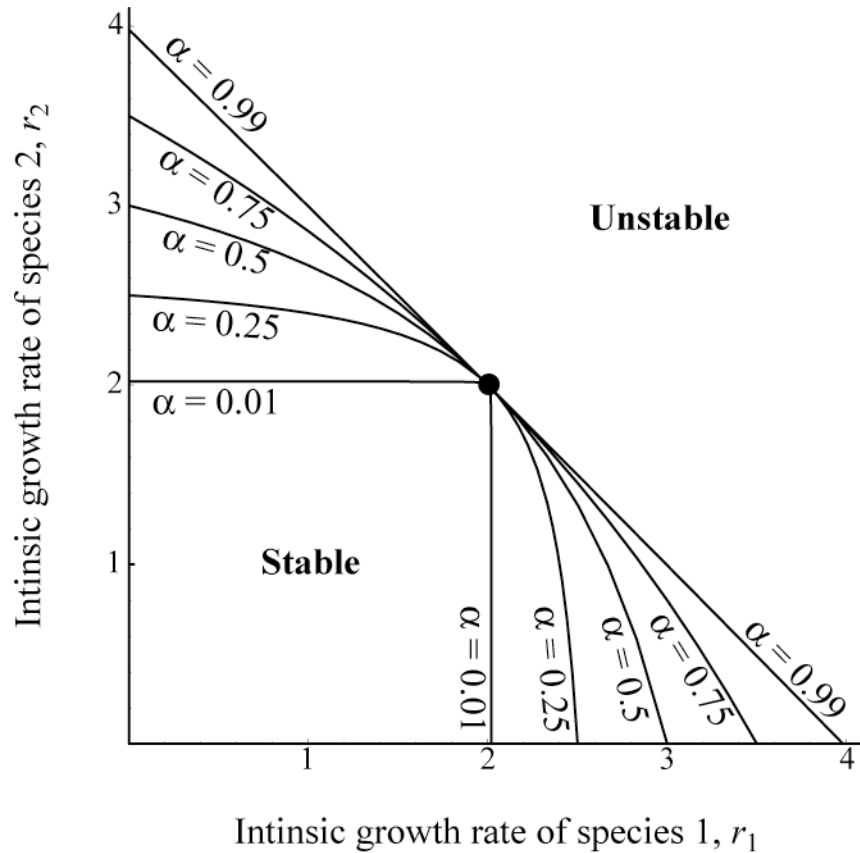
$$1 - \alpha_{12} \alpha_{21} > 0 \quad (\text{from Condition 1})$$

$$0 < \frac{r_1^* + r_2^*}{2} < \min \left[1 + \frac{r_1^* r_2^* (1 - \alpha_{12} \alpha_{21})}{4}, 2 \right] \quad (\text{from Conditions 2 - 4})$$

Although the equilibrium exists with both species present when competition is weak and when competition is strong, condition 1 tells us that the equilibrium is unstable when competition is strong (S8.1.4b). For the equilibrium to exist under strong competition requires that the resources of species 1 are entirely consumed by the competitor when species 2 is at its carrying capacity ($K_1 < \alpha_{12} K_2$) and vice versa ($K_2 < \alpha_{21} K_1$). So it makes sense that the two species should not coexist.

But why do we also see a restriction on the intrinsic growth rates (Conditions 2 – 4)? The reason is the same as in the logistic model in discrete-time. If the growth rates are too high, the number of individuals can grow so much within a time step that one or both species overshoots the equilibrium. Indeed, if $r_1 = r_2 = \hat{r}$, it can be shown that the second restriction reduces to $0 < \hat{r} < 2$, exactly as found in the logistic model (Chapter 5, section 5.3.1). If one species grows rapidly and the other slowly (e.g., $r_1 < 2 < r_2$), we need Conditions 2 – 4 to determine whether growth is so rapid that the equilibrium is overshoot and unstable (Figure S8.1.2).

Figure S8.1.2: Stability condition for coexistence in the Lotka-Volterra model. Stability in the discrete-time model requires that the intrinsic growth rates of two competing species be sufficiently low. When r_1 and r_2 are similar, both intrinsic growth rates must be less than ~ 2 for stability (near filled circle). If one of the growth rates is higher than two, the equilibrium can still be stable as long as the other growth rate is small enough. Here, we assume equal carrying capacities ($K_1 = K_2$) and competitive effects ($\alpha_{12} = \alpha_{21} = \alpha$) in the two species. In this case, when inter-species competition is strong ($\alpha = 0.99$), the *average* intrinsic growth rate must be less than ~ 2 for stability. When inter-species competition is weak ($\alpha = 0.01$), *each* intrinsic growth rate must be less than ~ 2 for stability.



A similar graphical procedure can be used to analyze continuous-time models, but the conditions are the same as the Routh-Hurwitz conditions described in Box 8.3. Nevertheless, it can help to have a more intuitive feel of the Routh-Hurwitz conditions by imagining what a graphical analysis would require. For example, if we consider the shape of the 2nd degree polynomial given by $r^2 + a_1r + a_2 = 0$, where now r represents the eigenvalue. This polynomial

will necessarily have a root greater than zero if the polynomial is negative at $r = 0$. But the value of the polynomial at $r = 0$ is just a_2 . So stability requires that a_2 be positive. Similarly, if the slope at $r = 0$ is negative, then either both roots will be real and positive or both roots will be complex with a positive real part¹. In either case, the equilibrium is unstable. But the slope of the polynomial at $r = 0$ is just a_1 . Thus, stability also requires that a_1 be positive. These two conditions for stability are the Routh-Hurwitz conditions for a two-variable model (8.3.3).

In Problem 8.11, we apply these conditions to the Lotka-Volterra model in continuous-time. While the growth rates of the two species matter in a discrete-time model, they do not affect stability in the continuous-time model, as you might expect based on the behavior of the logistic model. Once again, this is because the growth of each species is continuously updated, reducing the chance that the equilibrium is overshoot.

For the 2×2 stability matrices considered so far, it is possible to use the quadratic formula to derive the eigenvalues. The graphical method really earns its keep, however, when analyzing larger matrices whose eigenvalues cannot be directly calculated. Unfortunately, as the degree of the characteristic polynomial increases, it becomes more difficult to prove that all of the roots satisfy the stability criterion ($-1 < \lambda < 1$ for a discrete-time model, $r < 0$ for a continuous-time model). While proving that an equilibrium is stable becomes more difficult, it is often easier to prove that an equilibrium is unstable. For example, if you can show that P is negative at $\lambda = 1$ in a discrete-time model (or at $r = 0$ in a continuous-time model) under a specific set of conditions, then you have proven that the equilibrium is unstable under these conditions. For certain biological questions, this result might be enough. For example, you might find that P is always negative at $\lambda = 1$ for a particular equilibrium of interest, which then proves that this equilibrium is always unstable.

¹ When the roots of a quadratic equation are complex, the real part of the roots can be found from a plot of the characteristic polynomial as a function of the eigenvalue. The real part is given by the position along the horizontal axis where the minimum occurs.