

# Interference competition and species coexistence

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Interference competition is ubiquitous in nature. Yet its effects on resource exploitation remain largely unexplored for species that compete for dynamic resources. Here, I present a model of exploitative and interference competition with explicit resource dynamics. The model incorporates both biotic and abiotic resources. It considers interference competition both in the classical sense (i.e. each species suffers a net reduction in per capita growth rate via interference from, and interference on, the other species) and in the broad sense (i.e. each species suffers a net reduction in per capita growth rate via interference from, but can experience an increase in growth rate via interference on, the other species). Coexistence cannot occur under classical interference competition even when the species inferior at resource exploitation is superior at interference. Such a trade-off can, however, change the mechanism of competitive exclusion from dominance by the superior resource exploiter to a priority effect. Now the inferior resource exploiter can exclude the superior resource exploiter provided it has a higher initial abundance. By contrast, when interference is beneficial to the interacting species, coexistence is possible via a trade-off between exploitation and interference. These results hold regardless of whether the resource is biotic or abiotic, indicating that the outcome of exploitative and interference competition does not depend on the exact nature of resource dynamics. The model makes two key predictions. First, species that engage in costly interference mechanisms (e.g. territoriality, overgrowth or undercutting, allelopathy and other forms of chemical competition) should not be able to coexist unless they also engage in beneficial interference mechanisms (e.g. predation or parasitism). Second, exotic invasive species that displace native biota should be superior resource exploiters that have strong interference effects on native species with little or negative cost. The first prediction provides a potential explanation for patterns observed in several natural systems, including plants, aquatic invertebrates and insects. The second prediction is supported by data on invasive plants and vertebrates.

**Keywords:** biotic resource; abiotic resource; interference competition; exploitative competition; coexistence

## 1. INTRODUCTION

Competition between species occurs in two ways. Exploitative competition involves indirect negative interactions arising from the use of a common resource (Case & Gilpin 1974). Each consumer affects others solely by reducing resource abundance (Vance 1984). Interference competition involves direct negative interactions arising from territoriality, overgrowth, undercutting, predation or chemical competition (Schoener 1983). Each consumer alters others' ability to exploit the resource at any level of abundance (Vance 1984).

Most theories on interspecific competition have focused on exploitative competition (e.g. Volterra 1926; Lotka 1932; MacArthur & Levins 1964; Armstrong & McGehee 1976; Levins 1979; Case & Casten 1979; Armstrong & McGehee 1980; Tilman 1982). This contrasts with the ubiquity of interference competition in nature. For instance, interspecific territoriality and other aggressive behaviours (Walls 1990; Kennedy & White 1996), allelopathy (Rice 1974; Harper 1977; Nilsson 1994), overgrowth (Connell 1961; Paine 1966) and predation of young (Eaton 1979; Leving & Franks 1982; Rytí & Case 1988; Polis *et al.* 1989) occur in a wide variety of taxa, from invertebrates to mammals. Moreover, exotic invasive species that displace native fauna and flora appear to do so via superiority in interference competition (e.g. Case *et*

*al.* 1994; Huenneke & Thomson 1995; Ridenour & Callaway 2001).

There is little theory on interference competition (Case & Gilpin 1974; Schoener 1976, 1978; Case *et al.* 1979; Hsu 1981; Vance 1984), virtually all of which follows the Lotka–Volterra tradition of considering resource dynamics to be implicit. The resource is assumed not to accumulate within the system, so it can be treated as an input rather than a state variable (Vance 1984). The interaction between exploitative and interference competition remains largely unexplored for species that exploit dynamic resources.

Here, I present a model of exploitative and interference competition with explicit resource dynamics. I consider both abiotic (i.e. with a constant resource supply rate) and biotic (i.e. with resource reproduction and self-limitation) resources. I derive the conditions under which the interplay between exploitation and interference leads to coexistence versus exclusion. I discuss the implications of these results for invasive species.

## 2. THE MODEL

Consider two consumer species that exploit a common resource. The resource can be biotic, i.e. it grows and reproduces (typically on the same time-scale as its consumers), and its supply rate is influenced by the con-

sumers (MacArthur & Levins 1964; Armstrong & McGehee 1980; Vance 1984). Examples include plants that support herbivores, insects or other hosts that support parasites or parasitoids, and prey species that support predators. The resource can also be abiotic, i.e. with a constant supply rate that is not influenced by consumers. Examples include water, and nutrients such as nitrogen, phosphorous and iron that are essential for the growth and reproduction of plants and phytoplankton.

The consumer species interact indirectly through exploitative competition. They also interact directly via interference competition.

In the classical definition of interference competition, interacting species incur only costs, but no benefits, due to interference. For instance, each consumer species suffers a reduction in its per capita growth rate because acts of interference (e.g. the aggressive defence of a territory or a food item, the production of allelochemicals, overgrowth or undercutting) divert time and energy from resource exploitation, and could in some cases cause injury or death (Case & Gilpin 1974; Schoener 1983; Vance 1984). In nature, however, many organisms, particularly non-territorial species, tend to use predation as a mechanism of interference. For instance, aquatic invertebrates and fishes tend to prey on eggs and larvae of their resource competitors (see examples in Polis *et al.* (1989)). In parasites and parasitoids, within-host larval competition involves one species killing and consuming the other (Force 1970; Zwolfer 1971; Munster-Swendsen 1979; Mills 1994). Such acts of intraguild predation or parasitism can benefit the aggressor by increasing its per capita growth rate.

The model I present considers interference competition in the broad sense, as incurring costs or accruing benefits depending on the actual mechanism of interference. The model thus encompasses a broad range of interference mechanisms, and can yield predictions about how the exact nature of the interference mechanism influences species coexistence.

Let  $R$ ,  $C_1$  and  $C_2$  denote, respectively, the abundances of the resource, consumer 1 and consumer 2. The following model describes the dynamics of a two-consumer-single-resource interaction with exploitation and interference:

$$\begin{aligned} \frac{dR}{dt} &= R\gamma(R) - f_{C_1}(R)C_1 - f_{C_2}(R)C_2 \\ \frac{dC_1}{dt} &= C_1 \left[ e_1 f_{C_1}(R) - d_1 - \left( g_{12}(C_2) \pm \beta_1 g_{21}(C_2) \right) \right] \\ \frac{dC_2}{dt} &= C_2 \left[ e_2 f_{C_2}(R) - d_2 - \left( g_{21}(C_1) \pm \beta_2 g_{12}(C_1) \right) \right]. \end{aligned} \quad (2.1)$$

The function  $\gamma(R)$  describes resource growth, and  $f_{C_i}(R)$  the functional response of consumer  $i$  ( $i = 1, 2$ ). The quantity  $e_i$  is the conversion efficiency (the number of offspring produced per unit of resource consumed) of consumer  $i$ , and  $d_i$  is its density-independent background mortality rate. The function  $g_{ij}(C_j)$  is the per capita effect of interference from consumer  $j$  on consumer  $i$ , and  $\beta_i g_{ji}(C_j)$  is the per capita cost or benefit to consumer  $i$  due to interference on consumer  $j$ . Both the effects and costs/benefits of interference are non-negative, i.e.  $g_{ij}(C_j) > 0$ ,  $g_{ij}(0) = 0$  ( $i, j = 1, 2, i \neq j$ ). When  $g_{ij}(C_j) + \beta_i g_{ji}(C_j)$ , both species incur a cost due to interference; when  $g_{ij}(C_j) - \beta_i g_{ji}(C_j)$ ,

one or both species gain a benefit from interference. When acts of interference are costly,  $\beta_i$  can be interpreted as a scaling constant. For example, when  $\beta_i = 1$ , the per capita effect on consumer  $j$  due to interference from consumer  $i$  is equal to the per capita cost that consumer  $i$  suffers due to interference on consumer  $j$ . When  $\beta_i < 1$ , the per capita effect that consumer  $i$  has on consumer  $j$  outweighs the per capita cost of interference. The reverse is true when  $\beta_i > 1$ . When acts of interference accrue a benefit to the aggressor,  $\beta_i$  can be interpreted as a conversion efficiency; it converts the benefit consumer  $i$  derives from interference into reproduction.

Interference between species can be unidirectional, particularly when it involves intraguild predation or parasitism (Holt & Polis 1997; Diehl & Feissel 2000). For instance, if consumer  $j$  interferes with consumer  $i$  and not vice versa,  $g_{ij}(C_j) > 0$  and  $g_{ji}(C_j) = 0$ .

The conditions under which the two consumer species can coexist can be derived as follows. Let  $F_i(R) = e_i f_{C_i}(R) - d_i$ . When it exists, an equilibrium of equation (2.1) ( $dC_i/dt = dC_j/dt = 0$ ) must satisfy

$$\begin{aligned} F_i(R^*) &= I_{C_i}(C_j^*) \\ F_j(R^*) &= I_{C_j}(C_i^*), \end{aligned} \quad (2.2)$$

where  $I_{C_i}(C_j^*) = g_{ij}(C_j^*) \pm \beta_i g_{ji}(C_j^*)$ ,  $I_{C_j}(C_i^*) = g_{ji}(C_i^*) \pm \beta_j g_{ij}(C_i^*)$  and  $R^*$  is the equilibrium level of the resource with all three species present.

Consider first the case when interference competition incurs only costs to both consumers, i.e.  $I_{C_i}(C_j^*) = g_{ij}(C_j^*) + \beta_i g_{ji}(C_j^*) > 0$  ( $i, j = 1, 2, i \neq j$ ). Then  $F_i(R^*)$ ,  $F_j(R^*) > 0$ , which means that given an ambient resource level of  $R^*$ , consumer species  $i$  and  $j$  can increase in abundance and depress resource levels to  $R_{C_i}^*$  and  $R_{C_j}^*$ , respectively. ( $R_{C_i}^*$  is the solution to  $F_i(R) = 0$ , and  $R_{C_j}^*$  is the solution to  $F_j(R) = 0$ , i.e. the resource level required for consumer  $i$  to persist in the absence of consumer  $j$  and vice versa.) Hence, in the absence of interspecific interference, the consumer species that drives resource abundance to the lowest level excludes the other ( $R^*$  rule (Tilman 1982)).

The key issue is whether interference can allow consumer species to coexist. For coexistence to be feasible ( $C_i^*$ ,  $C_j^* > 0$ ), it is necessary that  $F_i(R^*)$ ,  $F_j(R^*) > 0$ , which in turn implies that  $R^* > R_{C_i}^*$ ,  $R_{C_j}^*$ . In other words, consumer coexistence requires the equilibrium resource abundance to be greater than that required for each consumer to persist in isolation.

Coexistence also requires that each consumer species is able to invade when the other species is at equilibrium with the resource. Invasion is possible if each species can maintain a positive per capita growth rate when rare (i.e.  $(dC_i/dt)(1/C_i) > 0$  when  $C_i \approx 0$ ,  $i = 1, 2$ ). From equation (2.1), the invasion criteria for the two consumer species are, respectively

$$\begin{aligned} F_i(R_{C_j}^*) &> I_{C_i}(C_j^* |_{C_i=0}) \\ F_j(R_{C_i}^*) &> I_{C_j}(C_i^* |_{C_j=0}), \end{aligned} \quad (2.3)$$

where  $C_i^* |_{C_j=0}$  is the equilibrium abundance of consumer  $i$  in the absence of consumer  $j$ . Each consumer can persist on the resource in the absence of the other, i.e.  $C_i^* |_{C_j=0}$ ,  $C_j^* |_{C_i=0} > 0$ . Hence,  $I_{C_i}$ ,  $I_{C_j} > 0$ . Invasion will succeed if

each consumer species' resource exploitation ability ( $F_i$ ) exceeds the costs and effects from interference with the other ( $I_{C_i}$ ).

Assume, without loss of generality, that consumer  $i$  is the superior resource exploiter, i.e. it can persist at a lower resource level than consumer  $j$  ( $R_{C_i}^* < R_{C_j}^*$ ). This means that consumer  $j$  cannot maintain a positive growth rate at the resource level  $R_{C_i}^*$  i.e.  $F_j(R_{C_i}^*) < 0$ . As  $I_{C_j}(C_i^* |_{C_j=0}) > 0$ , it follows that  $F_j(R_{C_i}^*) < I_{C_j}(C_i^* |_{C_j=0})$ . Hence, when consumer  $i$  is the superior resource exploiter, consumer  $j$  cannot invade when rare.

From equations (2.3), consumer  $i$  can invade when rare if  $F_i(R_{C_j}^*) > I_{C_i}(C_j^* |_{C_i=0})$ . As shown previously, coexistence is feasible if  $F_i(R^*)$ ,  $F_j(R^*) > 0$ , i.e.  $R^* > R_{C_i}^*$ ,  $R_{C_j}^*$ . However, invasion by consumer  $i$  requires  $F_i(R_{C_j}^*)$  to exceed a positive quantity ( $I_{C_i}$ ), whereas feasibility of the coexistence equilibrium requires only that  $F_i(R^*)$  exceeds zero. Hence, invasion by consumer  $i$  means that  $F_i(R_{C_j}^*) > F_i(R^*)$ , i.e.  $R_{C_j}^* > R^*$ . This contradicts the feasibility condition for coexistence. Thus, conditions that allow consumer  $i$  to invade when rare preclude coexistence. The outcome is competitive dominance where the superior resource exploiter invades and excludes the inferior resource exploiter.

If consumer  $i$  cannot invade when rare i.e.  $F_i(R_{C_j}^*) < I_{C_i}(C_j^* |_{C_i=0})$ , then  $R^* > R_{C_i}^*$ ,  $R_{C_j}^*$  and the coexistence equilibrium is feasible. However, since neither consumer can invade when rare, the coexistence equilibrium will necessarily be unstable. The outcome is a priority effect where the consumer species with the higher initial abundance excludes the other.

The key result is as follows: when two consumer species that exploit a common resource also engage in interference competition in the classical sense (i.e. both species incur costs but gain no benefits), they cannot coexist at a point attractor. The only possible outcomes are competitive dominance or a priority effect.

Equations (2.1) can lead to persistent fluctuations in the abundance of the resource and consumers if the latter exhibit type II functional responses. Resource fluctuations can allow consumers to coexist in the absence of interference (Armstrong & McGehee 1976, 1980). I do not consider this situation because my goal is to determine whether the interplay between exploitation and interference can lead to coexistence in the absence of alternative mechanisms (see § 3).

Consider now the case when interference competition accrues a benefit to the interacting species. Now the interference parameters,  $I_{C_i}(C_j^*) = g_{ij}(C_j^*) - \beta_j g_{ji}(C_j^*)$  and  $I_{C_j}(C_i^*) = g_{ji}(C_i^*) - \beta_i g_{ij}(C_i^*)$ , can be positive or negative. There are three situations to consider.

- (i) Both consumer species can persist on the basal resource in the absence of interference, i.e.  $F_i(R^*)$ ,  $F_j(R^*) > 0 \Rightarrow R_{C_i}^*, R_{C_j}^* < R^*$ . For both species, the negative effect due to interference from the other species is greater than the benefit gained by interference on it, i.e.  $I_{C_i}(C_j^*)$ ,  $I_{C_j}(C_i^*) > 0$ . Here, the outcome is the same as for classical interference competition. Conditions that allow consumer species to invade when rare are incompatible with feasibility conditions for the coexistence equilibrium.
- (ii) Neither consumer can persist on the basal resource

alone, i.e.  $F_i(R^*)$ ,  $F_j(R^*) < 0 \Rightarrow R_{C_i}^*, R_{C_j}^* > R^*$ , and  $I_{C_i}(C_j^*)$ ,  $I_{C_j}(C_i^*) < 0$ . This case, therefore, is of little biological relevance.

- (iii) Consumer  $i$  can subsist on the basal resource alone but consumer  $j$  cannot, i.e.  $F_i(R^*) > 0$ ,  $F_j(R^*) < 0 \Rightarrow R_{C_i}^* < R^* < R_{C_j}^*$ . Consumer  $j$  accrues a net gain from interference, and consumer  $i$  a net loss, i.e.  $I_{C_i}(C_j^*) > 0$  and  $I_{C_j}(C_i^*) < 0$ . Coexistence can occur provided the species inferior at interference is superior at resource exploitation. Both consumer species can invade when rare under such a trade-off.

Consider the invasion criteria (equations (2.3)) for the two species. Proceeding with the assumption that consumer  $i$  is the superior resource exploiter ( $R_{C_i}^* < R_{C_j}^* \Rightarrow F_j(R_{C_i}^*) < 0$  and  $I_{C_j}(C_i^*) < 0$ ), it can be seen that consumer  $j$  can invade when rare if  $|F_j(R_{C_i}^*)| < |I_{C_j}(C_i^* |_{C_j=0})|$ . In biological terms, consumer  $j$  can invade when rare as long as its superiority in interference is sufficient to maintain a positive per capita growth rate in spite of its inferiority in resource exploitation.

Consumer  $i$ , the superior resource exploiter ( $F_i(R_{C_j}^*) > 0$  and  $I_{C_i}(C_j^*) > 0$ ), can invade when rare if  $F_i(R_{C_j}^*) > I_{C_i}(C_j^* |_{C_i=0})$ . In biological terms, consumer  $i$ 's superiority in resource exploitation should be sufficient to maintain a positive per capita growth rate in the face of interference from consumer  $j$ .

In summary, when two species compete for a dynamic resource, a trade-off between exploitation and interference cannot lead to coexistence as long as interference involves only costs and no benefits. It can, however, change the mechanism of competitive exclusion from competitive dominance to a priority effect such that the species superior at interference competition can exclude the species superior at resource exploitation when it has a higher initial abundance. By contrast, when interference competition confers a benefit to the interacting species, coexistence is possible via a trade-off between exploitation and interference.

In § 2a,b, I investigate specific examples of each of these situations for both biotic and abiotic resources.

**(a) Case 1: interference and exploitative competition for a biotic resource**

Consider two consumer species that compete for a single, biotic resource. Resource dynamics occur on the same time-scale as those of the consumers and the resource species experiences self-limitation in the absence of consumption. The consumer species interact via both exploitation and interference.

The dynamics of the three species system are given by

$$\begin{aligned} \frac{dR}{dt} &= R \left( r \left( 1 - \frac{R}{K} \right) - a_1 C_1 - a_2 C_2 \right) \\ \frac{dC_1}{dt} &= C_1 \left( e_1 a_1 R - d_1 - (\alpha_{12} \pm \beta_1 \alpha_{21}) C_2 \right) \\ \frac{dC_2}{dt} &= C_2 \left( e_2 a_2 R - d_2 - (\alpha_{21} \pm \beta_2 \alpha_{12}) C_1 \right), \end{aligned} \tag{2.4}$$

where  $r$  and  $K$  are the growth rate and the carrying capacity of the resource, respectively, and  $a_i$  is the attack rate of consumer  $i$ . The quantity  $\alpha_{ij}$  is the per capita effect

of interference from consumer  $j$  on consumer  $i$ , and  $\beta_i\alpha_{ji}$  is the per capita cost or benefit to consumer  $i$  due to interference on consumer  $j$ . In the interests of analytical tractability, exploitation and interference are considered to be linear functions of resource and consumer abundance, respectively.

Equations (2.4) can be expressed in non-dimensionalized quantities. Non-dimensional analysis reduces the number of parameters that describe the system. It also sheds light on the scaling relations among the various processes that underlie system dynamics (Murray 1993). I use the following substitutions:

$$\begin{aligned} \hat{R} &= \frac{R}{K}, & \hat{C}_i &= \frac{C_i}{e_i K}, & \hat{a}_i &= \frac{a_i e_i K}{r}, \\ \hat{d}_i &= \frac{d_i}{r}, & \hat{\alpha}_{ij} &= \frac{\alpha_{ij} e_j K}{r}, & \hat{\beta}_i &= \frac{e_j \beta_i}{e_i}, \\ \tau &= rt \quad (i, j = 1, 2, i \neq j) \end{aligned}$$

to transform the original variables into non-dimensional quantities. These quantities have the advantage that the units used in the analysis are unimportant and the expressions ‘small’ and ‘large’ have clear relative meaning (Murray 1993). The non-dimensional time-metric  $\tau$  expresses time in terms of the resource population growth rate. This time-scaling allows for easy comparison among systems that vary in their natural time-scales. Resource abundance is expressed as a fraction of the resource carrying capacity, and varies from 0 to 1. A particular value of the carrying capacity may not be all that informative, but knowing how close the resource abundance is to carrying capacity is. For example,  $R \ll 1$  indicates that the resource is depressed well below the carrying capacity and that resource self-limitation is weak, whereas  $R \rightarrow 1$  indicates the opposite.

The abundances of the two consumers are scaled by their respective conversion efficiencies and the resource carrying capacity. Large  $C_i$  and small  $C_j$  signify that for any given resource carrying capacity, consumer  $i$  has a lower conversion efficiency than consumer  $j$ . The non-dimensionalized attack rates of the two consumers ( $\hat{a}_i$ ) depend on both resource growth rate and carrying capacity, highlighting the importance of resource parameters on consumer population growth.

The quantity  $\hat{d}_i$  is the density-independent mortality rate of consumer  $i$  relative to the resource growth rate. Again, a particular value of the consumer death rate may not have much meaning, but whether or not consumer death rate approaches or exceeds resource growth rate (i.e.  $\hat{d}_i \rightarrow 1$  or  $\hat{d}_i > 1$ , respectively) has direct consequences on consumer–resource dynamics. Similarly, the non-dimensionalized interference parameter  $\hat{\alpha}_{ij}$  shows that the per capita inhibitory effect of consumer  $j$  on consumer  $i$  (or vice versa) depends on its conversion efficiency as well as resource growth rate and carrying capacity.

The quantity  $\hat{\beta}_i$  is a metric that scales conversion efficiencies for resource exploitation and interference. For instance, large  $\hat{\beta}_i$  imply that for any value of  $\beta_i$ ,  $e_i \ll e_j$ , i.e. consumer  $i$  receives relatively little benefit from resource exploitation compared with consumer  $j$ .

I substitute the non-dimensional quantities into equations (2.4) and drop the hats for convenience. Unless otherwise noted, all parameters from this point on are

expressed as non-dimensional quantities. The substitutions yield the non-dimensional system

$$\begin{aligned} \frac{dR}{d\tau} &= R(1 - R) - a_1 RC_1 - a_2 RC_2 \\ \frac{dC_1}{d\tau} &= a_1 RC_1 - d_1 C_1 - I_{C_1} C_1 C_2 \\ \frac{dC_2}{d\tau} &= a_2 RC_2 - d_2 C_2 - I_{C_2} C_1 C_2 \end{aligned} \tag{2.5}$$

where  $I_{C_1} = \alpha_{12} \pm \beta_1 \alpha_{21}$  and  $I_{C_2} = \alpha_{21} \pm \beta_2 \alpha_{12}$ .

Equation (2.5) yields five feasible equilibria. The trivial equilibrium  $[(R^*, C_1^*, C_2^*) = (0, 0, 0)]$  is unstable for all positive values of  $R, C_1$  and  $C_2$ . The equilibrium with both consumers extinct  $(1, 0, 0)$  is stable if and only if neither consumer is able to maintain a positive growth rate when the resource is at carrying capacity. One or both consumers can invade when rare if  $d_i/a_i < 1$  ( $i = 1, 2$ ). There are two boundary (two-species) equilibria with the resource and consumer  $i$  in the absence of consumer  $j$   $(R^*, C_i^*, C_j^*) = (d_i/a_i, (a_i - d_i)/a_i^2, 0)$ , and a unique interior equilibrium with all three species present

$$\begin{aligned} R^* &= \frac{a_1 d_2 I_{C_1} + a_2 d_1 I_{C_2} + I_{C_1} I_{C_2}}{a_1 a_2 (I_{C_1} + I_{C_2}) + I_{C_1} I_{C_2}} \\ C_1^* &= \frac{I_{C_1} (a_2 - d_2) - a_2 (a_1 d_2 - a_2 d_1)}{a_1 a_2 (I_{C_1} + I_{C_2}) + I_{C_1} I_{C_2}} \\ C_2^* &= \frac{I_{C_2} (a_1 - d_1) - a_1 (a_2 d_1 - a_1 d_2)}{a_1 a_2 (I_{C_1} + I_{C_2}) + I_{C_1} I_{C_2}}. \end{aligned} \tag{2.6}$$

Three species coexistence requires that:

- (i) each consumer species is able to invade when the other species is at equilibrium with the resource; and
- (ii) the coexistence equilibrium is stable to small perturbations in the abundance of all three species.

From equations (2.5), the invasion criteria for the two consumers are  $a_2(a_1 d_2 - a_2 d_1) > (a_2 - d_2)I_{C_1}$  and  $a_1(a_2 d_1 - a_1 d_2) > (a_1 - d_1)I_{C_2}$ , respectively. Assume, without loss of generality, that consumer 1 is superior at resource exploitation i.e.  $d_1/a_1 < d_2/a_2 < 1$ .

When interference competition incurs only costs ( $I_{C_1} = \alpha_{12} + \beta_1 \alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} + \beta_2 \alpha_{12} > 0$ ),  $a_2 d_1 < a_1 d_2$  and  $a_1(a_2 d_1 - a_1 d_2) < (a_1 - d_1)I_{C_2}$ . Hence, consumer 2 cannot invade when rare. This is because inferiority in resource exploitation prevents consumer 2 from maintaining a positive growth rate even in the absence of interference. From equation (2.6) it can be seen that  $C_2^* > 0$  only if consumer 2 cannot invade when rare.

Consumer 1 can invade when rare provided  $a_2(a_1 d_2 - a_2 d_1) > (a_2 - d_2)I_{C_1}$ . In biological terms, consumer 1 can invade if the cost of interference on consumer 2 and effect of interference from consumer 2 are both small ( $I_{C_1} \rightarrow 0$ ), and consumer 2 is an inefficient exploiter of the resource ( $a_2 \sim d_2 \Rightarrow R_{C_2}^* \rightarrow 1$ ). As consumer 2 cannot invade at all, the outcome is competitive dominance by consumer 1, the superior resource exploiter.

If  $a_2(a_1 d_2 - a_2 d_1) < (a_2 - d_2)I_{C_1}$ , then consumer 1 cannot invade when rare. As can be seen from equations

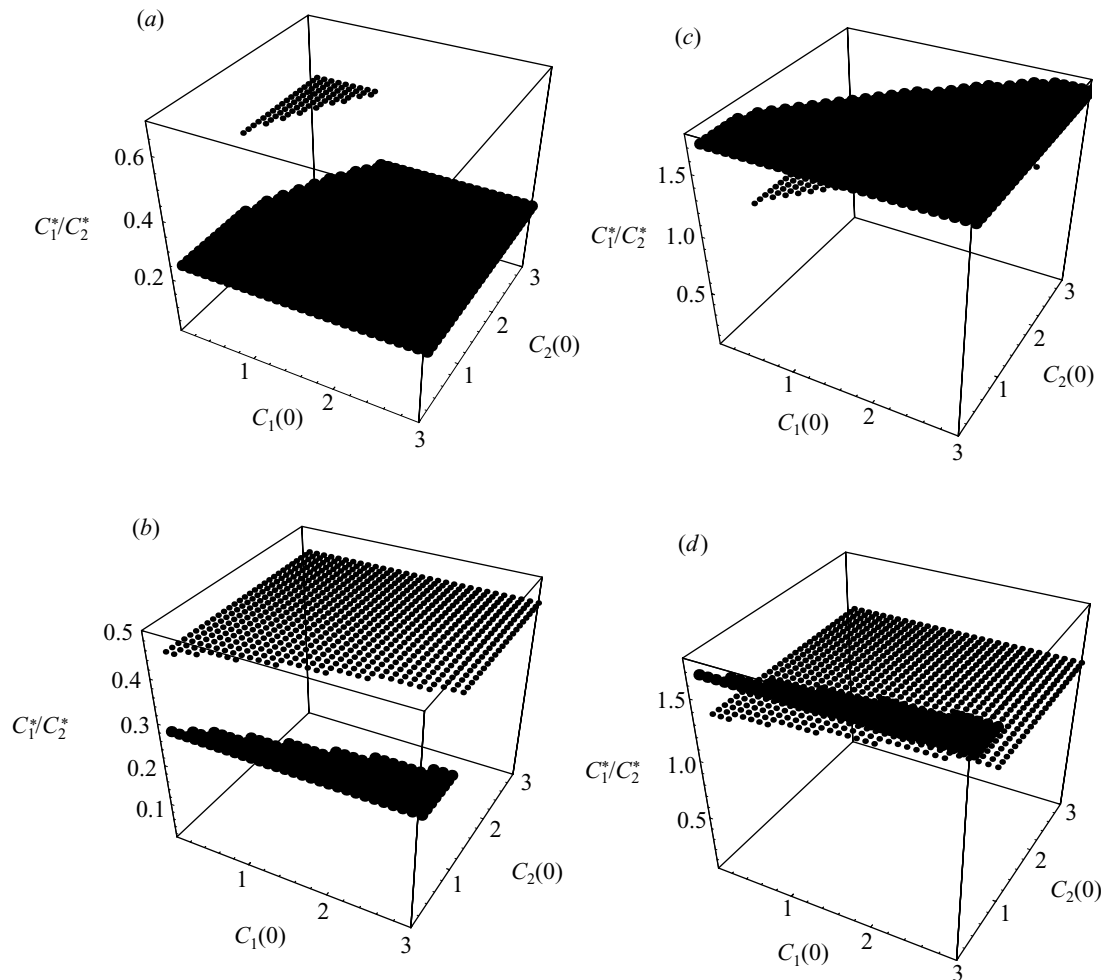


Figure 1. The range of initial abundances for which consumer 2 (inferior resource exploiter) excludes consumer 1 (superior resource exploiter) via a priority effect. The axes are, respectively, initial abundance of consumer species 1 [ $C_1(0)$ ], initial abundance of consumer species 2 [ $C_2(0)$ ], and equilibrium abundance of the species that excludes the other. The large black circles represent  $C_1^*$  and the small black circles,  $C_2^*$ . (a) and (b) are for a biotic resource and (c) and (d) for an abiotic resource. (a) and (c) represent a situation where consumer 2 cannot exclude consumer 1 except when its initial abundance is quite high. This occurs when the superior resource exploiter suffers little impact from interference from the inferior resource exploiter, and incurs little or no cost from interference on the latter. (b) and (d) represent a situation where consumer 2 can exclude consumer 1 even when its initial abundance is quite small. This occurs when the inferior resource exploiter has a strong effect on the superior resource exploiter by way of interference, and the latter suffers high costs due to its interference on the former. The parameter values used are: (a) and (c)  $a_1 = 3.5$ ,  $a_2 = 1.0$ ,  $d_1 = d_2 = 0.5$ ,  $\alpha_{12} = 1.2$ ,  $\alpha_{21} = 1.5$ ,  $\beta_1 = 0.9$ ,  $\beta_2 = 0.3$ ; (b) and (d)  $a_1 = 3.0$ ,  $a_2 = 1.5$ ,  $d_1 = d_2 = 0.5$ ,  $\alpha_{12} = 3.5$ ,  $\alpha_{21} = 0.1$ ,  $\beta_1 = 3.5$ ,  $\beta_2 = 0.1$ .

(2.6), this is the only condition under which  $C_1^* > 0$ . Thus, feasibility of the coexistence equilibrium [ $(C_1^*, C_2^*) > (0, 0)$ ] requires that neither consumer species can invade when rare. It is straightforward to show (see Appendix A) that the coexistence equilibrium is unstable when it exists. Under these conditions, the two species' boundary equilibria [ $(R^*, C_1^*, C_2^*) = (d_i/a_i, (a_i - d_i)/a_i^2, 0)$ ] ( $i, j = 1, 2, i \neq j$ ) are both globally stable. As neither consumer species can invade when rare, the outcome is a priority effect where the species with the higher initial abundance excludes the other.

How likely is it that a trade-off between exploitation and interference changes the outcome from competitive dominance of the superior resource exploiter to a priority effect? When the two consumer species exhibit large differences in resource exploitation efficiency, the range of initial conditions that lead to the exclusion of the superior exploiter becomes correspondingly small (figure 1). Even when inter-

ference competition is strong, exclusion of the superior resource exploiter is not guaranteed unless the initial abundance of the inferior resource exploiter is quite large.

When interference competition accrues benefits to both species (i.e.  $I_{C_i} = \alpha_{ij} - \beta_i \alpha_{ji}$  and  $I_{C_j} = \alpha_{ji} - \beta_j \alpha_{ij}$ ) mutual invisibility is possible provided  $I_{C_i}$  and  $I_{C_j}$  are not both positive. Assuming as before that consumer 1 is the superior resource exploiter (i.e.  $d_1/a_1 < d_2/a_2 < 1$ ), it can invade when rare if  $a_2(a_1 d_2 - a_2 d_1) > (a_2 - d_2)I_{C_1}$ . Consumer 2 can invade when rare if  $a_1(a_2 d_1 - a_1 d_2) > (a_1 - d_1)I_{C_2}$ . A necessary condition for mutual invisibility is that consumer 1 suffers a net loss from interference ( $I_{C_1} > 0$ ) while consumer 2 accrues a net benefit ( $I_{C_2} < 0$ ). Unlike the situation when interference incurs only costs, conditions for mutual invisibility are also the conditions for feasibility of the coexistence equilibrium [ $(C_1^*, C_2^*) > (0, 0)$ ; equations (2.6)]. Appendix A investigates the stability of the coexistence equilibrium.

The key results are as follows. When two consumer species compete for a single biotic resource via exploitative and interference competition, and interference involves mechanisms that incur a net cost, they cannot coexist at a point attractor even when the inferior resource exploiter is superior at interference. If the superior resource exploiter suffers little impact from interference from the inferior resource exploiter and/or incurs little or no cost from interference on the latter, then interference cannot alter the outcome of competitive dominance by the superior resource exploiter. If the cost and effect of interference are sufficiently high that the superior resource exploiter cannot invade a community consisting of the resource and the inferior resource exploiter, then a priority effect occurs and the consumer species with the higher initial abundance excludes the other.

By contrast, when interference involves mechanisms that provide a benefit to the interacting species, coexistence is possible provided competing species exhibit an interspecific trade-off between exploitation and interference.

**(b) Case 2: exploitative and interference competition for an abiotic resource**

The results in § 2a were derived for two consumer species that compete for a biotic resource. An important issue is whether the outcome of competition is altered when the limiting resource is abiotic such as an essential nutrient or a mineral.

The dynamics of two consumers competing for an abiotic resource are given by

$$\begin{aligned} \frac{dR}{dt} &= r(S - R) - a_1C_1R - a_2C_2R \\ \frac{dC_1}{dt} &= C_1 \left( e_1a_1R - d_1 - (\alpha_{12} \pm \beta_1\alpha_{21})C_2 \right) \\ \frac{dC_2}{dt} &= C_2 \left( e_2a_2R - d_2 - (\alpha_{21} \pm \beta_2\alpha_{12})C_1 \right), \end{aligned} \tag{2.7}$$

where  $r$  is the resource turnover rate and  $S$  is the supply concentration of the resource, which is akin to the resource carrying capacity (Tilman 1982; Frank & Amarasekare 1998). The other quantities are as defined in case 1 (§ 2a).

Equations (2.7) can be non-dimensionalized using the following substitutions:

$$\begin{aligned} \hat{R} &= \frac{R}{S}, & \hat{C}_i &= \frac{C_i}{e_i S}, & \hat{a}_i &= \frac{a_i e_i S}{r}, \\ \hat{d}_i &= \frac{d_i}{r}, & \hat{\alpha}_{ij} &= \frac{\alpha_{ij} e_j S}{r}, & \hat{\beta}_i &= \frac{e_j \beta_i}{e_i}, \end{aligned}$$

$\tau = rt \quad (i, j = 1, 2, i \neq j).$

Substituting the non-dimensional quantities into equations (2.7), and dropping the hats, yields the non-dimensional system

$$\begin{aligned} \frac{dR}{d\tau} &= 1 - R - a_1RC_1 - a_2RC_2 \\ \frac{dC_1}{d\tau} &= a_1RC_1 - d_1C_1 - I_{C_1}C_1C_2 \\ \frac{dC_2}{d\tau} &= a_2RC_2 - d_2C_2 - I_{C_2}C_1C_2, \end{aligned} \tag{2.8}$$

where  $I_{C_1} = \alpha_{12} \pm \beta_1\alpha_{21}$  and  $I_{C_2} = \alpha_{21} \pm \beta_2\alpha_{12}$ .

Equation (2.8) also yields five equilibria, of which the ones of interest are the two-species boundary equilibria  $(R^*, C_i^*, C_j^*) = (d_i/a_i, (a_i - d_i)/a_i d_i, 0)$  and the interior, coexistence equilibrium

$$\begin{aligned} R^* &= \frac{a_1d_2I_{C_1} + a_2d_1I_{C_2} - I_{C_1}I_{C_2} + \sqrt{(a_1d_2I_{C_1} + a_2d_1I_{C_2} - I_{C_1}I_{C_2})^2 + 4a_1a_2I_{C_1}I_{C_2}(I_{C_1} + I_{C_2})}}{2a_1a_2(I_{C_1} + I_{C_2})} \\ C_1^* &= \frac{a_2R^* - d_2}{I_{C_2}} \\ C_2^* &= \frac{a_1R^* - d_1}{I_{C_1}}. \end{aligned} \tag{2.9}$$

The invasion criteria for the two consumers are  $d_2(a_1d_2 - a_2d_1) > (a_2 - d_2)I_{C_1}$  and  $d_1(a_2d_1 - a_1d_2) > (a_1 - d_1)I_{C_2}$ , respectively. Assume, as before, that consumer 1 is superior at resource exploitation, i.e.  $d_1/a_1 < d_2/a_2 < 1$ .

When interference competition incurs only costs (i.e.  $I_{C_1} = \alpha_{12} + \beta_1\alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} + \beta_2\alpha_{12} > 0$ ), consumer 2 cannot invade when rare. Consumer 1 can invade when rare provided  $d_2(a_1d_2 - a_2d_1) > (a_2 - d_2)I_{C_1}$ , in which case the two-species equilibrium  $(R^*, C_1^*, C_2^*) = (d_1/a_1, (a_1 - d_1)/a_1^2, 0)$  is globally stable. If  $d_2(a_1d_2 - a_2d_1) < (a_2 - d_2)I_{C_1}$ , consumer 1 cannot invade when rare. Then the coexistence equilibrium is feasible but unstable, and both boundary equilibria are stable (see Appendix B).

When interference is beneficial (i.e.  $I_{C_1} = \alpha_{12} - \beta_1\alpha_{21}$  and  $I_{C_2} = \alpha_{21} - \beta_2\alpha_{12}$ ), consumer 1 can invade when rare if  $a_2(a_1d_2 - a_2d_1) > (a_2 - d_2)I_{C_1}$ . Consumer 2 can invade if  $a_1(a_2d_1 - a_1d_2) > (a_1 - d_1)I_{C_2}$ . As before,  $I_{C_1} > 0$ ,  $I_{C_2} < 0$  is a necessary condition for mutual invasibility, which in turn guarantees the feasibility of the coexistence equilibrium. The stability properties of the coexistence equilibrium are similar to those for a biotic resource (see Appendix B).

These results parallel those obtained for the biotic resource. A trade-off between resource exploitation and interference cannot lead to coexistence unless interference confers a benefit to one or both competing species.

**3. DISCUSSION**

The interplay between resource exploitation and interference is likely to have significant consequences for species' coexistence. Most theories on the subject, however, have focused on implicit resources (e.g. Case & Gilpin 1974; Schoener 1976, 1978; Case *et al.* 1979; Vance 1984). The few studies that incorporate dynamic resources have focused on unidirectional intraguild predation rather than interference competition (Hochberg & Holt 1990; Briggs 1993; Holt & Polis 1997; Diehl & Feisnel 2000). What is missing is a comparative analysis of how interference influences coexistence when the mechanism of interference changes from being costly to beneficial.

I have presented a model of exploitative and interference competition with explicit resource dynamics. The model considers both biotic and abiotic resources, and incorporates the two basic types of interference mechanisms (costly versus beneficial). It yields two key results. When the interference competition is costly, coexistence cannot occur even when competing species exhibit a

trade-off between interference and exploitation. The only possible outcomes are competitive dominance by the superior resource exploiter, or a priority effect with the outcome determined by the initial abundances of the two species. By contrast, when interference is beneficial, coexistence is possible via a trade-off between exploitation and interference. These results hold for both biotic and abiotic resources, suggesting that the outcome of exploitation and interference does not depend on the exact nature of resource dynamics.

The difference between competitive outcomes for the two forms of interference hinges directly on opportunities for niche partitioning. When interference is costly, it simply compounds the mutually negative effects caused by exploitative competition. As there is no opportunity for niche partitioning, the only possible outcomes are competitive dominance or a priority effect. When interference confers a benefit that can be converted into offspring, the species inferior at exploiting the primary resource effectively gains a second resource through interference on its competitor. It is this resource partitioning that leads to coexistence (Briggs 1993; Holt & Polis 1997).

The model makes several predictions about species competing for a single resource (biotic or abiotic) via exploitation and interference. First, species that engage in costly interference mechanisms (e.g. territoriality, overgrowth or undercutting, allelopathy and other forms of chemical competition) should not be able to coexist (assuming no other ameliorating forces exist; see below) unless they also engage in beneficial interference mechanisms (e.g. predation or parasitism).

Data from aquatic invertebrates and insects support this prediction. One example involves the filter-feeding copepod species *Diaptomus tyrrelli* and *Epischura nevadensis* that inhabit Lake Tahoe (Folt & Goldman 1981). Although *Diaptomus* is the superior filter feeder, allelopathy from *Epischura* can reduce its feeding by 60%. Interference, however, is not restricted to allelopathy; *Epischura* also preys on nauplii and small copepodids of *Diaptomus*. These are exactly the conditions under which the model predicts coexistence. If benefits from predation outweigh the costs of allelopathy, and allelopathy has a strong effect on the superior filter feeder, then coexistence should be possible. A second example comes from insect host-parasitoid systems. Coexistence of multiple parasitoid species on a single host species appears to involve interference mechanisms (e.g. hyperparasitism or within-host larval competition) that provide a benefit to the inferior exploitative competitor (Zwolfer 1971; Force 1970; Munster-Swendsen 1979; Mills 1994; Amarasekare 2000).

The differential effects of the two interference mechanisms on coexistence have implications for species diversity. In general, one would expect communities in which species engage in costly interference mechanisms to exhibit lower diversity than communities in which species employ beneficial interference mechanisms. In fact, species that can coexist in the former case should be those that are immune to interference from co-occurring species. Case & Gilpin (1974) point out that interference competition is unlikely to evolve unless it confers some benefit or at least has a low cost-to-effect ratio such that the fitness of

the species or genotype is increased as a result of interference.

The second prediction of the model concerns competitive displacement of native biota by invasive species. Displacement can occur in two ways. The first mechanism, exclusion via competitive dominance, applies to both costly and beneficial interference. An invasive species that is superior at both resource exploitation and interference can exclude a native species regardless of whether interference is costly or beneficial. The second mechanism, exclusion via a priority effect, applies only to costly interference. An invasive species that is superior at interference can exclude a native species that is superior at resource exploitation, provided it has a higher initial abundance. The greater the effects of interference relative to the exploitation advantage of the native species, the smaller the initial abundance required. Two corollaries follow. First, if the native species is the superior resource exploiter, and interference competition involves costs and no benefits, it should be immune to invasion by an inferior resource exploiter even when the latter is superior in interference. Second, an invasive species that is inferior at resource exploitation but superior at beneficial interference should be able to invade but will be unable to exclude the native species. Under these conditions the native and exotic species should coexist.

Empirical evidence supports the model prediction that successful invasive species should be superior at both exploitation and interference. For example, the exotic grass *Centaurea maculosa* Lam. has excluded native plants completely and developed dense monospecific stands (Ridenour & Callaway 2001). *C. maculosa* interferes with the native bunchgrass *Festuca idahoensis* Elmer via root-mediated allelopathy. However, *C. maculosa* outperforms *F. idahoensis* even when allelopathic mechanisms are inhibited, suggesting that it is also superior at resource competition. The invasive fire ant *Solenopsis invicta* Buren has extirpated many a native ant community in the southeastern USA (Porter & Savignano 1996). The success of this species is attributed to its superiority in both resource exploitation and aggressive interference. A third example involves an invasive vertebrate species. The displacement of the native gecko *Lepidodactylus lugubris* by the common house gecko *Hemidactylus frenatus* throughout the Pacific (Case *et al.* 1994) is attributed to the latter's aggressive dominance. However, *H. frenatus* also appears to be a more efficient forager of the common resource (insects), which may explain its ability to exclude *L. lugubris* from large regions.

As these data show, exclusion of a native species by an exotic that is superior in both exploitation and interference is likely to occur in nature. Alternatively, exclusion by virtue of greater initial abundance of an aggressive exotic seems less likely because invasive species typically have lower initial abundances than native species. However, exclusion via a priority effect may occur in native species that are inherently rare (e.g. narrow endemics) or whose abundances have declined due to anthropogenic or other factors. The interaction between the endemic thistle *Cirsium vinaceum* [Woot. & Standl.] and the invasive exotic *Dispacus sylvestris* [Dipsacaceae] (Huenneke & Thomson 1995) is suggestive of this situation. The two species show similar germination responses and exhibit few demo-

graphic differences. Although *D. sylvestris* is superior at interference competition, it appears unable to establish in dense stands of *C. vinaceum*. This suggests that initial abundances may play a part in *D. sylvestris*'s ability to displace *C. vinaceum*.

These examples illustrate situations where invasive species extirpate native biota. There are also situations in which exotic species become part of the community they invade (Kareiva (1996) and references therein). While such situations may reflect ongoing, but slow, competitive exclusion, it is also possible that invaders coexist with native species by virtue of superiority in beneficial interference (e.g. Usher *et al.* 1992; Dick 1996). One would expect such coexistence to be more prevalent in animal rather than plant communities because beneficial interference is more likely to operate in animals than plants.

The result that coexistence is impossible when interference competition is costly raises the question of whether there are factors ignored by the model that could lead to coexistence. One possibility is self-limitation in the competing species. In models that consider exploitation and interference with implicit resource dynamics (e.g. Case & Gilpin 1974; Vance 1984) coexistence is possible if interspecific interference is greater than interspecific interference for both species, and the strength of self-limitation outweighs the advantage to the superior resource exploiter. Self-limitation has not been investigated in models of exploitation and interference with explicit resource dynamics (in part because the consumers are considered to be limited by the resource (Gurney & Nisbet 1998)), but is likely to lead to the same outcome as the implicit resource models given that the nature of resource dynamics does not appear to influence the outcome of competition.

In the absence of self-limitation, species engaging in exploitative and interference competition for a single resource are unlikely to coexist unless ameliorating forces external to the competitive interaction also operate. There are several possibilities. First, resource fluctuations could allow coexistence if the consumers partition the resource such that the superior resource exploiter is more efficient at low resource abundances and the inferior exploiter at high abundances (Armstrong & McGehee 1976, 1980). Second, keystone predation or parasitism on the superior resource exploiter can lead to coexistence (Paine 1966; Sih *et al.* 1985; Navarrete & Menge 1996). Third, competing species that exhibit a priority effect in isolation can coexist in a patchy environment provided local populations are linked by small amounts of dispersal and there is spatial variation in initial abundances (Levin 1974; Yu & Wilson 2001); species that exhibit competitive dominance can coexist via small amounts of dispersal provided there is spatial heterogeneity in competitive ability (Amarasekare & Nisbet 2001; Codeco & Grover 2001). While it is plausible that these mechanisms allow the coexistence of species competing for a dynamic resource, none of them has been investigated in models of exploitative and interference competition with explicit resource dynamics. Another important issue concerns how the outcome of exploitation and interference is altered when more than two consumer species are involved, and when consumers compete for more than one resource. Given the ubiquity of interference competition in natural

communities, investigations of these possibilities constitute an important future direction for competition theory.

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**APPENDIX A: LOCAL STABILITY ANALYSES FOR CASE 1: EXPLOITATIVE AND INTERFERENCE COMPETITION FOR A BIOTIC RESOURCE**

The Jacobian matrix of equations (2.4) is given by

$$\begin{bmatrix} 1 - 2R^* - a_1C_1^* - a_2C_2^* & -a_1R^* & -a_2R^* \\ a_1C_1^* & 0 & -C_1^*I_{C_1} \\ a_2C_2^* & -C_2^*I_{C_2} & 0 \end{bmatrix},$$

where  $I_{C_1} = \alpha_{12} \pm \beta_1\alpha_{21}$  and  $I_{C_2} = \alpha_{21} \pm \beta_2\alpha_{12}$ .

The eigenvalues of the Jacobian are the roots of the characteristic equation

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \tag{A 1}$$

where

$$A_1 = R^*, \tag{A 2}$$

$$A_2 = R^*(a_1^2C_1^* + a_2^2C_2^*) - C_1^*C_2^*I_{C_1}I_{C_2}, \tag{A 3}$$

$$A_3 = -R^*C_1^*C_2^*(a_1a_2(I_{C_1} + I_{C_2}) + I_{C_1}I_{C_2}). \tag{A 4}$$

The Routh–Hurwitz criteria for the stability of the three species equilibrium are  $A_1 > 0$ ,  $A_3 > 0$  and  $A_1A_2 - A_3 > 0$ . By inspection, it can be seen that when  $I_{C_1} = \alpha_{12} + \beta_1\alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} + \beta_2\alpha_{12} > 0$ ,  $A_1 > 0$  but  $A_3 < 0$  always. Hence, the coexistence equilibrium is unstable when it exists.

When  $I_{C_1} = \alpha_{12} - \beta_1\alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} - \beta_2\alpha_{12} < 0$  (or vice versa),  $A_3 > 0$  if  $a_1a_2(I_{C_1} + I_{C_2}) + I_{C_1}I_{C_2} < 0$ . The condition  $A_1A_2 - A_3 > 0$  is met if

$$R^* + \frac{a_1a_2C_1^*C_2^*}{a_1^2C_1^* + a_2^2C_2^*}(I_{C_1} + I_{C_2}) > 0. \tag{A 5}$$

The condition  $A_1A_2 - A_3 = 0$  determines oscillatory instability of the three-species system, i.e. the transition from damped to persistent oscillations (Gurney & Nisbet 1998). When  $A_1A_2 - A_3 < 0$ , the consumers may still coexist in a pattern of unstable oscillations. This has been demonstrated for a two consumer–single resource system in which only one consumer species benefits from interference (Holt & Polis 1997).

**APPENDIX B: LOCAL STABILITY ANALYSES FOR CASE 2: EXPLOITATIVE AND INTERFERENCE COMPETITION FOR AN ABIOTIC RESOURCE**

The Jacobian matrix of equations (2.7) is given by

$$\begin{bmatrix} -1 - a_1C_1^* - a_2C_2^* & -a_1R^* & -a_2R^* \\ a_1C_1^* & 0 & -C_1^*I_{C_1} \\ a_2C_2^* & -C_2^*I_{C_2} & 0 \end{bmatrix},$$



where  $I_{C_1} = \alpha_{12} \pm \beta_1 \alpha_{21}$  and  $I_{C_2} = \alpha_{21} \pm \beta_2 \alpha_{12}$ .

The Routh–Hurwitz criteria are

$$A_1 = \frac{1}{R^*}, \quad (\text{B } 1)$$

$$A_2 = R^*(a_1^2 C_1^* + a_2^2 C_2^*) - C_1^* C_2^* I_{C_1} I_{C_2}, \quad (\text{B } 2)$$

$$A_3 = -a_1 a_2 R^* C_1^* C_2^* I_{C_1} - a_1 a_2 R^* C_1^* C_2^* I_{C_2} - \frac{C_1^* C_2^* I_{C_1} I_{C_2}}{R^*}, \quad (\text{B } 3)$$

when  $I_{C_1} = \alpha_{12} \pm \beta_1 \alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} \pm \beta_2 \alpha_{12} > 0$ ,  $A_1 > 0$  but  $A_3 < 0$  always. Hence, the coexistence equilibrium is unstable when it exists.

When  $I_{C_1} = \alpha_{12} - \beta_1 \alpha_{21} > 0$  and  $I_{C_2} = \alpha_{21} - \beta_2 \alpha_{12} < 0$  (or vice versa),  $A_3 > 0$  if  $a_1 a_2 R^{*2} (I_{C_1} + I_{C_2}) + I_{C_1} I_{C_2} < 0$ . The  $A_1 A_2 - A_3 > 0$  is met if

$$a_1^2 C_1^* + a_1^2 C_2^* + a_1 a_2 C_1^* C_2^* (I_{C_1} + I_{C_2}) > 0. \quad (\text{B } 4)$$

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.