Species coexistence of communities with intraguild predation: The role of refuges used by the resource and the intraguild prey

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ABSTRACT

In this paper, we develop a three-species intraguild predation model which incorporates refuges used by the resource and the intraguild prey, and focus on the effects of refuges on the three species coexistence. The invasion condition and parameter region for coexistence are obtained using invasion analysis. The new invasion condition requires that all boundary states with one missing species can be invaded by the missing species. Numerical simulations show that refuges have a major influence on species coexistence of intraguild predation system, and the results strongly depend on the types of refuges introduced into the model. Our study also shows that prey's refuges are detrimental to species coexistence except the resource using refuges. In contrast to previous research, we find that spatial structure may play an important role in effects of refuges on species coexistence of intraguild predation systems. Our results may shed new light on understanding the mechanisms and the persistence of multi-species predators-prey system.

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1. Introduction

Intraguild predation (IGP) occurs when one predator species (IG predator) consumes or parasitizes another predator species (IG prey) with whom it also competes for a common resource (Polis et al., 1989; Amarasekare, 2008). Such a multi-trophic interaction is a commonly found module in many food webs, and it has important implications for diversity maintenance in the fields of community ecology, wildlife management programs (Longcore, 2003), spatial ecology and biological control (Holt and Polis, 1997; Su et al., 2008; Okuyama, 2008). The current theory predicts coexistence if the IG prey is the superior competitor for the common resource, but such coexistence is – if at all – only possible at intermediate levels of resource productivity (Holt and Polis, 1997; Diehl and Feissel, 2000), IG prey cannot persist at high productivity (usually described by resource renewal rate or carrying capacity). Although there is one study which supports these predictions in microbial systems (Diehl and Feissel, 2000), these predictions often conflict with the empirical data and recent meta-analyzes show that IGP is a common and stable form of species interaction (Polis et al., 1989). The narrow coexistence parameter region does not support the ubiquitous occurrence of IGP in ecological communities. This is called "a puzzle in species coexistence" by Holt and Polis (1997), which poses the question of whether we are missing some crucial parts of reality in current models.

There have been many studies which try to incorporate more realistic ecological factors, such as adaptive omnivory (Křivan and Diehl, 2005), age or stage structure (Rudolf, 2007), spatial heterogeneity (Janssen et al., 2007), additional species (Holt and Huxel, 2007) to ascertain mechanisms for coexistence in systems with strong IGP. The coexistence parameter region may or may not expand, that depends on the details of the models. Currently, it is still a challenge to search the mechanisms that explain the persistence of IGP systems.

One biological feature that allows the prey to escape predation in space or time is widely observed. Spatial or temporal refuges are well-known examples of this class of mechanisms (Amarasekare, 2008). Some empirical and theoretical studies have been done on understanding the effects of prey refuges, where the refuge habitats can include burrows (Clarke et al., 1993), trees (Dill and Houtman, 1989), cliff faces (Berger, 1991), thick vegetation (Cassini, 1991), or rock talus (Holmes, 1991). Most of these works have focused on how refuges add stability to the system with predator–prey interactions. It is concluded that the refuges used by prey can stabilize the coexistence equilibrium and prey extinction can be prevented by the addition of refuges (Mistro et al., 2009, and the references therein; Ma et al., 2009). In contrast, there are also some other studies which suggest that the refuges used by prey can destabilize the coexistence equilibrium under a very restricted set of conditions (McNair, 1986; Ma et al., 2009). Recently, the role of spatial refuges in IGP communities has been investigated by Finke and Denno (2006) and HilleRisLambers et al. (2006), and the role of temporal refuges has been investigated by Amarasekare (2008).

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For modeling purposes, the effects of prey refuges on the population dynamics consist of two components (González-Olivares and Ramos-Jiliberto, 2003). The first component, which affects positively the growth of prey and negatively that of predators, because the decrease of predation success can lead to the reduction of prey mortality. The second one may be the trade-offs and by-products of the hiding behavior of prey which could be either advantageous or detrimental for the involved populations. For example, the prey population in the refuges has a low birth rate due to rarely being offered feeding or mating opportunities.

Refugia are often modeled as a refuge that protects either a constant fraction (McNair, 1986; Collings, 1995; Sih, 1987) or constant number of prey (Křivan, 1998; González-Olivares and Ramos-Jiliberto, 2003; Ma et al., 2009). Hassell (1978) noted that in reality refugia fall between these extremes with those protecting a proportion of the prey population appearing to be more common. In addition, based on empirical evidence, Hochberg and Holt (1995) suggested that for most host–parasitoid systems part of the host population is in a constant proportion refuge, which is also the case considered in this paper.

The primary goal of this paper is to develop a three-species mathematical model which incorporates refuges used by the resource and the intraguild prey. In particular, we want to understand how refuges used by the resource or IG prey alter the parameter region for coexistence. To the end, we will use invasion analysis (Okuyama, 2008) to analyze our model. For a three-species system, one crucial condition requires that all boundary states with one missing species can be invaded by the missing species (Křivan and Diehl, 2005). We can obtain the condition that IG prey can invade when rare (i.e. its per capita growth rate at low density is positive) and the condition that the IG predator can invade when rare. When the invasion criteria are both satisfied, then three-species can coexist. Finally, it is worth noting that mutual invasibility is not a necessary condition for indefinite coexistence. The module can persist indefinitely even when the conditions do not hold. For instance, Ruggieri and Schreiber (2005) illustrated that stable coexistence can be achieved even though the invasibility conditions fail. Therefore, the coexistence guaranteed by the invasion analysis is a strong form coexistence, i.e., permanence. A mathematically rigorous justification of the coexistence statements presented here follow immediately from results in Schreiber (2000).

2. Models

We assume that the densities of all species populations change continuously with time, uniform distribution over space and having no stage structure. The model, we will consider is a general model of a tri-trophic food web consisting of resource (R), IG prey (C), and IG predator (P). The IG predator may feed on the resource and IG prey. The population dynamics are represented by the following system of differential equations:

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{a_1 CR}{1 + a_1 b_1 R} - \frac{a_2 PR}{1 + a_2 b_2 R + a_3 b_3 C},$$

$$\frac{dC}{dt} = \frac{c_1 a_1 RC}{1 + a_1 b_1 R} - m_c C - \frac{a_3 PC}{1 + a_2 b_2 R + a_3 b_3 C}, \quad (1)$$

$$\frac{dP}{dt} = \frac{c_2 a_2 RP + c_3 a_3 CP}{1 + a_2 b_2 R + a_3 b_3 C} - m_p P$$

where r and K are intrinsic rate of growth and carrying capacity of the resource, $a_i(i = 1, 2, 3)$ are the attack rate, $b_i(i = 1, 2, 3)$ are the handling time, $c_i(i = 1, 2, 3)$ measure the contribution of the victim to the growth of the IG prey and IG predators, $m_i(i = c, p)$ are the death rates. The above model is the natural extension of tritrophic Rosenzweig–MacArthur food chain model, and it is the same as the one explored in Křivan and Diehl (2005).

This paper extends the above model by incorporating a refuge protecting $\beta_1 R$ of the resource from IG prey and $\beta_2 R$ of the resource from IG predators, and $\beta_3 C$ of the IG prey from IG predators, where $\beta_1, \beta_2, \beta_3 \in [0, 1]$ is constant. Then, the modified system reads as:
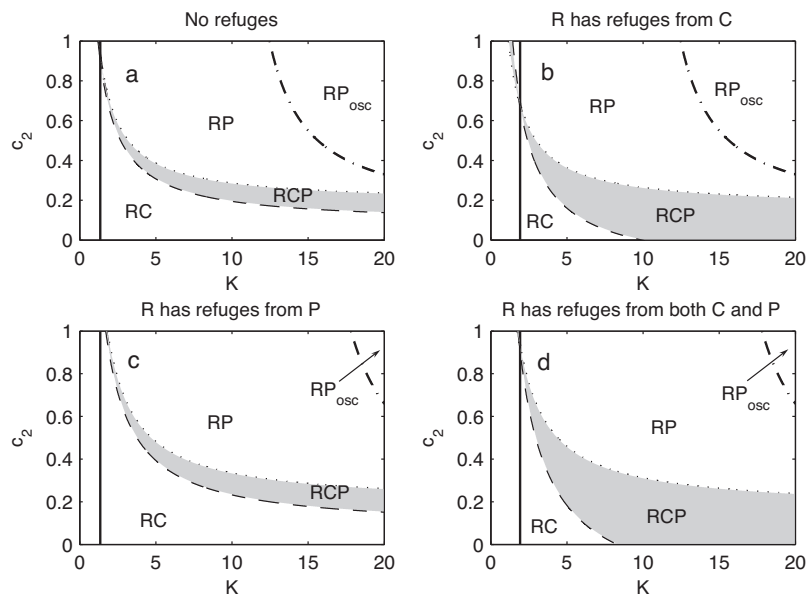

Fig. 1. Influence of conversion efficiencies of the IG prey into the IG predators (c_2), refuges used by the shared prey (β_1, β_2), and the carrying capacity of the resources (K) on species coexistence in IGP system. The dashed line denotes M_{RC} while the dotted line denotes M_{RP}. 3-species coexistence occurs in the shaded region. The vertical line is the threshold level below which the IG prey cannot survive (see (5)). Oscillating attractors are labeled "osc". Different asymptotic community states are labeled by their respective community members (R = the resource, C = the IG prey, P = the IG predator). (a): the system without any refuges ($\beta_1 = \beta_2 = \beta_3 = 0$), (b): the resources are protected only from the IG prey ($\beta_1 = 0.3$, and $\beta_2 = \beta_3 = 0$), (c): the resources are protected only from the IG predators ($\beta_1 = \beta_3 = 0$, and $\beta_2 = 0.3$), (d): the resources are protected from both the IG prey and IG predators ($\beta_1 = \beta_2 = 0.3$, $\beta_3 = 0$). Other parameter value: $c_3 = 0.25$.