J. theor. Biol. (2002) **214,** 49–62
doi:10.1006/jtbi.2001.2448, available online at http://www.idealibrary.com on IDEAL®

Effects of Intraguild Predation on Resource Competition

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(*Received on* 5 *March* 2001, *Accepted in revised form on* 18 *August* 2001)

In this work, a simple Lotka–Volterra model of intraguild predation with three species is analysed, searching for the effect of the top predator on the coexistence with its prey-competitor species. Apart from the well-known result that the intraguild prey must be superior in the competition for the shared prey in order to make coexistence possible, the magnitude of intraguild predation and the form by which the intraguild predator makes use of the intraguild prey have important consequences upon the dynamics, extending or restricting the possibilities of coexistence. These results are easily obtained by nullcline analysis. Also, some interesting results are obtained for the same model but including saturating functional response.

Introduction

Increasing attention has been devoted to the ecological relationship of intraguild predation, also known by some people as a form of omnivory. The review by Polis *et al.* (1989) and subsequent works (e.g. Holt & Polis, 1997) have set a solid background for additional studies. Polis *et al.* (1989) define intraguild predation as the killing and eating of species that use similar, often limiting, resources and are thus potential competitors.

The most simple model that we can use for the study of omnivory and/or intraguild predation is a Lotka–Volterra model of predation for the trophic relations depicted in Fig. 1. This situation was analysed by Hallam (1986), and the model equations are

$$\begin{aligned} \dot{N}_1 &= rN_1(1 - \tfrac{N_1}{K}) - a_{12}N_1N_2 - a_{13}N_1N_3, \\ \dot{N}_2 &= c_{12}a_{12}N_1N_2 - d_2N_2 - a_{23}N_2N_3, \qquad (1) \\ \dot{N}_3 &= c_{13}a_{13}N_1N_3 + c_{23}a_{23}N_2N_3 - d_3N_3. \end{aligned}$$

The meaning of the variables and parameters are: N_1: density of the shared prey or common resource, N_2: density of the intraguild prey (IG prey), N_3: density of the intraguild predator (IG predator) or omnivore, r: the resource's intrinsic growth rate, K: the resource's carrying capacity, a_{ij}: attack or predation rate of species j upon species i, c_{ij}: efficiency constant; converts eaten prey units of j into predator units of i, d_i: death rate of i (with $i \neq 1$).

One of the most important results for this model is that, for coexistence to be possible, the intraguild prey (IG prey/species 2) must be superior to the intraguild predator (IG predator/species 3) for the shared prey. If neither species 2 or 3 act as an intraguild predator and they only compete for one shared prey, coexistence is impossible. The mixed effect of competition and predation set by intraguild predation creates a niche difference between species 2 and 3.

Other properties of the simple Lotka–Volterra model for intraguild predation/omnivory have been studied. A recent work by Diehl & Feissel (2000) has focused on effects of enrichment on the

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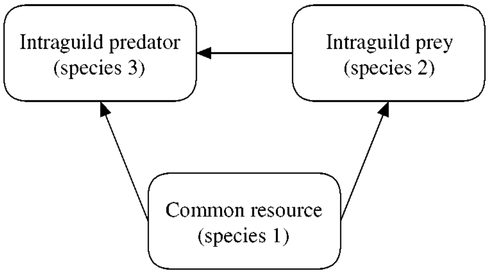

FIG. 1. Trophic relations for the model equation (1).

coexistence of species 2 and 3. As the carrying capacity (K) becomes larger, there can be a sequence of equilibria: only species 1 present, species 1 and 2 present, all the three species present, and only species 1 and 3 present. This prediction was tested in the laboratory by the authors (Diehl & Feissel, 2000), and the experimental results match most of the model predictions.

The condition that the IG prey must be a superior competitor to the IG predator for coexistence to be possible generates the following questions.

1. How large must the level of intraguild predation be in order to make possible the presence of species 3?
2. How large must the competitive superiority of species 2 be in order to make possible its presence?

An attempt will be made to answer both questions taking into account the fact that they are related.

Model Nullclines and Equilibria

The ordinary differential equation system (1) has the following nullclines that are planes in the $N_1N_2N_3$ phase space. For the resource we have

$$N_1 = \frac{K}{r}(r - a_{12}N_2 - a_{13}N_3), \tag{2}$$

for the IG prey:

$$N_1 = \frac{d_2}{c_{12}a_{12}} + \frac{a_{23}}{c_{12}a_{12}}N_3 \tag{3}$$

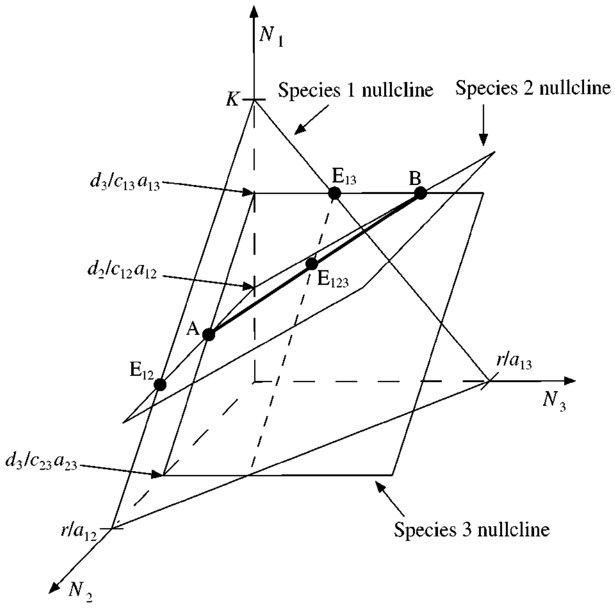

FIG. 2. Nullclines of species 1–3 for the Lotka–Volterra intraguild predation model equation (1). The nullclines for species 2 and 3 coincide along the line AB, that passes through the species 3 nullcline at the point E_{123}.

and for the IG predator:

$$N_1 = \frac{d_3}{c_{13}a_{13}} - \frac{c_{23}a_{23}}{c_{13}a_{13}}N_2. \tag{4}$$

The nullclines are shown in Fig. 2, supposing that a positive equilibrium with all three species present exists. There are five possible equilibria, the first of which is trivial:

$$\hat{N}_1 = 0, \qquad \hat{N}_2 = 0, \qquad \hat{N}_3 = 0, \tag{5}$$

with only the first level present:

$$\hat{N}_1 = K, \qquad \hat{N}_2 = 0, \qquad \hat{N}_3 = 0, \tag{6}$$

with only species 3 absent, the point E_{12} in the N_1N_2 plane:

$$\hat{N}_1 = \frac{d_2}{c_{12}a_{12}}, \qquad \hat{N}_2 = \frac{r}{a_{12}K}\left(K - \frac{d_2}{c_{12}a_{12}}\right),$$
$$\hat{N}_3 = 0, \tag{7}$$

with only species 2 absent, the point E_{13} in the N_1N_3 plane:

$$\hat{N}_1 = \frac{d_3}{c_{13}a_{13}}, \qquad \hat{N}_2 = 0,$$

$$\hat{N}_3 = \frac{r}{a_{13}K}\left(K - \frac{d_3}{c_{13}a_{13}}\right), \tag{8}$$

Equations (7) and (8) are the equilibria for the Lotka–Volterra model for one prey and one predator. These equilibria are positive if

$$K > \frac{d_i}{c_{1i}a_{1i}}, \tag{9}$$

where $i = 2, 3$. In that case, the equilibrium is approached monotonically or with damped oscillations.

Finally, there could be a positive equilibrium with the three species present (see Diehl & Feissel, 2000), the point E_{123} in the $N_1N_2N_3$ space:

$$\hat{N}_1 = K\,\frac{rc_{23}a_{23} + c_{23}a_{13}d_2 - a_{12}d_3}{rc_{23}a_{23} + Ka_{12}a_{13}(c_{13}c_{23} - d_2)},$$

$$\hat{N}_2 = \frac{d_3 - c_{13}a_{13}\hat{N}_1}{c_{23}a_{23}}, \tag{10}$$

$$\hat{N}_3 = \frac{c_{12}a_{12}\hat{N}_1 - d_2}{a_{23}}.$$

The conditions that ensure that eqn (10) defines a positive equilibrium were already depicted by Holt & Polis (1997). An illustrative way to obtain conditions for positive equilibria is by analysing the geometry of the nullclines [eqns (2–4)] in the three species space. With a pure geometrical perspective, the three-species equilibrium is the *unique coincidence point* for the nullclines because they are planes. For the coordinates of that point to be positive, the following must be true:

1. that nullclines for IG prey and IG predator coincide along a straight line that passes through the points A and B that belongs to the positive region of the N_1N_2 and N_1N_3 planes, respectively, and
2. that the straight line AB just mentioned passes through the plane nullcline of the resource in the positive octant.

Since the IG prey nullcline is parallel to the N_2-axis [N_2 does not appear in eqn (3)] with positive slope in the N_1N_3 plane, and the IG predator nullcline is parallel to the N_3-axis [N_3 does not appear in eqn (4)] with negative slope in the N_1N_2 plane, both planes coincide in the positive octant if and only if

$$\frac{d_3}{c_{13}a_{13}} > \frac{d_2}{c_{12}a_{12}}, \tag{11}$$

producing the points A and B just mentioned (see Fig. 2). This condition allows the first of the above requisites, but at the same time confirms that the IG prey is a superior competitor than the IG predator (because $d_i/c_{1i}a_{1i}$ is the minimal density of species 1 that supports growth for species i in a predator–prey Lotka–Volterra system), which is a necessary but not sufficient condition for coexistence in models of intraguild predation (Holt & Polis, 1997).

For the second requisite to be fulfilled, points A and B must lie at opposite sides of the resource nullcline. For the region enclosed by the resource nullcline and the N_1N_2, N_1N_3, N_2N_3 planes, I will call it "below" the resource nullcline and the other one "above" resource nullcline. Common sense says that there are two ways of placing points A and B at different sides, and two ways of placing them at the same side. These four situations will also determine if IG prey or predator can or cannot invade.

IG PREY INVASION CONDITION

The IG prey invasion condition is obtained doing $N_2 = 0$, plotting nullcline equations (2–4) in the N_1N_3 plane, and verifying that the equilibrium coordinates for the resident species, resource and IG predator (point E_{13}) lie in the region for which $dN_2/dt > 0$.

Since point B belongs to the IG prey nullcline and E_{13} to the resource nullcline, their relative positions will determine if E_{13} is in the $dN_2/dt > 0$ region or not, and, at the same time, if B is below or above the resource nullcline,

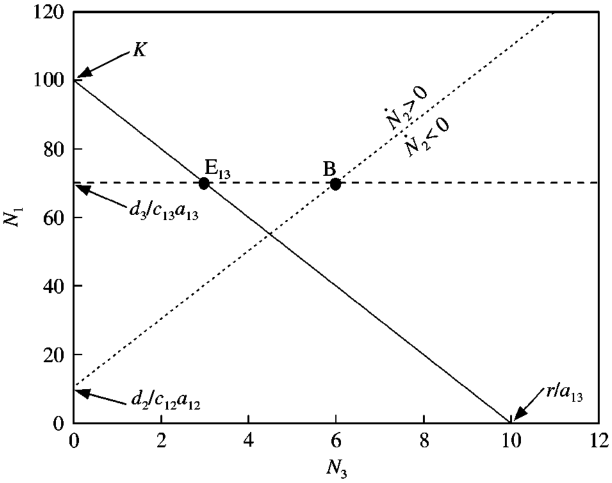

FIG. 3. The nullclines of species 1 (——), 2 (······) and 3 (- - - -) in the N_1N_3 plane of Fig. 2 for a case in which species 2 can invade when rare. Parameter values $r = 1$, $K = 100$, $a_{12} = a_{13} = c_{12} = c_{13} = 0.1$, $c_{23} = 0.9$, $d_2 = 0.1$, and $d_3 = 0.7$.

according to the convention stated. Figure 3 shows that the coordinates of E_{13} and B in the N_1-axis are the same and equal to $d_3/c_{13}a_{13}$ [eqn (8), because a Lotka–Volterra predator nullcline is perpendicular to the resource axis]. Then for the point E_{13} to be in the $\mathrm{d}N_2/\mathrm{d}t > 0$ region, and point B being above resource nullcline, the B coordinate at N_3 must be greater than $\hat{N}_3$ in eqn (8). That relation of coordinates results in the following inequality.

$$Q < \frac{1}{1 + (ra_{23}/Kc_{12}a_{12}a_{13})}, \qquad (12)$$

where Q is a combination of parameters that relates the competitive abilities of species 2 and 3 [see eqns (9, 11)]. The expression of Q is

$$Q = \frac{K - (d_3/c_{13}a_{13})}{K - (d_2/c_{12}a_{12})}. \qquad (13)$$

When Q equals 1, both species 2 and 3 can tolerate the same levels of scarcity of their common resource (species 1). Thus, in a situation of pure exploitative competition (with $a_{23} = 0$) coexistence is not possible. If $Q < 1$, then $d_3/c_{13}a_{13} > d_2/c_{12}a_{12}$: species 2 tolerates lower levels of resource than 3. On the other hand, if $Q > 1$, then $d_3/c_{13}a_{13} < d_2/c_{12}a_{12}$: species 3 is a better competitor than 2 and always excludes it. If condition (9) holds, Q cannot be negative [see in Appendix A how to obtain eqns (12) and (13)].

If the sign of eqn (12) is reversed, this means that B is below the resource nullcline, and at the same time, that E_{13} lies in the zone where $\mathrm{d}N_2/\mathrm{d}t < 0$, and IG prey could not invade a community composed by resource and IG predator at equilibrium.

IG PREDATOR INVASION CONDITION

The invasibility condition for species 3 is obtained doing $N_3 = 0$, plotting nullcline equations (2–4) in the N_1N_2 plane, and verifying that the equilibrium coordinates for the resident species, now resource and IG prey (point E_{12}), lie in the region for which $\mathrm{d}N_3/\mathrm{d}t > 0$.

Figure 4 shows that point A belongs to the IG predator nullcline, E_{12} to the resource nullcline, and the coordinates of E_{12} and A in the N_1-axis are the same and equal to $d_2/c_{12}a_{12}$ (because both points belong to the IG prey nullcline, which is perpendicular to the resource axis). Then, E_{12} will be in the $\mathrm{d}N_3/\mathrm{d}t > 0$ zone, and point A below the resource nullcline, if the coordinate of A in the N_2-axis is lower than $\hat{N}_2$ in eqn (7). The relation between these two

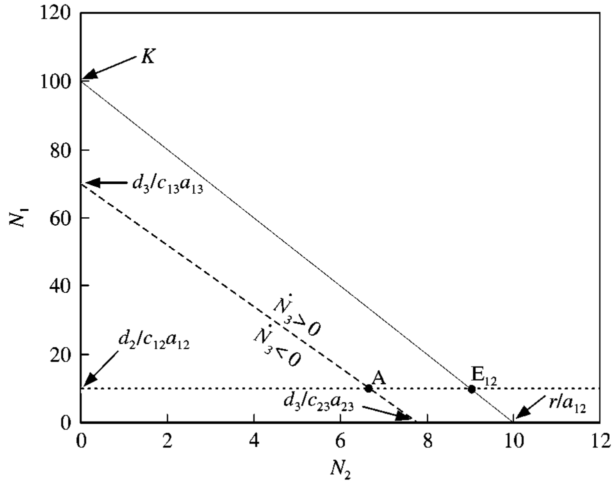

FIG. 4. The nullclines of species 1 (——), 2 (······) and 3 (- - - -) in the N_1N_2 plane of Fig. 2 for a case in which species 3 can invade when rare. Parameter values as in Fig. 3.

coordinates results in the inequality

$$Q > 1 - \frac{c_{23} r a_{23}}{K c_{13} a_{13} a_{12}}, \qquad (14)$$

If the sign of eqn (14) is reversed, that is because point A lies above the resource nullcline, and E_{12} in the $dN_3/dt < 0$ zone of the IG predator nullcline, making the invasion impossible. Appendix A shows how to obtain eqn (14) from the relation of coordinates.

INVASION OUTCOMES

On combining inequalities (12) and (14), four cases result.

- *Case* 1, *inequality* (12) *holds*, *inequality* (14) *does not hold*. Points A and B are above the resource nullcline and there is no positive equilibrium (E_{123}). In this case, species 2 can invade when rare, but species 3 cannot.
- *Case* 2, *inequality* (12) *does not hold*, *inequality* (14) *holds*. Points A and B are below the resource nullcline and there is no positive equilibrium (E_{123}). Species 2 cannot invade when rare, but species 3 can invade.
- *Case* 3, *inequalities* (12) *and* (14) *hold*. Points A and B are below and above the resource nullcline, respectively, and line AB [intersection between eqns (3) and (4)] passes through the resource nullcline giving the positive equilibrium (E_{123}, as shown in Fig. 2). Both species 2 and 3 can invade when rare.
- *Case* 4, *inequalities* (12) *and* (14) *do not hold*. Points A and B are above and below the resource nullcline, respectively, and the line AB gives a positive equilibrium (E_{123}), but neither species (2 or 3) can invade when rare.

These cases resemble the four cases of the Lotka–Volterra model of competition. The first two correspond to species 2 only or species 3 only winning. The remaining two are the situations where a positive three-species equilibrium exists. It is obvious that case 4 does not promote coexistence, and the three-species equilibrium shall be unstable [see Holt & Polis (1997) for the local stability analysis].

Case 3 allows the two boundary equilibria (E_{12} and E_{13}) to be invasible, but does not tell us anything about the stability of the three-species equilibrium. Numerical analysis (Holt, 1996; Holt & Polis, 1997) shows that the system can display limit-cycle behavior. So the analogy with the four classical competition cases is not perfect.

Parameter Space Analysis

Inequalities (12) and (14) of the last section can be plotted in a plane with Q and ra_{23} as axes, providing a useful parameter space. The Q-axis measures the competitive ability of species 2: lower values, below 1, mean that species 2 is a better competitor, and for Q greater than 1, species 2 is always excluded by species 3. On the other hand, the product ra_{23} describes the effect of resource intrinsic growth rate and, more importantly, the effect of the magnitude of intraguild predation (a_{23}). In a plot of Q against ra_{23} [Fig. 5(a)], the right-hand side of eqn (12) is a decreasing positive hyperbolic function that tends to zero with infinity and is equal to 1 when $ra_{23} = 0$; the right-hand side of eqn (14) is a straight line with negative slope, equal to 1 when $ra_{23} = 0$, and zero when $ra_{23} = (c_{13}/c_{23}) K a_{12} a_{13}$.

It is important to consider that the expression for Q [eqn (13)] depends on the parameters $K, a_{12}, a_{13}, c_{12}$, and c_{13}, that also appear at the right-hand sides of eqns (12) and (14). So the only way to vary Q without changing them is to vary d_2 and d_3. This is a limitation because we cannot consider the influence of the other parameters on coexistence. However, the d's are good predictors of the competitive ability because they can be considered proportional to the minimal energetic requirements for growth in isocline models such as those studied by León & Tumpson (1982) and Tilman (1982). Thus, r, a_{23} and c_{23} [they do not appear in eqn (13)] are free to vary.

In the following sections, it is supposed that condition (9) holds for both consumers. Nevertheless this is not strictly necessary, and the relation could be inverted for the IG predator, a situation that does not prevent the existence of a three-species equilibrium, but means that the top predator cannot grow on the common resource alone.

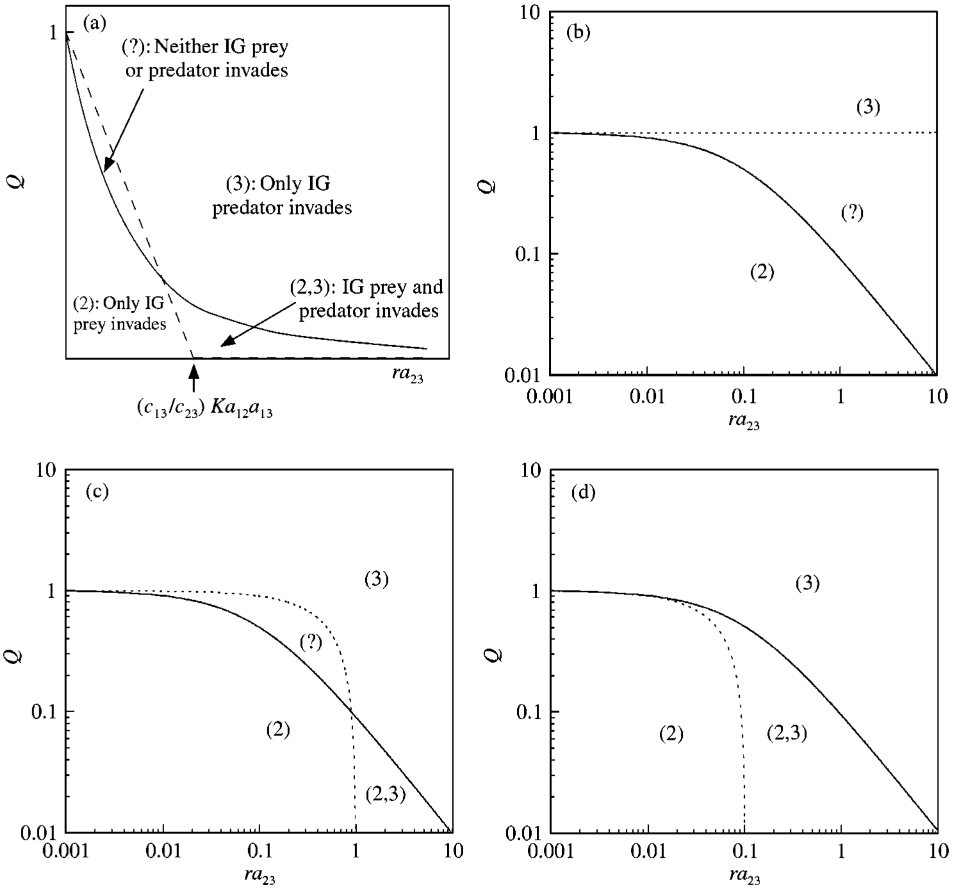

FIG. 5. Parameter space Q against ra_{23}, from conditions (12, 14). Part (a) shows the invasibility regions and the convention to name them. For $ra_{23} > (c_{13}/c_{23})Ka_{12}a_{13}$, the right-hand side of eqn (14) is set to zero (see dashed lines). Parts (b)–(d) present numerical examples plotted in a double logarithmic scale using fixed parameters: $K = 100$, $a_{12} = a_{13} = c_{12} = c_{13} = 0.1$, with $c_{23} = 0$, 0.1, and 1 in (b), (c), and (d), respectively.

COEXISTENCE REGION

Figure 5(a) shows that both boundary equilibria are invasible when the right-hand side of eqn (12) is greater than the right-hand side of eqn (14), that is

$$\Delta Q = \left(1 + \frac{ra_{23}}{Kc_{12}a_{12}a_{13}}\right)^{-1} - \left(1 - \frac{c_{23}ra_{23}}{Kc_{13}a_{13}a_{12}}\right) > 0, \quad (15)$$

for $ra_{23} < (c_{13}/c_{23})Ka_{12}a_{13}$. If $ra_{23} > (c_{13}/c_{23})Ka_{12}a_{13}$, the right-hand side of eqn (14) becomes negative. Condition (9) sets Q as positive, then zero must be substracted in eqn (15) giving

$$\Delta Q = \left(1 + \frac{ra_{23}}{Kc_{12}a_{12}a_{13}}\right)^{-1} - 0 > 0. \quad (16)$$

There is always a nonnegative ra_{23} solution for $\Delta Q > 0$ [eqns (15, 16)] because the right-hand side of eqn (12) is always positive. This means that there is always a set of values for ra_{23} that allow for the invasion of IG prey and IG predator.

Figure 5(a) also shows that for $ra_{23} < (c_{13}/c_{23})Ka_{12}a_{13}$, the right-hand side of eqn (14) decreases faster than the right-hand side of eqn (12). But for $ra_{23} > (c_{13}/c_{23})Ka_{12}a_{13}$, the right-hand side of eqn (14) was set to zero and ΔQ [eqn (16)] only decreases. So the following is true:

$$\partial\Delta Q/\partial(ra_{23}) > 0 \quad \text{for } ra_{23} < (c_{13}/c_{23})Ka_{12}a_{13},$$

$$\partial\Delta Q/\partial(ra_{23}) < 0 \quad \text{for } ra_{23} > (c_{13}/c_{23})Ka_{12}a_{13}. \quad (17)$$

Then ΔQ is maximal at $ra_{23} = (c_{13}/c_{23})Ka_{12}a_{13}$.

If we derivate ΔQ with c_{23}, the result is

$$\partial \Delta Q/\partial c_{23} = ra_{23}/Kc_{13}a_{12}a_{13} > 0 \qquad (18)$$

for $ra_{23} < (c_{13}/c_{23})Ka_{12}a_{13}$, thus the increase of c_{23} broadens the coexistence region. If $ra_{23} > (c_{13}/c_{23})Ka_{12}a_{13}$, the derivative is zero [compare eqns (15) and (16)].

EQUILIBRIA

The three-species equilibrium values [eqn (10)] also depend on r, a_{23} and c_{23}. The derivatives of $\hat{N}_2$ and $\hat{N}_3$ with respect to r, a_{23} and c_{23} depends on the same derivatives for $\hat{N}_1$ which are more complex.

Let

$$\alpha = rc_{23}a_{23} + c_{23}a_{13}d_2 - a_{12}d_3, \qquad (19)$$

$$\beta = rc_{23}a_{23} + Ka_{12}a_{13}(c_{13}c_{23} - d_2). \qquad (20)$$

then $\hat{N}_1$ from eqn (10) is rewritten as

$$\hat{N}_1 = K\frac{\alpha}{\beta}. \qquad (21)$$

Since the resource density could never be greater than K (it is indeed lower than K for a feasible three-species equilibrium):

$$\alpha < \beta. \qquad (22)$$

Using eqns (19–21) the partial derivatives of $\hat{N}_1$ with a_{23}, r and c_{23} are

$$\partial\hat{N}_1/\partial a_{23} = rKc_{23}(\beta - \alpha)/\beta^2, \qquad (23)$$

$$\partial\hat{N}_1/\partial r = Kc_{23}a_{23}(\beta - \alpha)/\beta^2, \qquad (24)$$

$$\partial\hat{N}_1/\partial c_{23} = K\frac{\beta(\partial\alpha/\partial c_{23}) - \alpha(\partial\beta/\partial c_{23})}{\beta^2}. \qquad (25)$$

Inequality (22) makes $\partial\hat{N}_1/\partial a_{23}$ and $\partial\hat{N}_1/\partial r$ positive; eqns (19, 20) show that α and β depends linearly on a_{23} and r, but the difference $\beta - \alpha$, is independent of them. Then, the magnitude of $\partial\hat{N}_1/\partial a_{23}$ and $\partial\hat{N}_1/\partial r$ decrease with the squares of a_{23} and r, respectively.

TABLE 1
Variation of equilibrium densities with respect to the free parameters in eqns (12) *and* (14)

	$\partial/\partial a_{23}$	$\partial/\partial r$	$\partial/\partial c_{23}$
$\widehat{N_1}$	>0	>0	>0
$\widehat{N_2}$	<0	<0	<0
$\widehat{N_3}$	>0 or <0	>0	>0

There is no easier way to determine if $\partial\hat{N}_1/\partial c_{23}$ is positive or negative because the relative magnitudes of $\partial\alpha/\partial c_{23}$ and $\partial\beta/\partial c_{23}$ are unknown. Nevertheless, with the aid of geometry we can guess the sign of $\partial\hat{N}_1/\partial c_{23}$. From Figs 2 and 4, it can be observed that as c_{23} grows the slope of the IG predator nullcline becomes more negative [eqn (4)], moving point A towards the N_1-axis. E_{123} is part of the line AB and of the resource nullcline at the same time, so if c_{23} increases and A moves towards the N_1-axis, then $\hat{N}_1$ must increase in order to coincide with the resource nullcline. Then it is implicit that $\partial\hat{N}_1/\partial c_{23} > 0$ for a three-species equilibrium when both two species boundary equilibria are invasible (Case 3).

The signs of the derivatives of $\hat{N}_2$ and $\hat{N}_3$ with respect to a_{23}, r and c_{23} are shown in Table 1 (see the equations in Appendix A). The sign of $\partial\hat{N}_3/\partial a_{23}$ depends on the numerator of its expression (see Appendix A), which is

$$c_{12}a_{12}a_{23}(\partial\hat{N}_1/\partial a_{23}) - (c_{12}a_{12}\hat{N}_1 - d_2).$$

We found above that $\partial\hat{N}_1/\partial a_{23}$ decreases with the square of a_{23}. Then, as a_{23} increases, the sign of $\partial\hat{N}_3/da_{23}$ changes from positive to negative, having a maximum.

Model Simulations

Figure 5(b)–(d) shows three numerical examples of the parameter space in which the value of the conversion constant for the IG predator, c_{23}, is varied starting with zero ($c_{23} = 0$), through an intermediate value ($c_{23} = 0.1$), and finally reaching a very high value ($c_{23} = 1$). The behavior of the model changes dramatically. The graphs are in a double logarithmic scale.

The case with $c_{23} = 0$, depicted in Fig. 5(a) occurs when species 3 attacks but does not eat species 2 (or eats species 2 with no positive effect on its population density). Under this condition, there are regions in which either species 2 or 3 can invade, and also a region in which neither can invade when rare. So coexistence is impossible.

In Fig. 5(b), for $c_{23} = 0.1$, there are regions in which species 2 or 3 invade, both invade or neither invade. Under this situation, coexistence is possible for $Q < 1$, and intermediate values of ra_{23}.

Finally, if $c_{23} = 1$, the indeterminate region for invasion disappears and the coexistence region is larger [Fig. 5(d)].

Increases in c_{23} will extend the zone in which species 3 can invade [eqn (14)] and do not affect the species 2 invasion zone [eqn (12)], which extends the region of coexistence for lower values of the product ra_{23}.

In Fig. 6, equilibrium densities for species 1–3 are shown as a function of a_{23} for different values of Q and with $c_{23} = 0.9$. The graphs show that as Q becomes lower [graphs (a)–(f)], the zone of coexistence expands, mainly towards greater values of a_{23}. Thus, two of the conditions for coexistence, that species 2 is a better competitor than species 3 (Q value) and an intermediate magnitude of intraguild predation (a_{23} value), are not independent. From graphs (a)–(f), we see that resource grows and IG prey decreases with a_{23}. For IG predator, graphs (a)–(d) show that its density grows with a_{23}, but (e) and (f) shows that it decreases for higher values, having a maximum as predicted in the section above. This maximum does not appear from (a) to (d), because for a_{23} outside the coexistence region, the three-species equilibrium does not exist.

To complete the numerical results, Fig. 7 shows examples of invasion dynamics for three

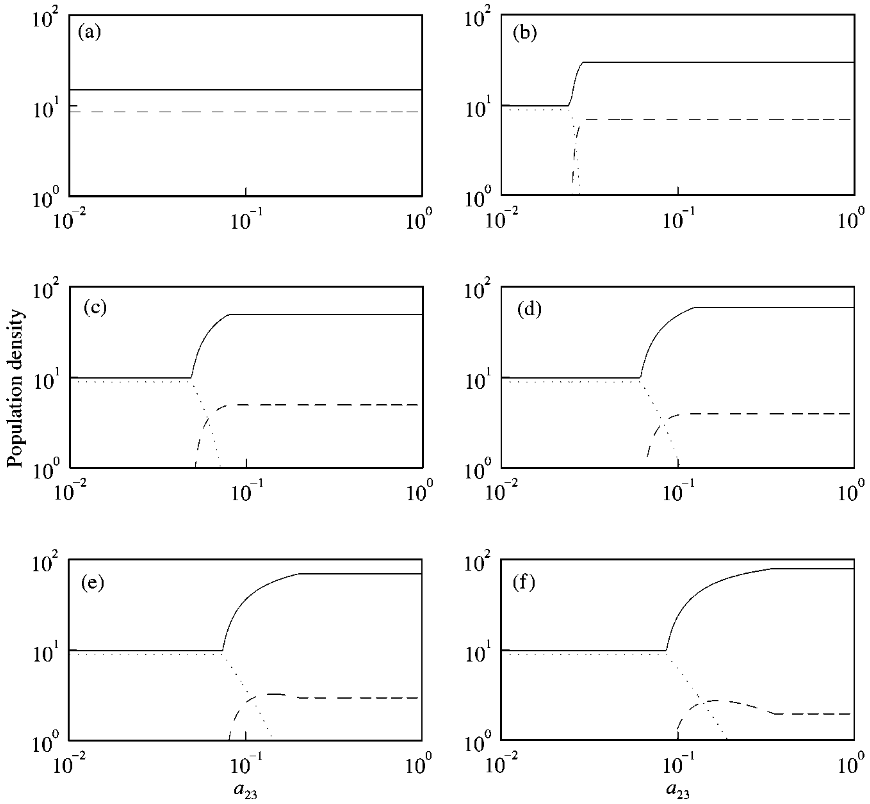

FIG. 6. Densities of species 1 (——), 2 (······) and 3 (- - - -) as a function of a_{23} in a double logarithmic scale, for a sequence of values for Q, obtained changing d_3: (a) $Q = 8.5/9$ ($d_3 = 0.15$), (b) $Q = 7/9$ ($d_3 = 0.30$), (c) $Q = 5/9$ ($d_3 = 0.50$), (d) $Q = 4/9$ ($d_3 = 0.60$), (e) $Q = 3/9$ ($d_3 = 0.70$), (f) $Q = 2/9$ ($d_3 = 0.80$). The remaining parameter values are: $r = 1$, $K = 100$, $a_{12} = a_{13} = c_{12} = c_{13} = 0.1$, $c_{23} = 0.9$ and $d_2 = 0.1$. In the regions with horizontal lines only boundary equilibria, E_{12} [eqn (7)] and E_{13} [eqn (8)], are valid.

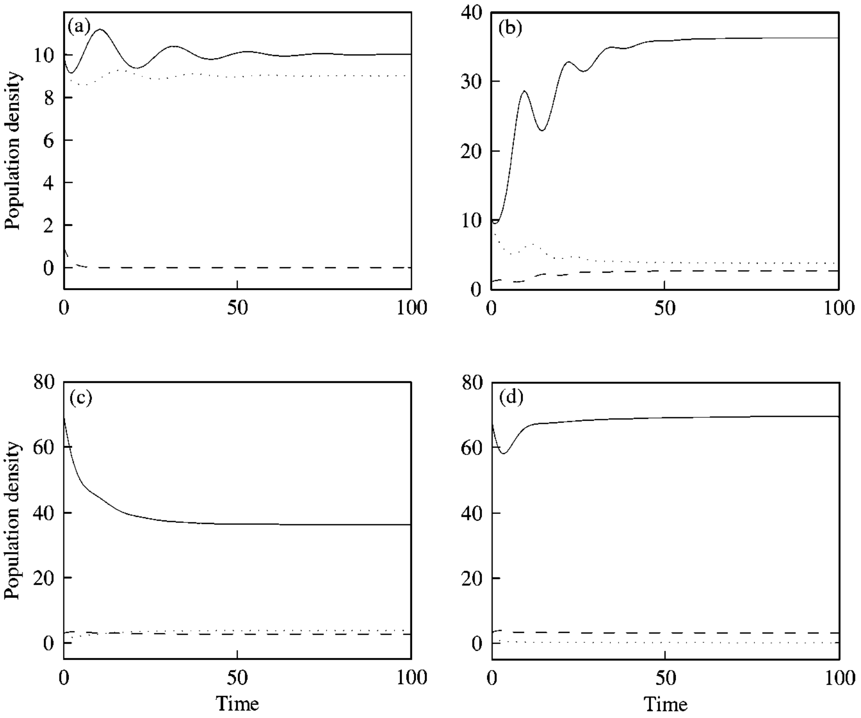

FIG. 7. Simulation of invasion dynamics for model (1): (a) species 3 cannot invade the equilibrium between species 1 and 2 with $a_{23} = 0.01$. In (b) and (c), species 3 and 2 can invade the resident equilibrium, respectively, with $a_{23} = 0.10$, leading to the same positive equilibrium. In (d), species 2 cannot invade the equilibrium between species 1 and 3 with $a_{23} = 0.20$. Parameter values: $r = 1$, $K = 100$, $a_{12} = a_{13} = c_{12} = c_{13} = 0.1$, $c_{23} = 0.9$ and $d_2 = 0.1$, $d_3 = 0.7$. Species 1 (——), 2 (⋯⋯) and 3 (- - - -).

values of a_{23} taken from the density profile shown in graph (e) of Fig. 6. We see that for intermediate values of a_{23}, both species 2 and 3 can invade the equilibrium of the other two reaching a new equilibrium state, but that at extreme values of a_{23} the original two-species equilibria are restored.

Models with Saturating Functional Responses

The relative simplicity of the Lotka–Volterra model of IGP [eqn (1)] makes it easier to obtain the above results, because the nullclines are linear (planes in a 3D space). It is possible to include nonlinearities such as Holling type II functional response:

$$\dot{N}_1 = rN_1\left(1 - \frac{N_1}{K}\right) - \frac{a_{12}N_1}{1 + h_{12}N_1}N_2 - \frac{a_{13}N_1}{1 + h_{13}N_1 + h_{23}N_2}N_3,$$

$$\dot{N}_2 = \frac{c_{12}a_{12}N_1}{1 + h_{12}N_1}N_2 - d_2N_2 - \frac{a_{23}N_2}{1 + h_{13}N_1 + h_{23}N_2}N_3, \qquad (26)$$

$$\dot{N}_3 = \left(\frac{c_{13}a_{13}N_1 + c_{23}a_{23}N_2}{1 + h_{13}N_1 + h_{23}N_2} - d_3\right)N_3$$

with (h_{ij}) being the handling time of species j upon species i. The above model equations give curved nullclines for common resource and IG prey, but the IG predator nullcline is a plane.

When one of the consumers is absent, the minimum resource density needed for the resident consumer is equal to $d_i/(c_{1i}a_{1i} + h_{1i}d_i)$, in model eqn (26). As IG predator density increases, the resource density needed for IG prey growth must increase to compensate for predation pressure. On the other hand, as IG prey density increases, the amount of common resource needed for IG predator growth decreases. Then both nullclines will coincide only if $d_2/(c_{12}a_{12} - h_{12}d_{12}) < d_3/(c_{13}a_{13} - h_{13}d_3)$. Again, a necessary condition for a positive equilibrium involves the competitive superiority of the IG prey.

The resource nullcline will have the general form depicted in Fig. 8, given that carrying capacity is high enough to allow the presence of "humps" for the boundary two species communities. The competitive superiority condition gives lower N_1 coordinates for the resource and IG prey equilibrium. Thus, it is more likely to have limit cycle behavior for a resource–IG prey interaction, than in the other consumer–resource dynamics. Curvature causes the IG prey and predator nullclines to coincide along a curved line AB, that could cross resource nullcline more than one time giving more than one three-species equilibrium, as Fig. 8 shows, via bifurcation.

Although a set of invasibility conditions like eqns (12) and (14) were not found, the question is the same: Is the combined density of resident species located in the $\mathrm{d}N_i/\mathrm{d}t > 0$ zone for invader species (i) nullcline? But now there is the possibility that resident species do not have a constant combined density, having a limit cycle that switch between the $\mathrm{d}N_i/\mathrm{d}t > 0$ and the < 0 zone for the invader. Figure 9 shows an example simulation of model (26), in which the boundary community of resource and IG prey undergo a predator–prey limit cycle but a stable equilibrium is the attractor for the resource and IG predator community. Invasion of both resident pairs leads to a stable three-species equilibrium.

Discussion

For the simple Lotka–Volterra model of intraguild predation, described by eqn (1), a necessary but not sufficient condition for coexistence is that the intraguild prey must be a better competitor than the intraguild predator in the consumption of their shared prey [eqn (11)]. This result is common to previous models with intraguild predation. Polis *et al.* (1989) and Holt & Polis (1997) present examples using Lotka–Volterra models with or without a resource equation, and also with Schoener's nonlinear model for exploitative competition (Schoener, 1974, 1976). However, the complexity of natural food webs can make this rule of competitive superiority for the IG prey too simple to be applicable. Indeed, Navarrete *et al.* (2000), working with an intertidal food web found coexistence, being the IG predator the best competitor. These authors attribute this to the open nature of the IG prey and IG predator populations (for example, IG predators are not strictly dependent on local resources), and to the large differences in body size in the IG prey and predator populations.

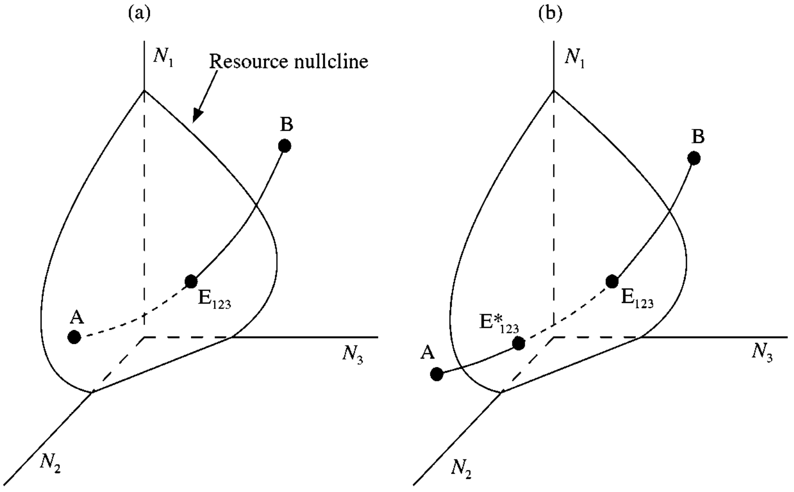

FIG. 8. With model equations like eqn (26), IG prey and predator nullclines cut forming the curved line AB, such a curve can pass through the resource nullcline one or more times giving simple (a) or multiple (b) equilibrium points (E_{123}, E^*_{123}). The dotted section of AB is below the resource nullcline.

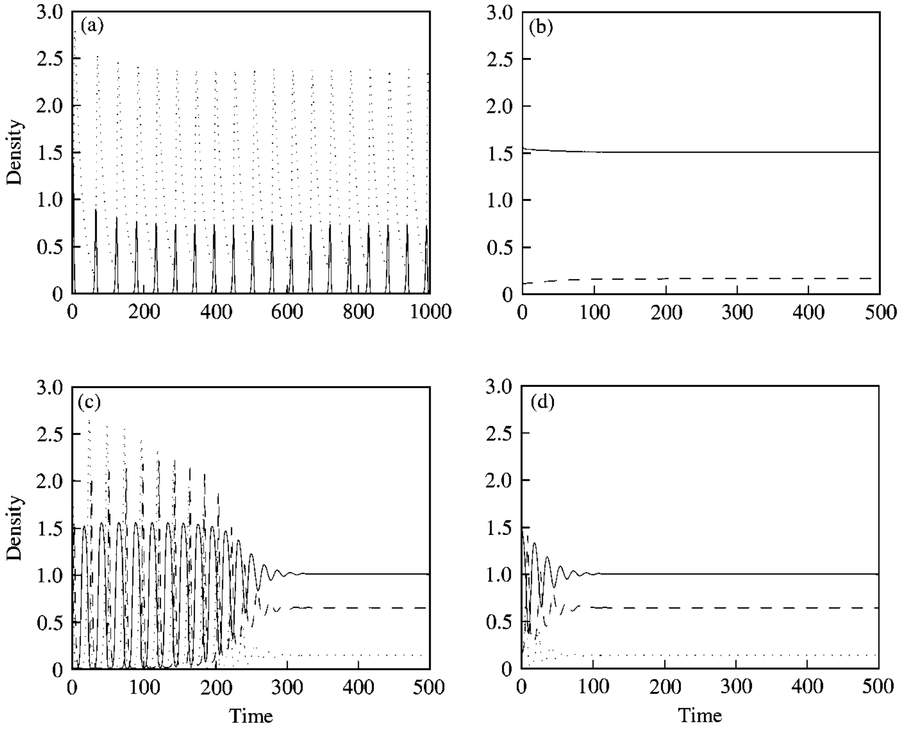

FIG. 9. Simulation of invasion dynamics for model (26): (a) species 1 and 2 with limit-cycle dynamics, (b) equilibrium dynamics between species 1 and 3, (c) invasion of species 1 and 2 community by species 3 leads to a stable three-species equilibrium, and (d) invasion of species 1 and 3 equilibrium by species 2 leads to the same equilibrium as (c). Parameter values: $r = 1$, $K = 1.6$, $a_{12} = a_{13} = c_{12} = 1$, $a_{23} = c_{13} = 1.5$, $c_{23} = 2$, $h_{12} = h_{13} = h_{23} = 1$ and $d_2 = 0.05$, $d_3 = 0.9$. Species 1 (——), 2 (······) and 3 (- - - -).

The main new result of the present work is to show that, with the aid of the nullcline analysis it is possible to obtain a set of analytical conditions, in the form of explicit inequalities (12, 14), for invasion of both intraguild prey and predator, and thus for coexistence that includes the earlier "competitive" condition, in the form of the Q value, plus a "predatory" condition in the form of the magnitude of intraguild predation measured by a_{23}. Working with such inequalities, some other analytical results can be obtained [inequalities (17, 18), Table 1]. With this approach, it is not necessary to perform a local stability analysis of the three-species equilibrium if we accept the following.

1. Species 1, the common resource is always present. So the problem of coexistence is for species 2 and 3.
2. Coexistence means that both species 2 and 3 can invade, no matter which is the resulting global dynamics.

These two statements also help to explain that the outcomes of model equations (1) are similar to those of the Lotka–Volterra competition model: species 2 win, species 3 win, both coexists, and either can win. The asymmetrical conditions experienced by both species, prevents them from occupying the same niche.

When coexistence is possible, it is achieved at intermediate values of ra_{23} [eqn (17)]: the negative effect that intraguild predator imposes on intraguild prey must be high enough to prevent competitive dominance of intraguild prey, but not so high as to exclude it. The range of intermediate values depends on the value of Q, that must be lower than 1, as seen in Fig. 5(a)–(d): as Q decreases, the zone of coexistence becomes greater.

As was mentioned in the introduction, the model equations (1) were tested by Diehl & Feissel (2000). These authors were interested in the effect of enrichment upon coexistence, and found that as K becomes larger species 2 excludes

3, species 2 and 3 coexist, and finally species 3 excludes 2. In terms of the parameter space of Fig. 5, this is equivalent to the increase of Q [Q grows with K to a plateau of $Q = 1$, see eqn (13)] that compares the competitive abilities of species 2 and 3. As K becomes larger (and then Q), the competitive advantage of species 2 decreases in relation to species 3. This is easy to see in Figs 2–4: as K grows, the upper corner of the resource nullcline moves up and the E_{12} and E_{13} coordinates increase in the N_2 and N_3 direction, respectively, giving the following sequence: A and B are above resource nullcline (Case 1), A and B are opposite (Case 3 in the example of Fig. 2), and A and B are below the resource nullcline (Case 2).

An experimental approach is needed to test the predictions about the effect of the parameter a_{23}, the intraguild predation pressure, and to know how wide or narrow is the coexistence region for this parameter for a fixed or variable value of K. Attack rate parameters such as a_{23} can be changed by reducing the frequency of contact between individuals by a method such as that used by Luckinbill (1973). Unfortunately, this will also affect a_{12} and a_{13}.

The magnitude of c_{23} changes the extent of the coexistence region [eqn (18)]. As seen in Fig. 5(b), with $c_{23} = 0$ coexistence is not possible for any value of Q. Holt & Polis (1997) have used a general additive model in which the role of c_{23} was modeled with a function which describes how the *per capita* growth rate of the IG predator is enhanced by consuming the IG prey. In the words of these authors: "This net demographic effect encompasses both direct caloric effects provided by the consumption of the IG prey and any costs due to reduced intake of the basal resource (e.g., because of time spent handling the IG prey, reducing the time available to search for the basal resource)." Thus the IG predator must achieve a positive effect ($c_{23} > 0$). A situation in which c_{23} is equal or near to zero occurs when the IG predator kills but does not eat IG prey (which corresponds to an extreme form of interference competition), or eats it but the energy taken is low, and as a consequence, the energetic costs of intraguild predation exceeds its benefits. So as c_{23} grows and the benefits are greater, the zone in which IG predator dominates also becomes greater as seen in Fig. 5(c) and (d).

In models with nonlinear functional response like eqn (26), a great difference is that resident species could have unstable dynamics, and this raises some interesting questions. For example, suppose an invasion of the IG predator when both resource and IG prey undergo a limit cycle. It is possible to have one part of that cycle inside the $\mathrm{d}N_3/\mathrm{d}t > 0$ region of the IG predator nullcline and the remaining inside the $\mathrm{d}N_3/\mathrm{d}t < 0$ region. Does this implie that there is a succession of "good" and "bad" times to invade? But numerical simulations perhaps are not a good way to explore this, because in models like eqns (1) and (26) extinction is asymptotic, so, when the residents return to the invasion favorable conditions, there will be always a reduced but non-zero density of the invader awaiting to grow. Of course, the whole cycle could be inside the $\mathrm{d}N_3/\mathrm{d}t > 0$ or < 0 region. It is possible that the final answer would be related to a sort of "mean transit time" of the resident cycle into the invasion favorable region defined by the invader's nullcline.

Given the lower resource demands of IG prey (if the hypothesis of competitive superiority holds), in a system governed by eqn (26) the resource–IG prey equilibrium would become less stable than the resource–IG predator one if the carrying capacity increases (enrichment effect in a predator–prey system with self-limitation in the prey, and saturating predator functional response). Then, an invasion of the IG predator is likely to lead the system to a stable situation [Fig. 9(c)]. But this is not a general conclusion, because the internal equilibrium could also be unstable; or there could be more than one three-species equilibrium if bifurcation phenomena are present given the nullcline curvatures (Fig. 8), a situation that does not happen with planar nullclines.

It is important to note that in this paper, what is termed invasibility is not necessarily equivalent to stable internal equilibria. Actually, it is possible that all species can invade when rare but instead of a stable internal equilibria we have a stable limit cycle (Holt & Polis, 1997). Then, when there is invasibility it is better to talk about uniform persistence instead of ecological stability.

I am very grateful to Diego Rodríguez for assistance with the writing. The paper benefited from conversations with Jesús Alberto Leon and Peter Abrams. This work was supported by Grant PG-033143361999 of Consejo de Desarrollo Científico y Humanístico of Universidad Central de Venezuela to Diego Rodriguez.

REFERENCES

Diehl, S. & Feissel, M. (2000). Effects of enrichment on three level food chains with omnivory. *Am. Nat.* **155,** 200–218.

Hallam, T. G. (1986). Community dynamics in a homogeneous environment. In: *Mathematical Ecology* (Hallam, T. G. & Levin, S. A., eds), pp. 241–285. Berlin: Springer.

Holt, R. D. (1996). Community Modules. In: *Multitrophic Interactions* (Begon, M., Gange, A. & Brown, V., eds), pp. 333–350. London: Chapman & Hall.

Holt, R. D. & Polis, G. A. (1997). A theoretical framework for intraguild predation. *Am. Nat.* **149,** 745–764.

León, J. A. & Tumpson, D. B. (1975). Competition between two species for two complementary or substitutable resources. *J. theor. Biol.* **50,** 185–201.

Luckinbill, L. S. (1973). Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum. Ecology* **54,** 1320–1327.

Navarrete, S. A., Menge, B. A. & Daley, B. A. (2000). Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? *Ecology* **81,** 2264–2277.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* **20,** 297–330.

Schoener, T. W. (1974). Competition and the form of the habitat shift. *Theor. Popul. Biol.* **6,** 265–307.

Schoener, T. W. (1976). Alternatives to Lotka–Volterra competition: models of intermediate complexity. *Theor. Popul. Biol.* **10,** 309–333.

Tilman, D. (1982). *Resource Competition and Community Structure.* Princeton, NJ: Princeton University Press.

APPENDIX A

Invasion Conditions for Species 2

In Fig. 3, the equilibrium point E_{13} has a coordinate on the N_3-axis equal to [from eqn (8)]:

$$N_3 \text{ at } E_{13} = \frac{r}{a_{13}K}\left(K - \frac{d_3}{c_{13}a_{13}}\right). \qquad (A.1)$$

The coordinate of E_{13} on the N_1-axis,

$$\hat{N}_1 = \frac{d_3}{c_{13}a_{13}}.$$

Substituting this expression into the equation of the species 2 nullcline [eqn (3)], yields the coordinate of B on the N_3-axis:

$$N_3 \text{ at } B = \frac{c_{12}a_{12}}{a_{23}}\left(\frac{d_3}{c_{13}a_{13}} - \frac{d_2}{c_{12}a_{12}}\right). \qquad (A.2)$$

The species 1–species 3 equilibrium is invasible by species 2 if N_3 at $E_{13} < N_3$ at B (see Fig. 3), which translates to

$$\frac{c_{12}a_{12}}{a_{23}}\left(\frac{d_3}{c_{13}a_{13}} - \frac{d_2}{c_{12}a_{12}}\right) > \frac{r}{a_{13}K}\left(K - \frac{d_3}{c_{13}a_{13}}\right). \qquad (A.3)$$

It is useful to define the following quantities:

$$D_{12} = K - \frac{d_2}{c_{12}a_{12}},$$

$$D_{13} = K - \frac{d_3}{c_{13}a_{13}},$$

$$D_{23} = \frac{d_3}{c_{13}a_{13}} - \frac{d_2}{c_{12}a_{12}}.$$

Thus, it is true that

$$D_{12} = D_{13} + D_{23}. \qquad (A.4)$$

With the aid of eqn (A.4), the invasion condition for species 2 [eqn (A.3)] becomes

$$Q = \frac{D_{13}}{D_{12}} < \frac{1}{1 + (ra_{23})/(Kc_{12}a_{12}a_{13})},$$

Invasion Conditions for Species 3

In Fig. 4, the equilibrium point E_{12} has a coordinate on the N_2-axis equal to [from eqn (7)]

$$N_2 \text{ at } E_{12} = \frac{r}{a_{12}K}\left(K - \frac{d_2}{c_{12}a_{12}}\right), \qquad (A.5)$$

and the coordinate of point A on the same axis is obtained by substituting the coordinate of E_{12} on the N_1-axis,

$$\hat{N}_1 = \frac{d_2}{c_{12}a_{12}},$$

in the equation of the species 3 nullcline [eqn (4)], and the result is

$$N_2 \text{ at } A = \frac{c_{13}a_{13}}{c_{23}a_{23}}\left(\frac{d_3}{c_{13}a_{13}} - \frac{d_2}{c_{12}a_{12}}\right). \quad \text{(A.6)}$$

Now, the species 1–species 2 equilibrium is invadible by species 3 if N_2 at $\mathrm{E}_{12} > N_2$ at A (see Fig. 4), which translates to

$$\frac{c_{13}a_{13}}{c_{23}a_{23}}\left(\frac{d_3}{c_{13}a_{13}} - \frac{d_2}{c_{12}a_{12}}\right) < \frac{r}{a_{12}K}\left(K - \frac{d_2}{c_{12}a_{12}}\right). \quad \text{(A.7)}$$

Using eqn (A.4) inequality (A.7) becomes the condition invasion for species 3:

$$Q = \frac{D_{13}}{D_{12}} > 1 - c_{23}(ra_{23})/(Kc_{13}a_{13}a_{12}).$$

Derivatives of $\hat{N}_2$ and $\hat{N}_3$ with Respect to a_{23}, r and c_{23}

The derivatives of $\hat{N}_2$ and $\hat{N}_3$ from eqn (10) depend on $\hat{N}_1$, then:

$$\partial\hat{N}_2/\partial a_{23} = -\frac{(d_3 - c_{13}a_{13}\hat{N}_1) + c_{13}a_{13}a_{23}(\partial\hat{N}_1/\partial a_{23})}{c_{23}a_{23}^2}, \quad \text{(A.8)}$$

$$\partial\hat{N}_2/\partial r = -\frac{c_{13}a_{13}}{c_{23}a_{23}}(\partial\hat{N}_1/\partial r), \quad \text{(A.9)}$$

$$\partial\hat{N}_2/\partial c_{23} = -\frac{(d_3 - c_{13}a_{13}\hat{N}_1) + c_{13}c_{23}a_{13}(\partial\hat{N}_1/\partial c_{23})}{c_{23}^2 a_{23}}, \quad \text{(A.10)}$$

$$\partial\hat{N}_3/da_{23} = \frac{c_{12}a_{12}a_{23}(\partial\hat{N}_1/\partial a_{23}) - (c_{12}a_{12}\hat{N}_1 - d_2)}{a_{23}^2}, \quad \text{(A.11)}$$

$$\partial\hat{N}_3/\partial r = \frac{c_{12}a_{12}}{a_{23}}(\partial\hat{N}_1/\partial r), \quad \text{(A.12)}$$

$$\partial\hat{N}_3/\partial c_{23} = \frac{c_{12}a_{12}}{a_{23}}(\partial\hat{N}_1/\partial c_{23}). \quad \text{(A.13)}$$

The signs of the $\hat{N}_1$ derivatives makes $\partial\hat{N}_2/\partial a_{23}$, $\partial\hat{N}_2/\partial r$, and $\partial\hat{N}_2/\partial c_{23}$ negative, $\partial\hat{N}_3/\partial r$, $\partial\hat{N}_3/\partial c_{23}$ positive, and $\partial\hat{N}_3/\partial a_{23}$ undetermined.