Online Appendix 1: phase portraits analysis of isoclines

The isocline of species 1 (I_1), can be found by setting equation 4a equal to zero, after setting irrelevant parameters to zero. I_1 can take on several shapes, as a result it is useful to distinguish shapes that arize when species 2 has no effect on species 1, species 2 harms species 1 and species 2 benefits species 1.

Neutral interactions

When species 2 has no effect on species 1 the isocline for species 1 can be found by setting $q_1 = c_1 = 0$ in equation 4a, giving an isocline of:

$$N_1 = \frac{g_1}{d_1} \tag{S.1}$$

This is as a vertical line figure 2 A.

Harmful interactions

So long as we restrict ourselves to positive population densities ($N_1, N_2 > 0$), I_1 can have two shapes when species 1 is harmed by species 2. I_1 will either be a strictly decreasing function figure 2 C or a function that increases initially, reaches a local maximum then decreases figure 2 D. In this subsection we explain how these two shapes emerge and how to distinguish them. To find I_1 take equation 4a, set $c_1 = 0$ then solve for $dN_1/dt = 0$ giving:

$$I_1 : N_2 = -\frac{(g_1 - d_1 N_1)(e_1 q_1 N_1 + 1)}{q_1(a_2(g_1 - d_1 N_1) - 1)} \tag{S.2}$$

To determine the shape of I_1 predicted by S.2, we first note that this function is a ratio of two polynomials. This type of function known as a rational function can be plotted using information on its asymptotes, and intercepts (Forbes et al. 1989).

To find the N_2 intercept set $N_1 = 0$. equation S.2 reduces to:

$$N_2^{intercept} = -\frac{g_1}{q_1(a_2 g_1 - 1)}. \tag{S.3}$$

Equation S.2 includes two N_1 intercepts, which can be found by identifying values which make the numerator of equation S.2 equal to 0. The first intercept can be found by solving $g_1 - d_1 N_1$ giving:

$$N_1^{intercept_1} = \frac{g_1}{d_1} \tag{S.4}$$

in this section we are concerned with cases where harm inflicted by species 2 eliminates species 1. As a result we need only consider cases where $N_1^{intercept_1} > 0$

(i.e. species 1 could be present in the absence of species 2).

The second intercept can be found by solving $e_1 q_1 N_1 + 1 = 0$ giving:

$$N_1^{intercept_2} = \frac{-1}{e_1 q_1} \tag{S.5}$$

We have already assumed that $e_1, q_1 > 0$, as a result $N_1^{intercept_2}$ is always less than zero.

Equation S.2 has a single, vertical asymptote when species 1 is harmed by species 2 (i.e. when $q_1 > 0$). This can be found by finding values where the denominator of S.2 is equal to 0. By re-arranging we obtain:

$$VerticalAsymptote : N_1 = \frac{a_2 g_1 - 1}{d_1 a_2} \tag{S.6}$$

To understand the shapes of I_1, it is important to note that the vertical asymptote always has an opposite sign as the $N_2^{intercept}$. This is because the vertical asymptote is the same sign as $a_2 g_1 - 1$ (we have assumed that d_1 and a_2 are never negative), while $N_2^{intercept}$ will be the opposite sign as $a_2 g_1 - 1$ (q_1, a_2 and g_1 are presumed to be non-negative).

Next, we check for diagonal asymptotes (**?**). To do this we first expand the numerator and denominator of equation S.2 giving:

$$I_1 : N_2 = -\frac{\overbrace{-d_1 e_1 q_1 N_1^2}^{\text{largest power}} + g_1 e_1 q_1 N_1 - d_1 N_1 + g_1}{\underbrace{-q_1 a_2 d_1 N_1}_{\text{largest power}} + q_1 a_2 g_1 - q_1} \tag{S.7}$$

In the numerator the largest power of N_1 is N_1^2 while in the denominator the largest power of N_1 is N_1^1. Such a rational function has a diagonal asymptote (**?**). The slope of this asymptote can be found by comparing the leading coefficients associated with the largest power in the numerator and denominator:

$$N_2 = -\frac{-d_1 e_1 q_1 N_1^2}{-q_1 a_2 d_1 N_1} \tag{S.8}$$

simplifying this gives:

$$N_2 = -\frac{e_1 N_1}{a_2}, \tag{S.9}$$

equation S.9 indicates that the slope of the diagonal asymptote is $-e_1/a_2$. Since $e_1, a_2 \geq 0$, the slope is never positive.

As we move from small values of N_1 to larger values, the intercepts always occur in the same order because $N_1^{intercept_2} < 0$, $N_2^{intercept}$ occurs at 0, while $N_1^{intercept_1} > 0$. This observation is illustrated in figure S.1 where $N_1^{intercept_2}$ is a triangle, $N_2^{intercept}$ is a square and $N_1^{intercept_1}$ is a circle.

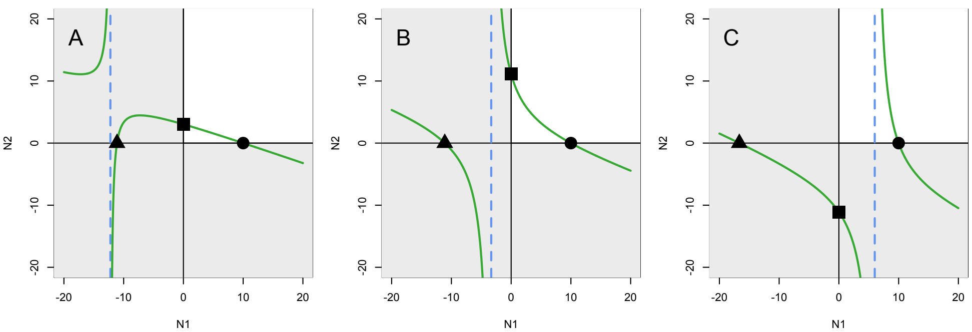

Figure S.1: Ilustrations of three qualitatively different shapes possible for I_1 (green), including the vertical asymptote (blue dotted line), $N_1^{intercept_2}$ (triangle), $N_2^{intercept}$ (square) and $N_1^{intercept_1}$ (circle). The positive quadrants of each plot (i.e. the portions where $N_1, N_2 > 0$) are white. Portions in grey represent other quadrants, and hence population densities we would not observe in nature.

We can distinguish three qualitatively different shapes for I_1 based on the position of the vertical asymptote. In case A, the asymptote occurs at a lower N_1 value than any of the intercepts (figure S.1 A). Since the vertical asymptote is less than 0 ($N_1 < 0$), the $N_2^{intercept}$ is positive ($N_2 > 0$). So, starting slightly the right of the vertical asymptote, I_1 starts at negative infinity, moves through $N_1^{intercept_2}$, then $N_2^{intercept}$, down through $N_1^{intercept_1}$ and approaches its diagonal asymptote as N_1 becomes large. In case B, the asymptote occurs between $N_1^{intercept_2}$ and $N_2^{intercept}$ (figure S.1 B). Here again, $N_2^{intercept} > 0$, because the vertical asymptote is less than 0. To the right of the vertical asymptote I_1 begins at positive infinity, then moves down through $N_2^{intercept}$, $N_1^{intercept_1}$ then approaches its diagonal asymptote as N_1 gets large. In case C, the vertical asymptote occurs between $N_2^{intercept}$ and $N_1^{intercept_1}$. Here $N_2^{intercept}$ is less than zero because the vertical asymptote is greater than zero. As a result, starting from to the right of the vertical asymptote, I_1 decreases, crosses $N_1^{intercept_1}$, then approaches the diagonal asymptote as N_1 gets large.

In each of the cases listed above, the portion of I_1 to the left of the vertical asymptote has no direct effect on the population dynamics. In cases A and B, this branch only occurs for values of $N_1 < 0$. In case C this branch never reaches feasible population densities where $N_1, N_2 > 0$. Starting at $N_1 = -\infty$, the branch is close to its diagonal asymptote, moves through $N_1^{intercept_2}$ (at this point $N_1 < 0$), I_1 then moves through $N_2^{intercept}$ (at this point $N_2 < 0$), I_1 then approaches negative infinity as it nears the vertical asymptote.

Does I_1 have local maxima?

In the previous section we described the behavior of I_1 in coarse terms. We did not determine if it has local turning points (maxima or minima), which could lead to an isocline with a local maximum, which in turn alters population dynamics. To investigate this later question we consider the derivative of I_1 (i.e. equation S.2) with respect to N_1:

$$\frac{dI_1}{dN_1} = -\frac{e_1 d_1^2 a_2 N_1^2 q_1 - 2e_1 d_1 a_2 g_1 N_1 q_1 + 2e_1 d_1 N_1 q_1 + e_1 a_2 g_1^2 q_1 - e_1 g_1 q_1 + d_1}{q_1(-d_1 a_2 N_1 + a_2 g_1 - 1)^2}. \tag{S.10}$$

For there to be a local maximum somewhere on I_1, $\frac{dI_1}{dN_1}$ must be equal to zero. $\frac{dI_1}{dN_1} = 0$ occurs when the numerator of equation S.12 is equal to zero. The numerator of equation S.12 can be expressed as a quadratic equation (i.e. it can be expressed as $\alpha N_1^2 + \beta BN_1 + \kappa$, where α, β, and κ are constants). Quadratic equations have no more than two solutions. As a result I_1 has no more than two turning points.

We can break I_1 into a branch to the left to its asymptote and a branch to the right of its asymptote. It is impossible for one such branch to have two turning points. If one branch did, then there would need to be an inflection point between the two turning points. This would imply that there was a location where the d^2I_1/d^2N_1. However the second derivative of I_1 is:

$$\frac{d^2I_1}{d^2N_1} = -\frac{2d_1(e_1q_1(1-a_1g_1)+d_1a_2)}{q_1(a_2(g_1-d_1N_1)-1)^3}, \tag{S.11}$$

and since no value of N_1 makes the numerator equal to zero, there are no inflection points.

I_1 can have a local maximum in the positive quadrant in the case illustrated in figure S.1 A. In this case, the right branch of I_1 starts at $-\infty$ reaches a single m then decreases as it approaches its diagonal asymptote (figure S.2 A). To determine if this maximum occurs in the positive quadrant, determine if $dI_1/dN_1 > 0$ when I_1 crosses into this quadrant by substituting $N_1 = 0$ into equation S.12, giving:

$$\frac{dI_1}{dN_1} = -\frac{e_1a_2g_1^2q_1 - e_1g_1q_1 + d_1}{q_1(a_2g_1-1)^2}. \tag{S.12}$$

This expression will be positive when $e_1a_2g_1^2q_1 - e_1g_1q_1 + d_1$, which can be rearranged to obtain:

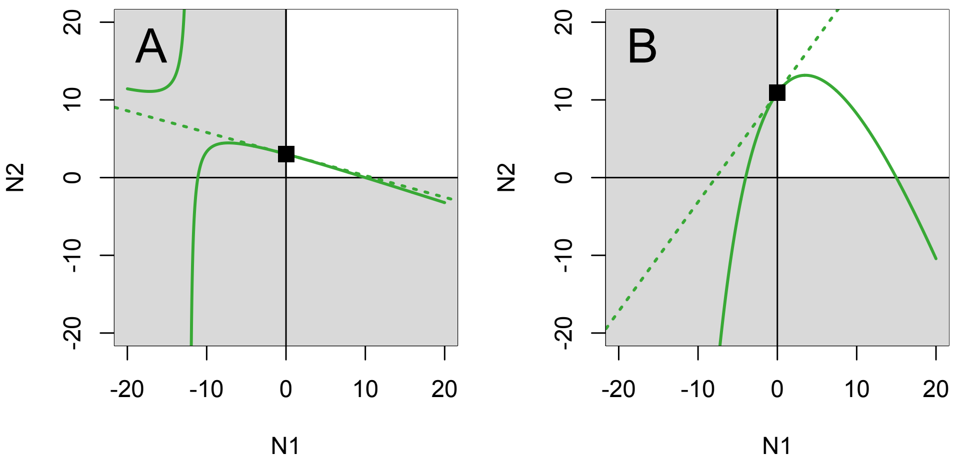

Figure S.2: The relationship between the shape of I_1 (green solid line) in the positive quadrant (white portions of the chart) and its derivative (the green dotted line) at its N_2 intercept (square). In A)

$$e_1 g_1 q_1 (1 - a_2 g_1) > d_1 \tag{S.13}$$

If inequality S.13 is true, I_1 has a local maximum in the positive quadrant figure S.2 B. If inequality S.13 is fase, I_1 decreases monotonically in the positive quadrant (figure S.2 A). Inequality S.13 is simply the reverse of inequality 6 in the main text.

We can also use inequality S.13 to test for local maxima in the other two cases illustrated in (figure S.1 B and C). In both cases, each branch of I_1 is strictly decreasing (implying both that $dI_1/dt < 0$ at $N_1 = 0$ and that I_1 has no local maxima). We know that each branch is strictly decreasing because each branch starts at $+\infty$ and finishes at $-\infty$ (figure S.1 B and C). This is only possible if each branch has zero turning points. If a single branch had a single turning point, it could not go from $+\infty$ to $-\infty$. We have already established that a single branch has no more than one turning point.

If we ignore a_2, inequality S.13 is easy to interpret, e_1, q_1 and g_1 all increase the left-hand side of this expression making an isocline with a local maximum more likely; high values of e_1 indicate that the harm species 2 inflicts on species 1 saturates when the density of species 1 is high. High values of g_1 indicate a high density independent growth rate for species 1; while high values of q_1 indicate that species 2 can dramatically harm species 1. High values of d_1 indicate strong density dependence for species 1, this makes an isocline with a local maximum less likely. High values of a_2 indicate that the the harm species 2 inflicts on species 1 saturates at high densities of species 2. Increasing $a_2 > 0$ makes a isocline with a local maximum likely. When $a_2 > 0$, increasing g_1 can make it either easier or harder to get a local maximum, depending on the size of g_1 versus g_1^2. Large values of g_1 make $e_1 g_1 q_1 (1 - a_2 g_1)$ negative, eliminating the maximum.

Interactions that benefit species 1

When biotic interactions benefit species 1, the isocline for species 1 can be found by taking equation 4a, setting $q_1 = 0$ then solving for $dN_1/dt = 0$ and re-arranging, giving:

$$N_2 = -\frac{(c_1 h_2 N_1 + 1)(g_1 - d_1 N_1)}{c_1(b_2(g_1 - d_1 N_1) + 1)} \tag{S.14}$$

The N_2 intercept of equation S.14 is:

$$I_1(N_1 = 0) : -\frac{g_1}{c_1(b_2 g_1 + 1)}. \tag{S.15}$$

Equation S.14 has two N_1 intercepts given by:

$$N_1 = -\frac{1}{c_1 h_2}, \tag{S.16}$$

which is always negative and:

$$N_1 = \frac{g_1}{d_1} \tag{S.17}$$

which is negative when species 1 cannot persist in the absence of species 2.

Equation S.14 approaches a vertical asymptote, so long as $b_2 > 0, d_1 > 0$. This asymptote is given by:

$$N_1 = \frac{g_1 + 1/b_2}{d_1}, \tag{S.18}$$

Note that this asymptote is equal to equation S.17 plus a positive constant. As such, the vertical asymptote is to the right of this intercept on a phase portrait.

Equation S.14 also has a slant asymptote with a slope of $-h_2/b_2$. This asymptote

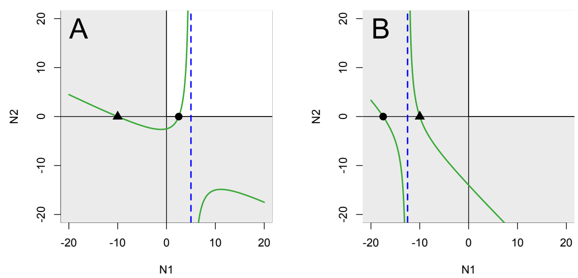

Figure S.3: Graphs of potential shapes for I_1.

always has a negative slope.

For I_1 to cross into the positive quadrant, the vertical asymptote must be to right of both N_1 intercepts (figure S.3 A). In this case the left most branch of I_1 starts at $N_2 = +\infty$ decreases, crosses the left most N_1 intercept, arrives at a turning point, crosses the right most intercept and increases towards $N_2 = +\infty$. This branch of I_1 can only reach the positive quadrant after crossing through the right most asymptote. As a result I_1 is increasing in the positive quadrant, or entirely absent from this quadrant. The right branch of I_1 does not reach the positive quadrant.

It is mathematically possible for the vertical asymptote to occur between the two N_1 intercepts (figure S.3). In this case the left and right branches of I_1 start at $N_2 = +\infty$ and decrease towards $N_2 = -\infty$. For this scenario to occur, both N_1 intercepts must be negative. Neither branch crosses into the positive quadrant. No other shapes occur because the vertical asymptote must be to the right of at least one of the intercepts.

Parameter values

Table S1. List of parameter values used in Figure 3 organized by panel.

	A	B	C	D	E	F	G	H	I
g_1	-9.50	-6.00	-9.50	5.00	5.00	5.00	5.00	5.00	4.00
g_2	5.00	3.00	5.00	5.00	3.50	5.00	5.00	5.00	8.00
c_1	2.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
c_2	0.00	10.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00
q_1	0.00	0.00	0.00	5.00	5.00	5.00	5.00	5.00	2.00
q_2	0.00	0.00	2.00	0.00	0.00	0.80	0.00	0.00	3.00
b_1	0.20	0.15	0.20	0.20	0.20	0.20	0.20	0.20	0.20
b_2	0.03	0.06	0.03	0.03	0.03	0.03	0.03	0.03	0.03
h_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
h_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
f_1	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.01
f_2	0.00	0.00	0.00	0.01	0.01	0.01	0.14	0.14	0.14
e_1	0.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00	0.00
e_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
d_1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
d_2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Online Appendix 2: the relationship between invasion and phase portraits

On a phase portrait, we can check if species 1 can increase in numhers when rare by examining the N_2 axis, which represents conditions where species 1 is rare enough to be essentially absent. Along the N_2 axis $I_2 = \hat{N}_2$ (the equilibrium density of species 2 in the absence of species 1), while the point where I_1 crosses the N_2 axis is the boundary between densities of species 2 where species 1 increases in numbers when rare $dN_1/dt > 0$, and densities at which species 1 decreases in numbers when rare $dN_1/dt < 0$.

When species 1 benefits from species 2, a value of I_1 above $\hat{N}_2$ indicates that when species 1 is rare, the benefit it obtains from species 2 is too low for species 1 to increase in numbers when rare. As a result species 1 cannot invade. A value of I_1 below $\hat{N}_2$ indicates that species 1 could increase in numbers, even if species 2 were less dense than $\hat{N}_2$. Thus, when species 1 benefits and I_1 is above I_2 at the N_2 axis, species 1 cannot invade. When I_1 is below I_2, species 1 can invade.

When species 1 is harmed by species 2, a value of I_1 above I_2 on the N_2 axis indicates that when species 1 is rare, it could resist extinction even if it were harmed by more individuals of species 2 than would be present at equilibrium ($dN_1/dt = 0$ at a point where $N_2 > \hat{N}_2$). Conversely, a value of I_1 below I_2 on the N_2 axis indicates that when species 1 is rare it could not resist extinction even if it were harmed by fewer individuals of species 2 than would be present at equilibrium ($dN_1/dt = 0$ at a point where $N_2 > \hat{N_2}$). Thus, when species 1 is harmed by species 2 and I_1 is above I_2 at the N_2 axis, species 1 can invade. When I_1 is below I_2, species 1 cannot invade.

References

Forbes, S., Morton, M., and Rae, H., 1989. Skills in Mathematics, volume 2. Forbes, Morton and Rae.