

# Productivity, dispersal and the coexistence of intraguild predators and prey

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## Abstract

A great deal is known about the influence of dispersal on species that interact via competition or predation, but very little is known about the influence of dispersal on species that interact via both competition *and* predation. Here, I investigate the influence of dispersal on the coexistence and abundance–productivity relationships of species that engage in intraguild predation (IGP: competing species that prey on each other). I report two key findings. First, dispersal enhances coexistence when a trade-off between resource competition and IGP is strong and/or when the Intraguild Prey has an overall advantage, and impedes coexistence when the trade-off is weak and/or when the Intraguild Predator has an overall advantage. Second, the Intraguild Prey's abundance–productivity relationship depends crucially on the dispersal rate of the Intraguild Predator, but the Intraguild Predator's abundance–productivity relationship is unaffected by its own dispersal rate or that of the Intraguild Prey. This difference arises because the two species engage in both a competitive interaction as well as an antagonistic (predator–prey) interaction. The Intraguild Prey, being the intermediate consumer, has to balance the conflicting demands of resource acquisition and predator avoidance, while the Intraguild Predator has to contend only with resource acquisition. Thus, the Intraguild Predator's abundance increases monotonically with resource productivity regardless of either species' dispersal rate, while the Intraguild Prey's abundance–productivity relationship can increase, decrease, or become hump-shaped with increasing productivity depending on the Intraguild Predator's dispersal rate. The important implication is that a species' trophic position determines the effectiveness of dispersal in sampling spatial environmental heterogeneity. The dispersal behavior of a top predator is likely to have a stronger effect on coexistence and spatial patterns of abundance than the dispersal behavior of an intermediate consumer. © 2006 Elsevier Ltd. All rights reserved.

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## 1. Introduction

The interplay between dispersal and species interactions is key to diversity maintenance in spatially structured environments (Levin, 1974; Holt, 1993; Leibold et al., 2004, 2005). Much is known about the impact of dispersal on communities characterized by non-trophic species interactions (e.g. competition, mutualisms; Bolker and Pacala, 1999; Amarasekare, 2004) and pairwise trophic interactions (e.g. predator–prey, host–parasitoid; Holt, 1985; Murdoch et al., 1992; Jansen, 2001). In contrast, very little is known about the effect of dispersal on communities

characterized by both trophic and non-trophic interactions. Yet, such multi-trophic interactions are the building blocks of all natural communities.

Multi-trophic communities are interesting because species within a trophic level can coexist in the absence of dispersal, but the operation of such coexistence mechanisms varies over space and time. There is thus the potential for simultaneous operation of local and spatial coexistence mechanisms, a situation that is typically not considered in spatial ecology. Intraguild predation (IGP), a multi-trophic interaction that is widespread in nature (Polis et al., 1989; Arim and Marquet, 2004), illustrates this situation well. Intraguild Predation results when two consumer species competing for a common resource also engage in a trophic interaction where one species can prey on or parasitize its

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competitor (e.g. Polis et al., 1989; Arim and Marquet, 2004). The two consumer species can coexist in the absence of dispersal provided they exhibit a trade-off between competition and predation: the inferior resource competitor gains a second resource by preying on its competitor. A key aspect of this trade-off is that its expression depends on the productivity of the basal resource. When resource productivity is low, exploitative competition dominates and only the superior resource competitor can persist; when resource productivity is high, predation dominates and only the intraguild predator (inferior resource competitor) can persist (Holt and Polis, 1997; Diehl and Feissel, 2000, 2001; Mylius et al., 2001). Hence, the trade-off between competition and predation can only be expressed at an intermediate level of resource productivity. Since coexistence is at best restricted, one would expect dispersal to play an important role in maintaining diversity in IGP systems.

Here, I investigate the role of dispersal in communities exhibiting IGP. I consider the most restrictive case for coexistence: a community that experiences spatial variation in resource productivity but no spatial variation in the life history traits of the consumers themselves. The consumer species can however sample spatial variation in resource productivity via dispersal. This study thus makes two novel contributions. First, it presents a theoretical framework for spatial dynamics of communities structured by competition and predation, a little studied area of spatial community ecology. Second, it investigates the impact of dispersal on the abundance–productivity relationships of interacting species, an aspect of spatial coexistence that has not previously been investigated.

## 2. The model

Consider a spatially structured environment consisting of a number of patches of suitable habitat embedded in an inhospitable matrix. Examples include patchily distributed host plants that support guilds of insect herbivores and their natural enemies (Harrison et al., 1995; Lei and Hanski, 1998; Amarasekare, 2000) and pond systems that support multi-trophic invertebrate communities (Chase and Leibold, 2002; Chase, 2003; Chase and Ryberg, 2004). There is permanent spatial heterogeneity in habitat quality as would occur if there were differences in soil, nutrient availability or moisture content that would make some host plant patches or ponds more productive than others. These spatial differences are assumed to occur within a spatial scale that can be traversed by the organisms occupying these habitats. For instance, host plant patches on opposing slopes of a canyon may be of different quality but in sufficiently close proximity to allow insects to disperse between patches.

Within each habitat patch we have a multi-trophic interaction characterized by unidirectional IGP: two consumer species compete for a common resource but one species (IGPredator) can prey on or parasitize its competitor (IGPrey). Examples of unidirectional IGP

include aquatic invertebrates such as amphipods (MacNeil et al., 2004) and larval caddisflies (Wissinger et al., 1996), and insect parasitoids engaging in multi-parasitism where within-host larval competition results in one species being consumed by another (Zwolfer, 1971; Polis et al., 1989; Amarasekare, 2000, 2003; Arim and Marquet, 2004). Coexistence of IGPrey and IGPredator can occur within a habitat patch (e.g. pond, host plant patch) if there is an interspecific trade-off that leads to resource partitioning: the IGPrey is the superior competitor for the basal resource but the IGPredator gains an additional resource by preying on or parasitizing the IGPrey. The expression of this trade-off, however, depends on the productivity of the basal resource. At very low or very high-productivity one species gains an overall advantage and excludes the other (Holt and Polis, 1997). Thus, coexistence is possible via local niche partitioning, but the operation of the niche partitioning mechanism is variable in space.

We thus have a patchy and spatially heterogeneous landscape where the outcome of IGP within a given habitat patch is determined by the ambient level of resource productivity. The simplest mathematical representation of such a system is a three-patch model with each patch at a level of resource productivity that leads to one of three outcomes: (i) resource productivity sufficiently low that the IGPredator cannot invade when rare, (ii) resource productivity sufficiently high that the IGPredator excludes the IGPrey, and (iii) resource productivity at an intermediate level that allows expression of the trade-off between resource exploitation and IGP.

I envision a situation where the resource does not disperse. This situation exemplifies communities where the basal resource is a plant species or an immobile life stage of insects and aquatic invertebrates (e.g. eggs, immobile adult stages of Coccinellids). The two consumers (IGPrey and IGPredator) disperse randomly, i.e. emigration and immigration are independent of species' or habitat characteristics. As this is the mode of dispersal commonly considered in spatial ecology, it provides a basis for comparing dispersal effects on IGP with previous work on dispersal effects on non-trophic and pairwise consumer–resource interactions (Holt, 1985; Murdoch et al., 1992; Bolker and Pacala, 1999; Jansen, 2001; Amarasekare and Nisbet, 2001).

These ideas are formalized by the following dynamical equations:

$$\begin{aligned} \frac{dR_j}{dt} &= r_j R_j \left(1 - \frac{R_j}{K}\right) - a_1 R_j C_{1j} - a_2 R_j C_{2j}, \\ \frac{dC_{1j}}{dt} &= e_1 a_1 R_j C_{1j} - d_1 C_{1j} - \alpha C_{1j} C_{2j} - \beta_1 C_{1j} + \frac{\beta_1}{3} \sum_{i=1}^3 C_{1j}, \\ \frac{dC_{2j}}{dt} &= e_2 a_2 R_j C_{2j} - d_2 C_{2j} + f \alpha C_{1j} C_{2j} - \beta_2 C_{2j} \\ &\quad + \frac{\beta_2}{3} \sum_{i=1}^3 C_{2j}, \end{aligned} \quad (1)$$

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