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Population ecology

A keystone effect for parasites in intraguild predation?

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Intraguild predation (IGP) is common in communities, yet theory suggests it should not often persist and coexistence of participating species should be rare. As parasitism can play keystone roles in interactions between competitors, and between predators and prey, here we examine the role of parasites in maintaining IGP. We used numerical exploration of population dynamic equations to determine coexistence and exclusion zones for two species engaged in IGP with shared parasitism. We demonstrate that parasitism increases the range of conditions leading to coexistence when the parasite exerts a greater deleterious effect on the 'stronger' species in terms of the combined effects of competition and predation. Such a parasite can enable an inferior competitor that is also the less predatory to persist, and may actually lead to numerical dominance of this species.

Keywords: coexistence; intraguild predation; keystone species; parasite-mediated

1. INTRODUCTION

Ecologists need to understand the processes involved in promoting population stability and species coexistence; recently, there has been increasing interest in the influence of parasitism on these processes (Thomas *et al.* 2005; Holt & Dobson 2006). One method of characterizing a community is to decompose it into subsets of strongly interacting species (community modules: Holt 1997). Although some modules have been examined in depth empirically and theoretically, there are still many areas of uncertainty, particularly where modules involving parasitism are concerned (Hatcher *et al.* 2006; Holt & Dobson 2006).

A frequent component module in communities is intraguild predation (IGP), predation between members of an ecological guild (species that exploit the same resources in similar ways, i.e. potential competitors; Holt & Polis 1997; Rosenheim 2007). IGP can be uni- or bidirectional; it often occurs among closely related species but can occur between disparate taxa, and is often associated with cannibalism (Dick *et al.* 1993; Rosenheim 2007). Recent analysis indicates that IGP is widespread in real food webs (Arim & Marquet 2004). However, this presents a paradox as mathematical models predict that IGP modules will frequently be unstable in ecological time (Holt 1997). For IGP to persist, the less predatory of the two species must be strongly competitively dominant, otherwise it will be eliminated by the stronger predator (Holt & Polis 1997). Yet, in many real systems, it is unclear whether the predicted pattern is upheld (Rosenheim 2007).

The frequency of trophic links involving parasites testifies to their potential importance in community ecology and ecosystem function (Hudson *et al.* 2006). Parasitism can play keystone roles in interactions between competitors and in predator–prey systems (Thomas *et al.* 2005; Hatcher *et al.* 2006). Here, we examine theoretically if parasitism stabilizes IGP through its effects on the competitive and predatory components of the association. We present a mathematical model combining IGP and parasitism, and ask if shared parasitism (where two species engaged in IGP are hosts of the same parasite species) can increase the range of conditions leading to coexistence.

2. THE MODEL

Our approach follows Dick *et al.* (1993) who examined mutual IGP and cannibalism, and Bowers & Turner (1997) concerning interspecific competition with shared parasitism. We assume overlapping generations for two host species with Lotka–Volterra competition; IGP is a linear function of the densities of both host species; parasite transmission is proportional to the densities of susceptible and infected individuals (i.e. it follows standard mass action principles), and the net rate of loss of infected individuals is composed of mortality due to parasitism, cannibalism and IGP. The model is broadly applicable to a range of invertebrate host–microparasite systems.

Our equations describing changes in population densities of two host species are

$$\frac{dN_1}{dt} = r_1N_1(1-\alpha_{11}N_1-\alpha_{12}N_2)-(1-e)k_1N_1^2 - (\gamma_{12}-e\gamma_{21})N_1N_2-\Omega_1I_1, \quad (2.1)$$

$$\frac{dI_1}{dt} = \beta_{11}(N_1-I_1)I_1+\beta_{12}(N_1-I_1)I_2 - (1-e)k_1N_1I_1-N_2I_1(\gamma_{12}-e\gamma_{21})-\Omega_1I_1, \quad (2.2)$$

$$\frac{dN_2}{dt} = r_2N_2(1-\alpha_{21}N_1-\alpha_{22}N_2)-(1-e)k_2N_2^2 - (\gamma_{21}-e\gamma_{12})N_1N_2-\Omega_2I_2, \quad (2.3)$$

$$\frac{dI_2}{dt} = \beta_{21}(N_2-I_2)I_1+\beta_{22}(N_2-I_2)I_2-(1-e)k_2N_2I_2 - N_1I_2(\gamma_{21}-e\gamma_{12})-\Omega_2I_2, \quad (2.4)$$

where N_i, total population density of host species i; I_i, density of the infected subpopulation of host species i; r_i, intrinsic *per capita* population growth rate; α_{ij}, competition coefficient (the effect on species i of species j); e, conversion efficiency of victims of predation or cannibalism into offspring; k_i, instantaneous rate of cannibalism; γ_{ij}, instantaneous rate of predation of species j on species i; Ω_i, *per capita* rate of parasite-induced mortality; and β_{ij}, parasite transmission efficiency to species i from species j.

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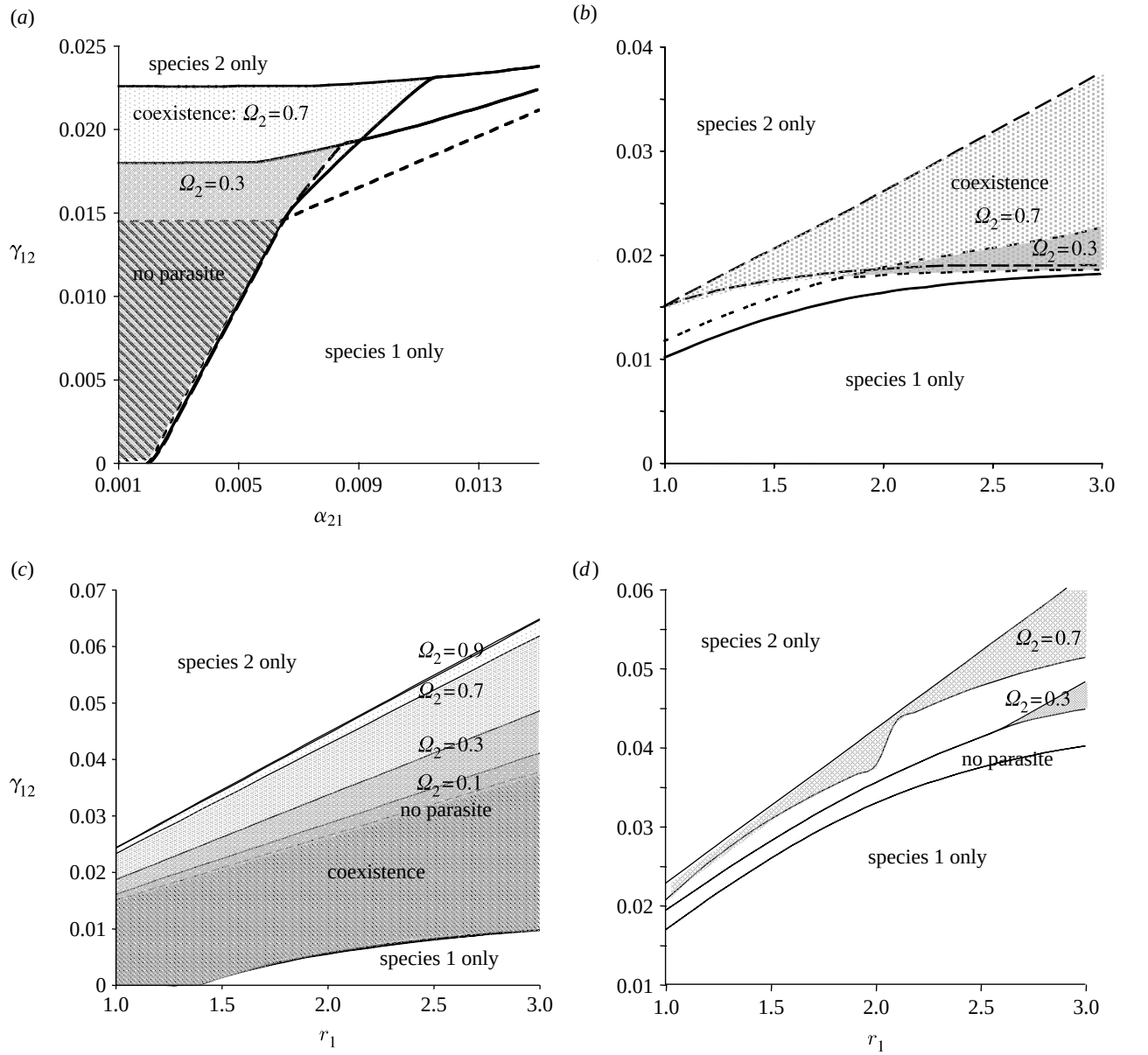

Figure 1. Zones of coexistence and exclusion for two species with a shared parasite and IGP. (*a*) IGP by species 2 against interspecific competition by species 1; (*b–d*) IGP by species 2 against intrinsic growth rate of species 1. In each case, regions of coexistence are shaded with parasite virulence to species 2 Ω_2 as marked. (*a*) $\alpha_{12}=0.0005$, $\alpha_{22}=\alpha_{11}=0.005$, $r_1=r_2=1$, $k_1=k_2=0.01$, $e=0.3$, $\beta_{11}=0.01$, $\beta_{12}=\beta_{21}=0.001$, $\beta_{22}=0.01$, $\Omega_1=0.1$, $\gamma_{21}=0.01$. Species 1 is superior at both competition and predation for $\alpha_{21}>0.005$ and $\gamma_{12}<0.01$; it persists alone below the lower boundary and is excluded above the upper boundary. (*b*) Symmetric interspecific competition without cannibalism ($\alpha_{21}=0.0005$, $k_1=k_2=0$, other parameters as in (*a*)); there is no coexistence without the parasite. (*c*) Symmetric interspecific competition with cannibalism ($k_1=k_2=0.01$; other parameters as in (*b*)). (*d*) Strong asymmetric competition (species 1 is the superior competitor, $\alpha_{11}=\alpha_{12}=0.0005$, $\alpha_{21}=\alpha_{22}=0.005$; other parameters as in (*c*)); there is no coexistence without the parasite.

As equations (2.1)–(2.4) cannot be solved algebraically (see also Bowers & Turner (1997) for a similar system without predation), population dynamic outcomes were examined using numerical exploration of the parametrized equations, with initial populations ($N_1=N_2=10$) iterated to equilibrium. Parameter values at which transitions between stable states occurred were bounded by binary search to an accuracy of (>) 5 decimal places.

Figure 1 characterizes the population dynamic outcomes for two competing species that share a parasite and perform mutual, asymmetric predation. Parasite virulence was kept relatively low in species 1 ($\Omega_1=0.1$), but set to higher levels in species 2. In the absence of parasitism, the results support Holt & Polis (1997): coexistence is most likely when the superior predator is the inferior competitor (bottom left of figure 1*a*; note, however, that our results include the effect of cannibalism). Moving along the *x*-axis of figure 1*a*, as interspecific competition by species 1 (α_{21}) increases, the outcome changes from coexistence to exclusion of species 2. Moving up the *y*-axis, as predation by species 2 (γ_{12}) increases, the outcome changes from coexistence to exclusion of species 1. Parasitism increases the range of conditions leading to coexistence, raising the level of IGP that can be tolerated by the weaker predator. At strong competition–IGP combinations (top right of graph), coexistence cannot occur; exclusion is determined by the relative strengths of IGP and competition. In the top left of figure 1*a*,

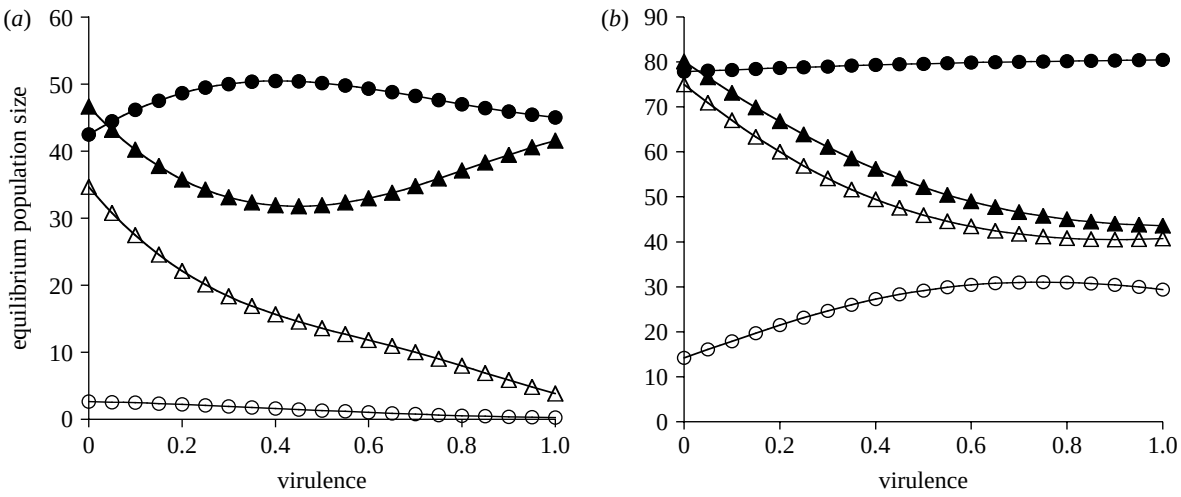

Figure 2. Equilibrium population sizes in relation to parasite virulence. (*a*) Parasites of intermediate virulence reverse the numerical dominance of a superior competitor and predator ($\alpha_{11}=0.005$, $\alpha_{12}=0.001$, $\alpha_{22}=0.005$, $\alpha_{21}=0.0045$, $\gamma_{12}=0.012$, $\gamma_{21}=0.01$; other parameters are the same as given in figure 1*a*). Filled circle, N_1; open circle, I_1; filled triangle, N_2; open triangle, I_2. (*b*) Effect of parasitism on the competitive and predatory components of IGP. Equilibrium population sizes ($\alpha_{11}=\alpha_{22}=0.005$, $\alpha_{12}=\alpha_{21}=0.0005$) are plotted in the presence ($\gamma_{12}=0.015$, $\gamma_{21}=0.01$) and absence ($\gamma_{12}=\gamma_{21}=0$) of IGP (other parameters are the same as given in figure 1*a*). The numerical impact of IGP on species 2 is slight, but the interaction between parasitism and IGP has a marked impact on species 1. Filled circle, N_1 (no IGP); open circle, N_1 (with IGP); filled triangle, N_2 (no IGP); open triangle, N_2 (with IGP).

species 1 is the weaker competitor and predator. Despite this, coexistence is sometimes possible even in the absence of parasitism, owing to the stabilizing influence of cannibalism (Rosenheim 2007). However, presence of a shared parasite that is more virulent in the superior species (2) dramatically increases the range of conditions leading to coexistence.

Competition coefficients were set to reflect definitive patterns of intra- and interspecific competition within the Lotka–Volterra framework. With α_{ij} fixed, the phase space was characterized with respect to the intrinsic growth rate of species 1 (r_1) and the level of IGP by species 2 (γ_{12}). When intraspecific competition exceeds interspecific competition for both species, Lotka–Volterra theory predicts coexistence in the absence of other forces. However, when mutual IGP is included, coexistence cannot occur in the absence of parasitism for the parameter ranges studied here (figure 1*b*). Once a shared parasite is included, coexistence occurs for sufficiently high r_1, counterbalancing strong predation by species 2. As parasite virulence for the superior predator is increased, the range of conditions leading to coexistence increases (figure 1*b*). If cannibalism is also included, coexistence occurs without parasitism, but parasitism increases the parameter range for coexistence (figure 1*c*). Higher virulence in the superior predator further promotes coexistence, raising the level of IGP that the inferior predator can tolerate before it is excluded. In figure 1*d*, intraspecific competition is weak for species 1 and strong for species 2 and interspecific competition is weak against species 1 and strong against species 2 ($\alpha_{12}<\alpha_{22}$ and $\alpha_{11}<\alpha_{21}$). Under these conditions, the Lotka–Volterra model predicts that species 1 will exclude species 2. The inclusion of cannibalism and IGP does not promote coexistence, but parasitism enables coexistence within a restricted range (the shape of the boundary was consistent when checked at a finer resolution). The zone for coexistence is narrower here compared with figure 1*a* where intraspecific competition was stronger than interspecific competition for both species.

3. DISCUSSION

Parasitism can influence both competitive and predatory interactions (Hatcher *et al.* 2006; Holt & Dobson 2006). Here we show theoretically that parasitism can also influence the outcome of IGP. We demonstrate that a shared parasite can increase the zone of coexistence for intraguild predators; coexistence is promoted if the parasite exerts a greater deleterious effect on the 'stronger' species in terms of the combined effects of competition and predation. Since relatively small levels of IGP override the effects of competition (Dick *et al.* 1993), we predict that parasitism is most likely to stabilize IGP if the stronger predator suffers more from the effects of the parasite. In this case the parasite acts as a keystone species promoting coexistence (Holt & Dobson 2006). If, however, the parasite has a greater negative impact on the 'weaker' species, most probably the least predatory, we predict that parasitism will exacerbate its decline, further destabilizing the module.

Within the zones for coexistence described here, both species maintain appreciable population frequencies away from the boundaries for species exclusion. In some cases, shared parasitism can lead to reversed numerical dominance with the weaker species attaining the higher population size (figure 2*a*). This process has an element of apparent competition (Bowers & Turner 1997; Thomas *et al.* 2005), as seen in figure 2*b*. In the absence of IGP, parasite-induced mortality reduces the equilibrium population size of species 2, allowing a slight increase in population size for species 1. Once IGP is included, an additional process occurs (figure 2*b*): parasitism reduces the predatory impact of species 2

via its effects on population size, enabling an increase in the equilibrium population size of species 1; similar effects occur in linear food chains (Holt 1997; Holt & Dobson 2006).

Parasite-mediated IGP may be another process influencing community structure and the outcome of biological invasions (Prenter *et al.* 2004; Thomas *et al.* 2005). This possibility has been examined empirically in a guild of native and invasive amphipods (MacNeil *et al.* 2003*a*,*b*). The native *Gammarus duebeni celticus* is under threat in Northern Ireland from the following three invasive species: *Gammarus pulex* (the stronger IG predator), *Gammarus tigrinus* and *Crangonyx pseudogracilis* (both smaller and weaker IG predators). IGP theory predicts that *G. pulex* should eliminate *G. d. celticus* and that invasions by *G. tigrinus* and *C. pseudogracilis* should fail. However, two parasite species may play keystone roles in this system. The microsporidian *Pleistophora mulleri* may facilitate invasion by the smaller species; it has no direct effect on the survival of *G. d. celticus*, but infected adults are less likely to prey on the two smaller invaders (however, infection also increases vulnerability to predation by *G. pulex*; MacNeil *et al.* 2003*a*). In addition, the acanthocephalan *Echinorynchus truttae* may promote coexistence as infection of *G. pulex* reduces its predation on *G. d. celticus* (MacNeil *et al.* 2003*b*). Other papers on apparent competition in arthropods also speculate that parasite-mediated IGP might be important (Hatcher *et al.* 2006).

We may have underestimated the influence of parasitism in our model as the effects of parasitism on the competing species are entirely population density-mediated. However, in many systems (including the *Gammarus* system above: MacNeil *et al.* 2003*a*), parasites modify the competitive or predatory traits of hosts via effects on behaviour or morphology. Such trait-mediated indirect effects (Werner & Peacor 2003) can potentially have powerful effects on the dynamics of species interactions (Hatcher *et al.* 2006) and warrant further study.

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