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 its own dispersal rate or that of the Intraguild Predator. 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.

Keywords: Competition; Intraguild predation; Spatial coexistence; Random dispersal; Productivity; Life history trade-offs

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 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
competing 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 IGPPrey and IGPPredator 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 IGPPredator 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 IGP Predator cannot invade when rare, (ii) resource productivity sufficiently high that the IGP Predator 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 IGP Predator) 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:

\[
\begin{align*}
\frac{dR_i}{dt} &= r_j R_j \left(1 - \frac{R_j}{K}\right) - a_1 R_j C_{1j} - a_2 R_j C_{2j}, \\
\frac{dC_{1j}}{dt} &= e_1 a_1 R_j C_{1j} - d_1 C_{1j} - xC_{1j} C_{2j} - \beta_1 C_{1j} + \frac{\beta_1}{3} \sum_{i=1}^{3} C_{1i}, \\
\frac{dC_{2j}}{dt} &= e_2 a_2 R_j C_{2j} - d_2 C_{2j} + f xC_{1j} C_{2j} - \beta_2 C_{2j} + \frac{\beta_2}{3} \sum_{i=1}^{3} C_{2i},
\end{align*}
\]

(1)
where $R_i$ is the resource abundance in patch $j$, and $C_{ij}$ is the abundance of Consumer species $i$ in patch $j$ ($i = 1, 2, j = 1, 2, 3$). The parameter $r_j$ is the per capita rate of resource production in patch $j$ and $K$ is the resource carrying capacity in each patch. Spatial heterogeneity in the environment affects resource productivity while the resource carrying capacity remains constant among patches. The parameter $a_i$ is the attack rate of Consumer $i$, $e_i$ is the number of its offspring resulting from resource consumption, and $d_i$ is its background mortality rate. The parameter $x$ is the attack rate of Consumer 2 on Consumer 1, and $f$ is the number of Consumer 2 offspring resulting from intraguild predation. Consumer 1 therefore is the IGPrey, and Consumer 2 is the IGPredator. Neither species exhibits spatial variation in their vital rates. Each species can however, sample spatial variation in resource productivity via dispersal. The parameter $\beta_i$ is the intrinsic or potential dispersal rate of Consumer $i$. Dispersal rate is species specific but not habitat specific, i.e. all individuals of a given species exhibit the same intrinsic dispersal rate.

I non-dimensionalize Eq. (1) using scaled quantities. Non-dimensional analysis allows the dynamics be characterized by fewer parameters, and also highlights biologically significant scaling relations between parameters (Nisbet and Gurney, 1982; Murray, 1993).

I use the following substitutions:

$$
\dot{R}_i = \frac{R_i}{K}, \quad \dot{C}_{ij} = \frac{C_{ij}}{c_iK}, \quad \dot{r}_j = \frac{r_j}{d_i},
$$

$$
\dot{a}_i = \frac{e_i\alpha_i K}{d_i}, \quad \dot{x} = \frac{e_2\alpha K}{d_2}, \quad \dot{\beta}_i = \frac{\beta_i}{d_i},
$$

$$
f = \frac{e_1 f}{e_2}, \quad \delta = \frac{d_2}{d_1}, \quad \tau = d_1 t \quad (d_i \neq 0, \quad i = 1, 2, j = 1, 2, 3)
$$

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 IGPrey’s death rate. This time scaling allows for 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 whether or not the resource abundance is close 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 ($\dot{a}_i$) depend on the resource carrying capacity and the consumer’s death rate ($d_i$). Similarly, the non-dimensionalized interference parameter $\dot{x}$ shows that the per capita inhibitory effect of the IGPredator on the IGPrey depends on the IGPredator’s conversion efficiency and mortality rate as well as the resource carrying capacity. The quantity $\dot{\beta}_i$ is the per capita emigration rate of consumer $i$ relative to its within-patch mortality rate. Again, a particular value of the consumer emigration rate may not have much meaning, but whether or not the emigration rate approaches or exceeds the local mortality rate (i.e. $\dot{\beta}_i \rightarrow 1$ or $\dot{\beta}_i > 1$, respectively) may have important consequences on consumer coexistence. The other interesting scaled quantity is the efficiency metric $f$. Taken separately, the efficiency parameters $e_i$ and $f$ have little meaning; taken together they reveal important scaling relationships between conversion efficiencies for resource exploitation and IGP. For instance, large values of $f$ imply that for any value of $e_1$, $f \gg e_2$, i.e. the IGPredator obtains a greater benefit from preying on the IGPrey than from exploiting the basal resource.

I substitute the non-dimensional quantities into (1) 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:

$$
\frac{dR_i}{d\tau} = r_j R_i (1 - R_j) - a_1 R_i C_{ij} - \delta a_2 R_i C_{2j},
$$

$$
\frac{dC_{ij}}{d\tau} = a_1 R_i C_{ij} - C_{ij} - \delta a_2 C_{ij} C_{2j} - \beta_1 C_{ij} + \frac{\beta_i}{3} \sum_{i=1}^{3} C_{ij},
$$

$$
\frac{dC_{2j}}{d\tau} = \delta a_2 R_j C_{2j} - C_{2j} + f a_2 C_{ij} C_{2j} - \beta_2 C_{2j}
$$

$$
+ \frac{\beta_i}{3} \sum_{i=1}^{3} C_{ij}.
$$

Because the goal is to understand the possible interplay between local coexistence mechanisms and those mediated by dispersal, I restrict attention to the situation where local coexistence via a competition–IGP trade-off is possible in at least one patch. The trade-off is such that the IGPrey is the superior resource competitor (i.e. it has a lower $R^*$; Tilman, 1982), but the IGPredator can prey on the IGPrey ($x > 0$). From Eq. (2) $R^*$ in the absence of dispersal is $1/a_i$, and hence competitive superiority of the IGPrey translates into having a higher attack rate than the IGPredator. Throughout, I use $a_i$ as the measure of competitive ability and $x$ as a measure of the strength of IGP while keeping the mortality ratio ($\delta$) and conversion efficiency ($f$) fixed. I later investigate the robustness of results to variation in these parameters. Rather than attempt an exhaustive exploration of the parameter space I focus on four situations that are biologically relevant: the trade-off between competition and IGP is strong or weak, and the IGPrey or the IGPredator has the overall advantage (Table 1). A strong trade-off means that coexistence via local niche partitioning can occur for a broad range of resource productivities, while a weak trade-off implies the opposite. When one
species has an overall advantage, the range of resource productivities for which one species excludes the other exceeds the range for which coexistence occurs.

I focus in particular on the effects of dispersal on the relationship between abundance and resource productivity for the IGPrey and IGPredator. I do so for two reasons. First, resource productivity is an easily manipulated parameter and abundance is a readily measured variable, which allows model predictions to be easily translated into empirical investigations. Second, the mechanisms shaping the productivity–abundance relationship have been discussed extensively, but mostly from the perspective of local species interactions (Leibold, 1989; Holt et al., 1994; Holt and Polis, 1997; Diehl and Feissel, 2000, 2001; Bonsall and Holt, 2003). Here, I elucidate the productivity–abundance relationship under dispersal, thus providing an alternative hypothesis for explaining the relationship.

The abundance–productivity relationship in the absence of dispersal is determined by deriving the per capita growth rates of the IGPrey and IGPredator when rare (i.e. their invasion criteria) as a function of resource productivity. Let \( r_j \) be the ambient resource productivity in habitat patch \( j \). The IGPrey can invade when rare (i.e. its per capita growth rate at low density is positive) if \( r_j < r_{C_1} \), the IGPredator can invade when rare if \( r_j > r_{C_2} \), and both species can invade when rare if \( r_{C_1} < r_j < r_{C_1} \). The quantities \( r_{C_1} \) and \( r_{C_2} \) are, respectively, the right-hand sides of the invasion criteria of the IGPrey and IGPredator in the absence of dispersal when solved in terms of \( r_j \) (see Appendix for details). The key point is that the IGPrey’s per capita growth rate when rare declines with increasing resource productivity, while the IGPredator’s per capita growth rate when rare increases with increasing resource productivity (Fig. 1a). The abundance–productivity relationship mirrors this pattern (Figs. 1b and c).

### 2.1. Model analyses

The three-patch model with dispersal does not lend itself to analytical results. I therefore used numerical methods to investigate the conditions for invasibility and coexistence. Eq. (2) was numerically integrated for 75,000 time steps using the method of Runge–Kutta step 5 with an adaptive step size (Press et al., 2002). If the abundance of any species fell below 0.001 (i.e. 1/1000th of the resource carrying capacity for a conversion efficiency \( e_i \) of unity) during any time step, that species was considered to have gone extinct in that patch. This allowed me to investigate the role of demographic stochasticity on invasibility and long-term coexistence. Long-term abundances were calculated as the average over the last 5000 time steps.

I investigated the influence of dispersal against the backdrop of spatial variation in resource productivity. I introduced spatial variation by setting the resource productivity in each patch to a level that leads to one of the three outcomes observed in the absence of dispersal: (i) IGPrey only, (ii) coexistence, (iii) IGPredator only. Adopting the convention that patches 1–3 represent increasing levels of resource productivity, we have \( r_1 = (0, r_{C_1}) \), \( r_2 = (r_{C_2}, r_{C_1}) \), and \( r_3 = (r_{C_1}, r_{max}) \) where \( r_{C_1} \) and \( r_{C_2} \), are, respectively, the threshold resource productivities required for the IGPrey and IGPredator to invade when rare (see Appendix), and \( r_{max} \) is the maximum resource productivity. (The maximum resource productivity is determined by the resource species’ life history traits as well as habitat characteristics; for instance, habitat attributes such as nutrient availability may reduce the fecundity of a resource species below the limit set by energy allocated to reproduction.) The \( r \) values thus obtained determine the strength of spatial variation in resource productivity, i.e. \( r_1 \rightarrow 0 \) and \( r_3 \rightarrow r_{max} \) imply strong spatial variation while \( r_1 \rightarrow r_{C_2} \) and \( r_3 \rightarrow r_{C_1} \) imply weak spatial variation. I used the following values as representing the baseline spatial variation in resource productivity:

\[
\begin{align*}
    r_1 &= r_{C_2}/2, \\
    r_2 &= (r_{C_1} + r_{C_1})/2, \\
    r_3 &= (r_{C_1} + r_{max})/2.
\end{align*}
\]

Because the focus is on the interplay between IGP and dispersal, I assumed that the two consumer species differ in their attack rates (\( a_j \)) and dispersal propensities (\( b_j \)) but have similar background mortality rates (i.e. \( \delta = 1 \)). The assumption of equal mortality rates is reasonable given that competitors within a guild are often subject to the same density-independent mortality factors (Zwolfer, 1971; Mills, 1994; Amarasekare, 2000). It allows all important life history traits to be scaled relative to the common

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### Table 1

<table>
<thead>
<tr>
<th>Competitive ability</th>
<th>Strength of IGP</th>
<th>Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a_1 &gt; a_2 )</td>
<td>( a &lt; a_2 )</td>
<td>Exploitative competition dominates, IGPrey has overall advantage(^a)</td>
</tr>
<tr>
<td>( a_1 &gt; a_2 )</td>
<td>( a &gt; a_2 )</td>
<td>Strong trade-off between competition and IGP(^b)</td>
</tr>
<tr>
<td>( a_1 &gt; a_2 )</td>
<td>( a &lt; a_2 )</td>
<td>Weak trade-off between competition and IGP(^c)</td>
</tr>
<tr>
<td>( a_1 &gt; a_2 )</td>
<td>( a &gt; a_2 )</td>
<td>IGP dominates, IGPredator has overall advantage(^d)</td>
</tr>
</tbody>
</table>

\(^a\)The IGPrey invades at relatively low resource productivity, but the IGPredator cannot invade except at high resource productivity. Coexistence is possible only for relatively high productivities. The IGPrey excludes the IGPredator for most of the productivity range.

\(^b\)Differences between species in competitive ability and IGP are large. Coexistence can occur for a broad range of resource productivities.

\(^c\)Differences between species in competitive ability and IGP are small. Coexistence occurs only for a narrow range of resource productivities.

\(^d\)The IGPredator can invade at relatively low resource productivity, and the IGPrey is excluded at relatively low productivity. Coexistence is possible for relatively low productivities. The IGPrey dominates the IGPredator for most of the productivity range.
mortality rate, which has the advantage of revealing the relative importance of local and spatial processes in coexistence.

3. Results

3.1. Summary of key results

The most notable result is the asymmetry between species in their response to dispersal. The abundance–productivity relationship of the IGPrey is strongly affected by the dispersal rate of the IGPredator, while the abundance–productivity relationship of the IGPredator is qualitatively unaffected by the dispersal rates of either the IGPrey or the IGPredator (Fig. 2). For instance, the IGPredator’s abundance increases monotonically with increasing productivity regardless of its dispersal rate (Fig. 3). In contrast, the IGPrey’s abundance–productivity relationship is highly sensitive to the IGPredator’s dispersal rate (Fig. 3). When the IGPredator’s dispersal rate is very low relative to the within-patch mortality rate (i.e. \( \beta_2 < 0.1 \)), the IGPrey’s abundance declines monotonically with increasing productivity. When the dispersal rate is low to moderate (0.1 < \( \beta_2 < 1 \)), the IGPrey’s abundance–productivity relationship becomes hump-shaped with the highest abundance at intermediate productivity. When the IGPredator’s dispersal rate is high relative to the within-patch mortality rate (i.e. \( \beta_2 > 1 \)), the IGPrey’s abundance increases monotonically with increasing productivity (Fig. 3). Thus, low IGPredator dispersal leads to inter-specific segregation with the IGPrey being concentrated in areas of low resource productivity and the IGPredator in areas of high resource productivity. In contrast, high IGPredator dispersal leads to inter-specific aggregation with both species being concentrated in areas of high-productivity (Fig. 3). These differences arise solely because of the IGPrey’s differential response to the magnitude of IGPredator’s dispersal. The IGPredator’s abundance–productivity relationship is qualitatively insensitive to changes in its own dispersal rate as well as that of the IGPrey’s (Figs. 2 and 3).

The mechanisms underlying these abundance–productivity relationships can be understood by looking at the long-term abundances of the IGPrey as a function of the IGPredator’s dispersal rate (Fig. 2). The key point to note is the existence of a threshold value of \( \beta_2 \) below which the IGPrey’s abundance is the lowest in the high-productivity patch, and above which the IGPrey’s abundance is the lowest in the low-productivity patch. Below this threshold the high-productivity patch is a sink for the IGPrey (i.e. it cannot maintain a positive growth rate when rare in the absence of dispersal; Holt and Polis, 1997; Fig. 1). It is rescued from extinction by immigration from the intermediate-productivity patch where local niche partitioning occurs in the absence of dispersal via the competition–IGP trade-off. Thus, at low dispersal rates of the IGPredator we have within-patch coexistence via a combination of source–sink dynamics in the IGPrey, and a trade-off between resource competition and IGP. Within-patch coexistence is still possible once the IGPredator’s dispersal rate exceeds the threshold, but it occurs via a combination of mechanisms that do not require the IGPrey’s dispersal. Coexistence in the intermediate-productivity patch occurs via the competition–IGP trade-off, while coexistence in the high-productivity patch occurs via high emigration of the IGPredator. The latter mechanism comes about because
Fig. 2. Long-term (equilibrium) abundances under random dispersal. The top graph depicts the IGPrey’s abundance as a function of the IGPredator’s intrinsic dispersal rate \( (\beta_2) \) and the bottom graph, the IGPredator’s abundance as a function of the IGPrey’s intrinsic dispersal rate \( (\beta_1) \). In each graph, the three lines with increasing thickness depict, respectively, abundances in the low, intermediate and high-productivity patches. The vertical dashed line in the top graph depicts the threshold dispersal rate below which the IGPrey’s abundance is the lowest in the high-productivity patch, and above which the IGPrey’s abundance is the lowest in the low-productivity patch. At this threshold the IGPrey has the same equilibrium abundance in both low- and high-productivity patches (i.e. \( C_{11}^o = C_{13}^o \)). Parameter values used are: \( a_1 = 10, a_2 = 2, z = 2, f = 2, \beta_1 = 0.2 \) (top panel) and \( \beta_2 = 0.2 \) (bottom panel).

Fig. 3. The abundance–productivity relationship of the IGPrey (top row) and the IGPredator (bottom row) under random dispersal. In each panel, the x-axis is the resource productivity \( (r_j) \) and the y-axis is long-term abundance. In each row, panels from left to right depict the abundance–productivity relationships for increasing levels of the IGPredator’s intrinsic dispersal rate \( (\beta_2) \). In the top row, the two graphs on the left depict the IGPrey’s abundance–productivity relationship when the IGPredator’s dispersal rate is below the threshold value of \( \beta_2 \) in Fig. 2, and the two graphs on the right depict the relationship when the IGPredator’s dispersal rate is above this threshold. Note the difference in scales for the two species: the IGPrey’s abundance is much lower than that of the IGPredator. The key point is that the IGPrey’s abundance–productivity relationship is highly sensitive to the IGPredator’s dispersal rate but the IGPredator’s abundance–productivity relationship is insensitive to its own dispersal rate. Parameter values used are: \( a_1 = 10, a_2 = 2, z = 2, f = 2, \beta_1 = 0.2 \).
random dispersal leads to a net movement of individuals from areas of higher to lower abundance. The IGPrey’s emigration out of the high-productivity patch, where it has the highest abundance, far exceeds immigration into it. This reduces the strength of IGP in the high-productivity patch and allows the IGPrey to invade when rare. This is equivalent to a mortality–IGP trade-off with the IGPrey experiencing a greater loss of individuals from the high-productivity patch, but the effect actually arises from high rates of random dispersal homogenizing IGPredator abundance across the landscape. The important point to note is that spatial coexistence of the IGPrey and IGPredator, and the resulting abundance–productivity relationships, arise from two different combinations of mechanisms. Which combination operates depends on the magnitude of the IGPredator’s dispersal rate.

The above results ensue when the trade-off between competition and IGP is relatively strong. I next investigate the robustness of these results to variation in the strength of the trade-off.

3.2. Strong trade-off vs. the IGPrey having an overall advantage

When the IGPrey has a strong competitive advantage (i.e. \( a_1 > a_2 \)), the trade-off is strong when \( x > a_2 \) (i.e. the IGPredator exploits the IGPrey at the same or a higher rate than the basal resource), and the IGPrey gains an overall advantage when \( x < a_2 \) (i.e. the IGPredator has a higher attack rate on the basal resource than on the IGPrey). When the emigration rate of the IGPrey is lower than its within-patch mortality rate (i.e. \( \beta_1 < 1 \)), the effects of the IGPredator’s dispersal rate (\( \beta_2 \)) on the IGPrey’s abundance–productivity relationship is qualitatively similar for both scenarios (Fig. 4). However, when the IGPrey’s emigration rate exceeds the within-patch mortality rate...
(\(\beta_1 > 1\)), low rates of the IGPrey’s dispersal causes the IGPrey’s abundance–productivity relationship to be monotonic decreasing when the two species exhibit a strong trade-off, and to be humped when the IGPrey has an overall advantage (Fig. 4). For high rates of the IGPredator’s dispersal both scenarios yield qualitatively similar abundance–productivity relationships. Somewhat paradoxically, both species exhibit greater overall abundances when the IGPrey has an overall advantage, a pattern that is robust to variation in \(\beta_i\) (Fig. 4).

### 3.3. Weak trade-off vs. the IGPredator having an overall advantage

When the IGPrey has only a weak competitive advantage (i.e. \(a_1 \simeq a_2\)), the trade-off is weak when \(\lambda < a_2\) (i.e. the IGPredator has a higher attack rate on the basal resource than the IGPrey), and the IGPredator gains an overall advantage when \(\lambda \gg a_2\) (i.e. the IGPredator has a higher attack rate on the IGPrey). Both scenarios yield qualitatively similar outcomes with regard to coexistence, with the IGPrey undergoing landscape-wide extinction at intermediate values of the IGPredator’s dispersal rate (Fig. 5). The range of IGPredator dispersal rates for which the IGPrey is extinct increases as the IGPrey’s dispersal rate itself increases (Fig. 5). Both scenarios also yield abundance–productivity relationships that are qualitatively similar. The overall abundances of both species are much higher when the two species exhibit a weak trade-off than when the IGPredator has an overall advantage, a pattern that is robust to variation in \(\beta_i\) (Fig. 5). Landscape-wide extinction of the IGPrey occurs because the IGPrey’s higher abundance in the low and intermediate-productivity patches results in a net movement into the high-productivity patch, while the IGPredator’s higher abundance in the high-productivity patches results in a net movement into the low and intermediate-productivity patches. The outcome is an increase in IGP, and hence greater mortality of the IGPrey, in all three patches. This predisposes the IGPrey to stochastic extinction when its abundances become low. Extinction, however, occurs only for intermediate values of the IGPredator’s dispersal rate. As the

![Fig. 5. Long-term abundances of the IGPrey and the IGPredator as a function of the IGPredator’s dispersal rate (\(\beta_2\)) when the IGPredator has an overall advantage vs. when the competition–IGP trade-off is weak. The three rows represent increasing levels of the IGPrey’s dispersal (\(\beta_1 = 0.1, 0.5\) and 2.0). In each graph, the three lines with increasing thickness depict, respectively, abundances in the low-, intermediate- and high-productivity patches. Both scenarios lead to qualitatively similar spatial distribution patterns for the two species. The overall abundances of both species are greater when trade-off is weak than when the IGPredator has an overall advantage. Parameter values used are: \(a_1 = 3, a_2 = 2, \lambda = 10, f = 2\) for when the IGPredator has an overall advantage, and \(a_1 = 3, a_2 = 2, \lambda = 0.5, f = 2\) for when the trade-off is weak.](image)
IGPredator’s dispersal rate increases the IGPrey is able to invade the high-productivity patch, immigration from which then maintains sink populations in the low and intermediate-productivity patches.

3.4. Strong vs. weak trade-off

The comparison between a strong and weak trade-off yields the most dramatic differences in both coexistence and abundance–productivity relationships (Fig. 6). When the trade-off is strong (i.e. $a_1 > a_2$, $x > a_2$) within-patch coexistence is possible for all levels of productivity even when dispersal rates exceed within-patch mortality rates ($\beta_1 > 1$). Thus, when a strong trade-off between resource competition and IGP allows coexistence in at least one patch, dispersal can allow stable within-patch coexistence across all patches and increase diversity above that in isolation. In contrast, when the trade-off is weak (i.e. $a_1 \approx a_2$, $x < a_2$) the IGPrey suffers landscape-wide extinction at intermediate dispersal rates of the IGPredator. Thus, when the trade-off allowing local coexistence is weak, dispersal prevents within-patch coexistence and decreases diversity below that in isolation. While the strength of the trade-off has a strong effect on coexistence, it has no qualitative effect on the abundance–productivity relationships of the two species (Fig. 6), which follow the general pattern described in the summary of key results section. Interestingly, the transition from a strong to weak trade-off increases the overall abundance of the IGPrey, and decreases the overall abundance of the IGPredator (Fig. 6).

3.5. Variation in conversion efficiency

The efficiency metric $f$ scales the two consumers’ resource exploitation efficiencies by the IGPredator’s efficiency in exploiting the IGPrey. Coexistence via a competition–IGP trade-off requires that $f$ exceed a threshold determined by $a_i$, $x$ and $r_j$ (see Appendix). The closer the value of $f$ to this threshold, the higher the resource productivity at which the IGPredator can invade, and the narrower the range of resource productivity that allows

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**Fig. 6.** Long-term abundances of the IGPrey and the IGPredator as a function of the IGPredator’s dispersal rate ($\beta_2$) when the IGPrey has an overall advantage vs. when the competition–IGP trade-off is strong. The three rows represent increasing levels of the IGPrey’s dispersal ($\beta_1 = 0.1$, 0.5 and 2.0). In each graph, the three lines with increasing thickness depict, respectively, abundances in the low-, intermediate- and high-productivity patches. Note the large qualitative changes between the two scenarios in the species’ spatial distribution patterns. Parameter values used are: $a_1 = 10, a_2 = 2, x = 2, f = 2$ for when the trade-off is strong, and $a_1 = 3, a_2 = 2, x = 0.5, f = 2$ for when the trade-off is weak.
coexistence. Hence it is important to investigate the sensitivity of the above results to variation in $f$.

When the competition–IGP trade-off is strong or when the IGPrey has an overall advantage, variation in $f$ yields similar outcomes (Fig. 7). For instance, an increase in $f$ has no effect on either species except for a reduction in the IGPrey’s overall abundance. A decrease in $f$ has no effect on the IGPredator except for a tendency for densities to become homogenized across patches as $\beta_2$ increases, resulting in a decline in the overall abundance. A decrease in $f$, however, causes the IGPrey to go globally extinct at intermediate values of $\beta_2$ (Figs. 7a and c). The range of values of $\beta_2$ leading to extinction increases as $\beta_1$ increases.

The one difference between a strong trade-off and the IGPrey having the overall advantage is that when $\beta_2$ is low and $\beta_1$ is high, source–sink dynamics in the IGPrey allows coexistence when the trade-off is strong, but not when the IGPrey has an overall advantage.

When the competition–IGP trade-off is weak or when the IGPredator has an overall advantage, a decrease in $f$ has the same effect while an increase in $f$ leads to different outcomes (Fig. 7). Under a weak trade-off, an increase in $f$ has no effect on either species except for a decrease in the IGPrey’s overall abundance. When the IGPredator has an overall advantage an increase in $f$ has no effect on the IGPredator but a large effect on the IGPrey (Figs. 7i and 7k).

![Figure 7](image-url)

Fig. 7. Long-term abundances of the IGPrey and the IGPredator as a function of the IGPredator’s dispersal rate ($\beta_2$) when there is variation in the conversion efficiency ($f$). The three rows represent, respectively, a strong trade-off, a weak trade-off, and the IGPredator having an overall advantage. Results for when the IGPrey has an overall advantage are not shown because they are indistinguishable from those for a strong trade-off. For a strong trade-off (top row) and weak trade-off (middle row), the two left panels are for $f$ just above the threshold that allows coexistence ($f = 0.6$ for strong trade-off and $f = 0.8$ for weak trade-off), and the two right panels are for $f$ well above the threshold for coexistence ($f = 2$ for both strong and weak trade-off). When the IGPredator has an overall advantage (bottom row), all four panels are for $f$ well above the coexistence threshold ($f = 2$ for the two left panels and $f = 3$ for the two right panels). In this case lowering $f$ down to 0.8, which is just above the coexistence threshold, increases the range of $\beta_2$ for which the IGPrey goes extinct, but otherwise gives results qualitatively similar to $f = 2$. In all panels, the IGPredator’s dispersal rate is equal to the within-patch mortality rate ($\beta_1 = 1$). The other parameters are the same as in Fig. 4 for a strong trade-off, and the same as in Fig. 5 for weak trade-off and the IGPredator having an overall advantage.
k). As the IGPrey’s dispersal rate exceeds the local mortality rate ($\beta_1 \geq 1$), the IGPrey goes extinct for all values of the IGPredator’s dispersal rate ($\beta_2$). This is to be expected since high $f$ implies that the IGPredator derives a greater benefit, in terms of reproduction, from the IGPrey than from the resource (i.e. $f > e_2$ in the original model), which intensifies the IGPrey’s overall disadvantage. Decreasing $f$ increases the range of $\beta_2$ for which global extinction of the IGPrey occurs. It also causes the IGPredator’s abundances to become homogenized as $\beta_2$ increases, leading to global extinction at high $\beta_2$ ($\beta_2 > 1$). The threshold $\beta_2$ at which extinction occurs increases as $\beta_1$ increases.

To summarize the key effects of variation in $f$, an increase in $f$ has no qualitative effect on either species except when the IGPredator has an overall advantage, in which case the IGPrey goes globally extinct. A decrease in $f$ affects only the IGPrey when the trade-off is strong or when the IGPrey has an overall advantage, and affects both species when the trade-off is weak or the IGPredator has an overall advantage. These results are obtained when $f$ is just above the threshold that allows the competition–IGP trade-off to operate, which is the most restrictive situation for coexistence in the absence of dispersal. For values of $f$ well above the threshold, the general outcomes discussed in the previous section ensue.

The important general result from all of the above analyses is that random dispersal enhances coexistence when the trade-off between competition and IGP is strong and/or when the IGPrey has an overall advantage, and impedes coexistence when the trade-off is weak and/or the IGPredator has an overall advantage. These results are unaltered by increasing the number of patches in the landscape as long as the proportion of patches in each productivity category remain the same (P. Amarasekare, unpublished results).

4. Discussion

A great deal is known about the spatial coexistence of species engaged in non-trophic interactions (e.g. competition, mutualisms; Boller and Pacala, 1999; Amarasekare, 2004) and pairwise trophic interactions (e.g. predator–prey, host–parasitoid; Holt, 1985; Murdoch et al., 1992; Jansen, 2001). Much less is known about the spatial coexistence of species engaged in both trophic and non-trophic interactions. This void exists despite the fact that multi-trophic interactions form the core of nearly all communities.

Here I have presented what is to my knowledge the first spatial model of a multi-trophic community characterized by competition and predation. I have focused on intraguild predation (IGP) as a representative multi-trophic interaction for two reasons. First, it is a widespread interaction in nature, occurring in a variety of taxa from microbes to mammals (Polis et al., 1989; Arim and Marquet, 2004). Second, while coexistence in the absence of dispersal is possible via a trade-off between competition and IGP, the trade-off operates only at intermediate levels of resource productivity. This suggests a potentially important role for dispersal in diversity maintenance.

A second novel feature of the model is the investigation of dispersal effects on the relationship between population abundance and resource productivity. This is an issue that has generated great interest because of the importance of abundance–productivity relationships to diversity maintenance and ecosystem functioning (Kinzig et al., 2001). Most existing work focuses on the roles of species interactions and abiotic factors in shaping abundance–productivity relationships (Leibold, 1989; Holt et al., 1994; Holt and Polis, 1997; Diehl and Feissel, 2000, 2001; Bonsall and Holt, 2003). This study complements this previous work by elucidating the role of spatial dynamics in shaping the abundance–productivity relationships in multi-trophic communities.

The study yielded two key results. The first is that random dispersal enhances coexistence when a trade-off between resource competition and IGP is strong and/or when the IGPrey has an overall advantage, and impedes coexistence when the trade-off is weak and/or the IGPredator has an overall advantage. Coexistence, and the resulting abundance–productivity relationships, occur from two different combinations of mechanisms. Which combination operates depends on the IGPredator’s dispersal rate. When the IGPredator’s dispersal is low, coexistence occurs via a combination of the competition–IGP trade-off and source–sink dynamics in the IGPrey. When the IGPredator’s dispersal is high, coexistence occurs via a combination of the competition–IGP trade-off and high emigration of the IGPredator from the high-productivity patch. High emigration of the IGPredator reduces the strength of IGP in the high-productivity patch and allows the IGPrey to invade when rare. Interestingly, when the IGPredator’s dispersal is high, coexistence occurs via a combination of mechanisms that do not require the IGPrey’s dispersal.

The second key result is the asymmetry between species in their response to each other’s dispersal. The IGPrey’s abundance–productivity relationship depends crucially on the dispersal rate of the IGPredator, but the IGPredator’s abundance–productivity relationship is unaffected by the dispersal rate of either the IGPrey or the IGPredator. This difference arises because the two species engage in both a competitive interaction as well as an antagonistic (predator–prey) interaction. The IGPrey, being the intermediate consumer, has to balance the conflicting demands of resource acquisition and predator avoidance, while the IGPredator has to contend only with resource acquisition. Thus, the IGPredator’s abundance increases monotonically with resource productivity regardless of either species’ dispersal rate, while the IGPrey’s abundance–productivity relationship can increase, decrease, or become hump-shaped with increasing productivity depending on the IGPredator’s dispersal rate. As a consequence, the
IGPredator’s dispersal behavior determines the spatial distributions of both species. For instance, low IGPredator dispersal leads to inter-specific segregation with the IGPrey being concentrated in areas of low resource productivity and the IGPredator in areas of high resource productivity. In contrast, high IGPredator dispersal leads to inter-specific aggregation with both species being concentrated in areas of high productivity.

These results have important implications for diversity maintenance in communities characterized by IGP. These communities present a puzzle because theory based on a competition–IGP trade-off predicts the exclusion of the IGPrey in productive environments, while data repeatedly show the coexistence of the IGPrey and IGPredator in such environments (Polis et al., 1989; Arim and Marquet, 2004). As shown here, dispersal provides a potential mechanism for coexistence in productive environments, particularly if the competition–IGP trade-off is strong or the IGPrey has an advantage over the IGPredator. Experiments in which dispersal rates are manipulated by varying distances among patches with differing resource productivities can test the role of dispersal in maintaining diversity in productive habitats.

The asymmetry between species in their response to each other’s dispersal is not observed in community modules with pure resource competition or apparent competition. Abrams and Wilson (2004) investigated a spatial model of resource competition with explicit resource dynamics, and Amarasekare et al. (2004) investigated a spatial model of resource competition with no resource dynamics. In neither case did one competitor’s dispersal behavior have a disproportionately large effect on the other. Holt and Barfield (2003) investigated a model of apparent competition with dispersal in one prey species, the results of which suggest that the impact of dispersal on apparent competition is qualitatively similar to that of resource competition. Thus, the asymmetry observed in this study appears to be a direct result of the species engaging in both competitive and predator–prey interactions. This suggests that dispersal impacts on community modules with more than one type of species interaction (e.g. IGP, selective predation) may be fundamentally different from those on community modules with only one type of interaction (e.g. resource competition, apparent competition).

The findings reported here also have broader implications for spatial community ecology. They suggest that a species’ trophic position determines the advantages of using dispersal to sample spatial environmental heterogeneity. Because the dispersal rate of a top predator can have a much stronger effect on the intermediate consumer than vice versa, dispersal behavior of top predators may drive the coexistence and spatial distributions of species in multi-trophic communities.

The observed trophic asymmetry in species’ responses to dispersal suggests two important future directions. First, the result that coexistence can occur without the IGPrey’s dispersal given high rates of IGPredator dispersal hinges on the IGPredator emigrating in large numbers from resource rich habitats that are most conducive to its reproduction. This is a maladaptive decision from the point of view of an individual organism, especially given that permanent spatial heterogeneity in resource productivity provides a predictable environment where bet-hedging does not confer an additional advantage. This outcome begs the question of whether there are non-random dispersal strategies that allow for more biologically realistic coexistence mechanisms. Investigation of such strategies is an important next step. Second, the results reported here are for IGP, which represents only one type of multi-trophic interaction. Investigating the role of dispersal in other multi-trophic interactions such as selective predation is necessary in order to establish whether a trophic asymmetry in the response to dispersal is a general feature of multi-trophic communities.

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Appendix A. Invasion criteria for the IGPrey and IGPredator in the absence of dispersal

When neither species disperses (i.e. $\beta_i = 0$ in Eq. (2)), five sets of equilibria can occur within a given habitat patch $j$: (i) the trivial equilibrium with all species extinct ($R^*, C^*_1, C^*_2 = (0, 0, 0)$), (ii) the resource at carrying capacity and the consumers extinct ($R^*, C^*_1, C^*_2 = (1, 0, 0)$), (iii) boundary equilibrium with the resource and IGPrey ($R^*, C^*_1, C^*_2 = (1/a_1, r_f(a_1 - 1)/a_1^2, 0)$), (iv) boundary equilibrium with the resource and IGPredator ($R^*, C^*_1, C^*_2 = (1/a_2, 0, r_f(a_2 - 1)/a_2^2)$) and (v) the coexistence equilibrium ($R^*, C^*_1, C^*_2$)

$$
R^* = \left( \frac{f(a_2 + r_f z) a_1 - a_2(a_1 - a_2) + r_f z(1 - a_2)}{a_1 a_2(f - 1) + r_f z}, \frac{a_1(a_2 - a_1) + r_f z(a_1 - 1)}{a_1 a_2(f - 1) + r_f z} \right).
$$

The invasion criteria for each species is obtained by computing the dominant eigenvalue of the Jacobian of Eq. (2) in the absence of dispersal ($\beta_i = 0$) evaluated at the appropriate boundary equilibrium. The invasion boundary for the IGPrey is $a_2(a_1 - a_2) + r_f z(1 - a_2)/a_2^2 = 0$ which can be solved in terms of $r_f$, ($j = 1, 2, 3$) to give $r_c_1 = a_2(a_2 - a_1)/a_1(1 - a_2)$. The IGPrey can invade when $r_f < r_c_1$. The invasion boundary for the IGPredator is $\delta f(a_2 - a_1) + r_f z(a_1 - 1) = 0$ which can be solved in terms of $r_f$ to give $r_c_2 = a_1(a_1 - a_2)/f z(a_1 - 1)$. The IGPredator can invade when $r_f > r_c_2$. Coexistence occurs in the region $r_c_2 < r_f < r_c_1$. 


Note that the numerator (or a part thereof) of each species' invasion criterion also appears in the numerator of their respective coexistence equilibrium. Given mutual invasibility, the feasibility of the coexistence equilibrium ($C_1^*, C_2^* > 0$) therefore requires that the common denominator $\delta a_1 a_2 (f - 1) + r_f a_2$ be positive. Since $\delta$ and $r$ are positive, this occurs when $f > a_1 a_2 / (a_1 a_2 + r_f a_2)$. Note that the IGPredator's invasibility requires that $f > a_1 (a_2 - a_2) / r_a (a_1 - 1)$, which is a less stringent condition than the threshold $f$ required for the coexistence equilibrium to be feasible. I therefore used the former condition when investigating the sensitivity of results to variation in $f$ (see section on Variation in conversion efficiency).

References


