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 arise 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:

$$N_1 = \frac{g_1}{d_1}$$  \hspace{1cm} (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:

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

$$N_2^{\text{intercept}} = -\frac{g_1}{q_1 (a_2 g_1 - 1)}.$$ (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:

$$N_1^{\text{intercept}_1} = \frac{g_1}{d_1}$$ (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 $N_1^{\text{intercept}_1} > 0$
(i.e. species 1 could be present in the absence of species 2).

The second intercept can be found by solving $e_1q_1N_1 + 1 = 0$ giving:

$$N_{1\text{ intercept}}^2 = -\frac{1}{e_1q_1}$$  \hspace{1cm} (S.5)

We have already assumed that $e_1, q_1 > 0$, as a result $N_{1\text{ intercept}}^2$ 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:

$$Vertical Asymptote : N_1 = \frac{a_2g_1 - 1}{d_1a_2}$$  \hspace{1cm} (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 $N_{2\text{ intercept}}$. This is because the vertical asymptote is the same sign as $a_2g_1 - 1$ (we have assumed that $d_1$ and $a_2$ are never negative), while $N_{2\text{ intercept}}$ will be the opposite sign as $a_2g_1 - 1$ ($q_1$, $a_2$ 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:
\[ I_1 : N_2 = - \frac{-d_1 e_1 q_1 N_1^2 + g_1 e_1 q_1 N_1 - d_1 N_1 + g_1}{-q_1 a_2 d_1 N_1^2 + q_1 a_2 g_1 - q_1} \]  \hspace{1cm} \text{(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:

\[ N_2 = -\frac{-d_1 e_1 q_1 N_1^2}{-q_1 a_2 d_1 N_1} \]  \hspace{1cm} \text{(S.8)}

simplifying this gives:

\[ N_2 = -\frac{e_1 N_1}{a_2} \]  \hspace{1cm} \text{(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 \( N_1^{\text{intercept}_2} < 0 \), \( N_2^{\text{intercept}} \) occurs at 0, while \( N_1^{\text{intercept}_1} > 0 \). This observation is illustrated in figure S.1 where \( N_1^{\text{intercept}_2} \) is a triangle, \( N_2^{\text{intercept}} \) is a square and \( N_1^{\text{intercept}_1} \) is a circle.
Figure S.1: Illustrations of three qualitatively different shapes possible for $I_1$ (green), including the vertical asymptote (blue dotted line), $N_1^{\text{intercept}_2}$ (triangle), $N_2^{\text{intercept}}$ (square) and $N_1^{\text{intercept}_1}$ (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 $N_2^{\text{intercept}}$ is positive ($N_2 > 0$). So, starting slightly the right of the vertical asymptote, $I_1$ starts at negative infinity, moves through $N_1^{\text{intercept}_2}$, then $N_2^{\text{intercept}}$, down through $N_1^{\text{intercept}_1}$ and approaches its diagonal asymptote as $N_1$ becomes large. In case B, the asymptote occurs between $N_1^{\text{intercept}_2}$ and $N_2^{\text{intercept}}$ (figure S.1 B). Here again, $N_2^{\text{intercept}} > 0$, 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 $N_2^{\text{intercept}}$, $N_1^{\text{intercept}_1}$ then approaches its diagonal asymptote as $N_1$ gets large. In case C, the vertical asymptote occurs between $N_2^{\text{intercept}}$ and $N_1^{\text{intercept}_1}$. Here $N_2^{\text{intercept}}$ 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 $N_1^{\text{intercept}_1}$, 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 $N_1^{\text{intercept}_2}$ (at this point $N_1 < 0$), $I_1$ then moves through $N_2^{\text{intercept}}$ (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 $N_1$:

$$\frac{dI_1}{dN_1} = \frac{-e_1d_2a_2N_1^2q_1 - 2e_1d_1a_2g_1N_1q_1 + 2e_1d_1N_1q_1 + e_1a_2g_1^2q_1 - e_1g_1q_1 + d_1}{q_1(-a_2N_1 + a_2g_1 - 1)^2}. \quad (S.10)$$

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 $\alpha$, $\beta$, and $\kappa$ 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:

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

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:

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

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)

$$e_1g_1q_1(1-a_2g_1) > d_1$$ \hspace{1cm} (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 false, $I_1$ 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 $e_1g_1q_1(1 - a_2g_1)$ 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:

$$N_2 = -\frac{(c_1h_2N_1 + 1)(g_1 - d_1N_1)}{c_1(b_2(g_1 - d_1N_1) + 1)} \quad (S.14)$$
The $N_2$ intercept of equation S.14 is:

$$I_1(N_1 = 0) : -\frac{g_1}{c_1(b_2g_1 + 1)}.$$  \hspace{1cm} (S.15)

Equation S.14 has two $N_1$ intercepts given by:

$$N_1 = -\frac{1}{c_1h_2},$$  \hspace{1cm} (S.16)

which is always negative and:

$$N_1 = \frac{g_1}{d_1}$$  \hspace{1cm} (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:

$$N_1 = \frac{g_1 + 1/b_2}{d_1},$$  \hspace{1cm} (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
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.
Table S1. List of parameter values used in Figure 3 organized by panel.

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Online Appendix 2: the relationship between invasion and phase portraits

On a phase portrait, we can check if species 1 can increase in numbers 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