BioSystems 152 (2017) 11–23

Contents lists available at ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

Effects of size refuge specificity on a predator–prey model

Hong Zhang [a,*], Feng Tian [b], Prince Harvim [c], Paul Georgescu [d]

[a] Department of Financial Mathematics, Jiangsu University, ZhenJiang, JiangSu 212013, PR China
[b] Faculty of Science, Jiangsu University, ZhenJiang, JiangSu 212013, PR China
[c] Faculty of Science, Jiangsu University, ZhenJiang, JiangSu 212013, PR China
[d] Department of Mathematics, Technical University of Iaşi, Bd. Copou 11A, 700506 Iaşi, Romania

ARTICLE INFO

Article history:
Received 17 July 2016
Received in revised form 1 November 2016
Accepted 6 December 2016
Available online 26 December 2016

Keywords:
Competitive refuge construction
Evolutionary outcome
Degree of specificity
Stability analysis
Invasibility criterion

ABSTRACT

Predation is a major cause of early-stage mortality for prey individuals, which are often forced to use refuges in order to reduce the risk of being consumed. The ability of certain genotypes in a prey population to reach a size refuge from predation may contribute significantly to the preservation of community diversity. We investigate how the specificity of this behavior affects the evolution of a given population by using a modified Lotka-Volterra model, in which the proportion of each genotype available for predation consists of two components: an intrinsic part and a combination from all genotypes present in the population. The trade-off of these components is characterized by a specificity parameter. From the viewpoint of population dynamics, we observe that the ability of the mutant to invade the resident population strongly depends on the values of this parameter. Finally, we describe the possible evolutionary outcomes, analytically and numerically.

1. Introduction

The encounters between competitors or between predator and prey may be shaped by the relative size of the interacting individuals (Olson et al., 1995; Wissinger, 1992). In a predator–prey interaction, the most important part of the prey survival strategy is the ability to find a refuge (Collings, 1995; Gonzalez-Olivares and Ramos-Jiliberto, 2003; Kar, 2005; Ma et al., 2009; Mcfadden, 1986; Ruxton, 1995; Sarwardi et al., 2012, 2013; Sih, 1987), especially a size refuge (Almeida et al., 2011; Rudolf, 2006; Rudolf and Armstrong, 2008), certain prey individuals having a size advantage to escape predation. However, due to ontogenetic changes in size, the prey individuals may be found in different trophic levels (Rudolf and Armstrong, 2008), which implies that the effect one species has on the other eventually may change throughout the ontogeny of those species (Werner and Gilliam, 1984). Different genotypes might reach different size refuges by virtue of expressing different phenotypes, which vary in their degree of adaptation to survive and may then contribute significantly to the preservation of community diversity and structure (Paine, 1976, 1977).

The dependence of predator–prey interactions on prey size has been well documented in marine benthic communities. For example, even if a sea pen (*Ptilosarcus gurneyi*) individual escapes its predators at small sizes, it may eventually grow too large and attract attention of some of its other predators which prefer larger individuals (Birkeland, 1974). Also, field experiments revealed that competitive interactions between *Mytilus edulis* species may change as the relative sizes of the competing individuals vary, those relative sizes being in turn greatly influenced by the predation from crabs (Almeida et al., 2011; Ebling et al., 1964).

In these examples, there is a possibility of free-riding on the genotype that facilitates the escape from predation. The prey ability to do so depends on the specificity of the refuge (Gonzalez-Olivares and Ramos-Jiliberto, 2003). If the modification of the size refuge mechanism is highly specific to the genotype that determines it, then it may be difficult for some other genotypes to survive, whereas a more general modification is easier to free-ride on, which implies that the refuge could promote predator–prey coexistence by preventing prey extinction (Connell, 1972; Murdoch and Oaten, 1975).

It has been concluded from both a theoretical and an experimental point of view that the availability of a prey refuge has a stabilizing effect on predator–prey interactions and also that the prey can escape extinction by using refuges (Anderson, 2001; Cressman and Garay,

---

[*] Corresponding author.
E-mail addresses: hongzhang@ujs.edu.cn (H. Zhang), tianfengcuocuo@sina.com (F. Tian), princeharvim@yahoo.com (P. Harvim), v.p.georgescu@gmail.com (P. Georgescu).

http://dx.doi.org/10.1016/j.biosystems.2016.12.001
0303-2647/

2009; Hochberg and Holt, 1995; Magalhaes et al., 2007; McNair, 1986; Rudolf and Armstrong, 2008; Sih, 1987). From an analytic viewpoint, the study of the influence of prey refuge on the dynamics of predator–prey interactions is now recognized as a significant and challenging issue (Collings, 1995; Gonzalez-Olivares and Ramos-Jiliberto, 2003; Kar, 2005; Huang et al., 2006; Sarwardi et al., 2013; Mukherjee, 2016; Tripathi et al., 2015).

A key question is how the specificity of size refuge construction alters the evolutionary dynamics of the system. A feasible way of modeling this issue is by accounting for the proportion of the each genotype, which is a sum of two components: an intrinsic proportion of each genotype available to the predator and a contribution from all genotypes present in the population. The relative impact of these components is described by the degree of specificity.

Also, to investigate the effect of the evolutionary dynamics of each genotype of prey on the predation behavior inheritance, one should understand mechanisms by which natural selection benefits from different size refuges. On one hand, an invading mutant with specific size refuge may outcompete the former resident and become the new resident. On the other hand, a prey population may adapt in such a way that it can no longer persist (Gyllenberg and Parvinen, 2001). If this is the case, natural selection will drive the species to extinction, phenomenon which is called evolutionary suicide (Ferrière, 2000).

2. Evolutionary results

2.1. The model

We denote by x_i the amount of prey individuals of genotype i, $i = 1, 2, \cdots, n$, and by y the amount of predator individuals. As our template for considering the effect of size refuge formation on predator–prey interactions, we use a modified Lotka-Volterra model, of the form

$$\begin{cases} \dfrac{dx_i}{dt} &= r_i x_i \left(1 - \dfrac{x_T}{K}\right) - pR_i(\mathbf{x})x_i y, \\ \dfrac{dy}{dt} &= qp\displaystyle\sum_{i=1}^{n} R_i(\mathbf{x})x_i y - \delta y,\ i = 1, 2, \cdots, n. \end{cases} \tag{1}$$

In the above, $r_i > 0$ is the genotype specific growth rate, $x_T = \Sigma_{i=1}^{n} x_i$ is the total size of the prey population, K is the total prey carrying capacity, p is the predation rate without size refuge, q and δ are the (density independent) conversion and death rates for predators, respectively. Also, $R_i(\mathbf{x})$, $\mathbf{x} = (x_1, x_2, \ldots, x_n)$, $1 \le i \le n$, describe the size refuge formation and represent the specific proportions of prey genotypes actually available for predation.

We assume that the proportion of each genotype available for predation is determined both by an intrinsic (local) and a combinational (global) component and then use a specificity parameter $\gamma \in [0, 1]$ to interpolate between these components. On one side of the spectrum, where the specificity is maximal, we have the situation in which each genotype has its own intrinsic size refuge and on the other side we have the case of minimal specificity, where prey availability R is given by the weighted mean of the constituent genotypes, i.e.,

$$R = \frac{1}{x_T}\sum_{j=1}^{n}(1 - \theta_j)x_j, \tag{2}$$

where $\theta_j x_j (j = 1, 2, \cdots, n)$ describes the size refuge mechanism protecting the proportion θ_j of the j-th genotype in the prey population, $\theta_j \in [0, 1)$.

We now define

$$R_i(\mathbf{x}) = \gamma(1 - \theta_i) + \frac{1 - \gamma}{x_T}\sum_{j=1}^{n}(1 - \theta_j)x_j. \tag{3}$$

In the above, $\gamma = 1$ corresponds to the local case, in which each genotype has its own intrinsic size refuge, and $\gamma = 0$ corresponds to the global case, in which each genotype uses the same size refuge. The model (1) may now be used to investigate the resilience of a resident population with respect to an invading mutant, considering the impact of the degree of specificity γ.

For the sake of simplicity, we shall consider only the case $n = 2$, situation in which the system (1) simplifies to

$$\begin{cases} \dfrac{dx_1}{dt} &= r_1 x_1 \left(1 - \dfrac{x_1 + x_2}{K}\right) - px_1 R_1(x_1, x_2)y, \\ \dfrac{dx_2}{dt} &= r_2 x_2 \left(1 - \dfrac{x_1 + x_2}{K}\right) - px_2 R_2(x_1, x_2)y, \\ \dfrac{dy}{dt} &= qp\left(x_1 R_1(x_1, x_2) + x_2 R_2(x_1, x_2)\right)y - \delta y \end{cases} \tag{4}$$

with

$$R_i(x_1, x_2) = \gamma(1 - \theta_i) + \frac{1 - \gamma}{x_1 + x_2}\left[(1 - \theta_1)x_1 + (1 - \theta_2)x_2\right], \quad i \in \{1, 2\}. \tag{5}$$

2.2. Invasibility criterion

Without loss of generality, we assume that the first genotype stands for the resident and the second one stands for the mutant. The Jacobian of (4) at an arbitrary point $(\hat{x}_1, \hat{x}_2, \hat{y})$ is given by

$$J = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

with

$$\begin{aligned}
a_{11} &= r_1\left(1 - \frac{2\hat{x}_1 + \hat{x}_2}{K}\right) - p\hat{y}\left(R_1 + \hat{x}_1\frac{\partial R_1}{\partial x_1}\right)\\
a_{12} &= -\frac{r_1\hat{x}_1}{K} - p\hat{x}_1\frac{\partial R_1}{\partial x_2}\hat{y}\\
a_{13} &= -p\hat{x}_1 R_1\\
a_{21} &= -\frac{r_2\hat{x}_2}{K} - p\hat{x}_2\frac{\partial R_2}{\partial x_1}\hat{y}\\
a_{22} &= r_2\left(1 - \frac{\hat{x}_1 + 2\hat{x}_2}{K}\right) - p\hat{y}\left(R_2 + \hat{x}_2\frac{\partial R_2}{\partial x_2}\right)\\
a_{23} &= -p\hat{x}_2 R_2\\
a_{31} &= qp\left(R_1 + \hat{x}_1\frac{\partial R_1}{\partial x_1} + \hat{x}_2\frac{\partial R_2}{\partial x_1}\right)\hat{y}\\
a_{32} &= qp\left(R_2 + \hat{x}_2\frac{\partial R_2}{\partial x_2} + \hat{x}_1\frac{\partial R_1}{\partial x_2}\right)\hat{y}\\
a_{33} &= qp\left(\hat{x}_1 R_1 + \hat{x}_2 R_2\right) - \delta.
\end{aligned}$$

In the above, $R_i = R_i(\hat{x}_1, \hat{x}_2)$ and $\frac{\partial R_i}{\partial x_j} = \frac{\partial R_i}{\partial x_j}(x_1, x_2)|_{(x_1=\hat{x}_1, x_2=\hat{x}_2)}$ for $i, j = 1, 2$. The characteristic equation of J is

$$\Delta(\lambda) = \lambda^3 + \kappa_1\lambda^2 + \kappa_2\lambda + \kappa_3 = 0,$$

where

$$\begin{aligned}
\kappa_1 &= -\mathrm{trace}(J),\\
\kappa_2 &= \begin{vmatrix} r_1(1 - \frac{2\hat{x}_1 + \hat{x}_2}{K}) - p\hat{y}(R_1 + \hat{x}_1\frac{\partial R_1}{\partial x_1}) & -\frac{r_1\hat{x}_1}{K} - p\hat{x}_1\frac{\partial R_1}{\partial x_2}\hat{y} \\ -\frac{r_2\hat{x}_2}{K} - p\hat{x}_2\frac{\partial R_2}{\partial x_1}\hat{y} & r_2(1 - \frac{\hat{x}_1 + 2\hat{x}_2}{K}) - p\hat{y}(R_2 + \hat{x}_2\frac{\partial R_2}{\partial x_2}) \end{vmatrix}\\
&\quad + \begin{vmatrix} r_1(1 - \frac{2\hat{x}_1 + \hat{x}_2}{K}) - p\hat{y}(R_1 + \hat{x}_1\frac{\partial R_1}{\partial x_1}) & -p\hat{x}_1 R_1 \\ qp(R_1 + \hat{x}_1\frac{\partial R_1}{\partial x_1} + \hat{x}_2\frac{\partial R_2}{\partial x_1})\hat{y} & qp(\hat{x}_1 R_1 + \hat{x}_2 R_2) - \delta \end{vmatrix}\\
&\quad + \begin{vmatrix} r_2(1 - \frac{\hat{x}_1 + 2\hat{x}_2}{K}) - p\hat{y}(R_2 + \hat{x}_2\frac{\partial R_2}{\partial x_2}) & -p\hat{x}_2 R_2 \\ qp(R_2 + \hat{x}_2\frac{\partial R_2}{\partial x_2} + \hat{x}_1\frac{\partial R_1}{\partial x_2})\hat{y} & qp(\hat{x}_1 R_1 + \hat{x}_2 R_2) - \delta \end{vmatrix};\\
\kappa_3 &= -\det J.
\end{aligned}$$

Note that a sufficient condition for a Hopf bifurcation to occur is that there exists a bifurcation parameter $\zeta = \zeta_B$ such that $\kappa_1(\zeta_B)\kappa_2(\zeta_B) - \kappa_3(\zeta_B) = 0$ with $\kappa_2 > 0$ and $\frac{d}{d\zeta}(Re(\lambda(\zeta)))|_{\zeta=\zeta_B} \neq 0$, in which λ is given by the characteristic equation $\Delta(\lambda) = 0$.

The monomorphic resident prey population steady states are then given by

$$M_1^* = (K, 0, 0), \quad M_2^* = \left(\frac{\delta}{qp(1-\theta_1)}, 0, \frac{r_1}{p(1-\theta_1)}\left[1 - \frac{\delta}{qp(1-\theta_1)K}\right]\right).$$

To assume that the second equilibrium is feasible, a precondition is given by

$$\theta_1 < \theta^* \doteq 1 - \frac{\delta}{qpK}. \tag{6}$$

The mutant can then invade the resident population if these equilibria are unstable, i.e., if at least one of the eigenvalues of the Jacobian evaluated at x_1^* and x_2^*, respectively, has a positive real part.

The Jacobian $J(M_1^*)$ at M_1^* is given by

$$J(M_1^*) = \begin{pmatrix} -r_1 & -r_1 - p(1-\gamma)(\theta_1 - \theta_2) & -p(1-\theta_1)K \\ 0 & 0 & 0 \\ 0 & 0 & qp(1-\theta_1)K - \delta \end{pmatrix}.$$

One notes that M_1^* is unstable if precondition (6) holds.

The Jacobian $J(M_2^*)$ at M_2^* is given by

$$J(M_2^*) = \begin{pmatrix} -\dfrac{r_1\delta}{qp(1-\theta_1)K} & -\dfrac{r_1\delta}{qp(1-\theta_1)K} - p(1-\gamma)(\theta_1-\theta_2) & -\dfrac{\delta}{q} \\ 0 & S(\gamma)r_1[1 - \dfrac{\delta}{qp(1-\theta_1)K}] & 0 \\ qr_1[1 - \dfrac{\delta}{qp(1-\theta_1)K}] & \dfrac{qr_1(1-\theta_2)}{1-\theta_1}[1 - \dfrac{\delta}{qp(1-\theta_1)K}] & 0 \end{pmatrix},$$

in which

$$S(\gamma) = \frac{r_2}{r_1} - \left[\gamma\left(\frac{1-\theta_2}{1-\theta_1} - 1\right) + 1\right]. \tag{7}$$

If precondition (6) holds, then it is obvious that the ability of the mutant to invade depends only on the sign of $S(\gamma)$. Hence, conditions

$$S(\gamma) > 0 \quad \text{and} \quad \theta_1 < \theta^* \tag{8}$$

altogether imply that the invading mutant succeeds under the pressure of predation.

In the following, we start by investigating the extremal values $\gamma = 1$ and $\gamma = 0$, corresponding to a locally determined versus globally determined size refuge. For the case of the maximal specificity ($\gamma = 1$), we obtain

$$S(1) = \frac{r_2}{r_1} - \frac{1-\theta_2}{1-\theta_1}, \tag{9}$$

which implies that the mutant can invade if

$$\frac{r_2}{r_1} > \frac{1-\theta_2}{1-\theta_1} \quad \text{and} \quad \theta_1 < \theta^*,$$

that is, the ratio $\frac{r_2}{r_1}$ of intrinsic growth rates of the mutant and the resident, respectively, called the relative growth rate, is greater than the ratio $\frac{1-\theta_2}{1-\theta_1}$ of population proportions available for hunting by a predator, called the relative hunting availability. Also, the protected proportion θ_1 of the resident prey is lower than an ecological threshold, which depends on the digestive and reproductive abilities of the predator, its death rate and the carrying capacity of the environment.

In the case of minimal specificity ($\gamma = 0$), we have

$$S(0) = \frac{r_2}{r_1} - 1, \tag{10}$$

which implies that the mutant can invade if $\theta_1 < \theta^*$ and $r_2 > r_1$.

This means that if the resident prey is subject to a maximal protection rate θ^*, then when the specific proportionality of the prey available to the predator is local and determined by its own genotype, there is a selection for mutants with a higher ratio of intrinsic growth rate to hunting availability, that is, with

$$\frac{r_2}{1-\theta_2} > \frac{r_1}{1-\theta_1},$$

while if the specific proportionality of the prey available to the predator is global and determined by all genotypes, there is a selection for mutants with a higher growth rate, that is, with

$$r_2 > r_1.$$

In order to get a better understanding of the impact of the degree of specificity upon the ability of the mutant to invade, we plot the curve $S(\gamma) = 0$ in the $(\frac{1-\theta_2}{1-\theta_1}, \gamma)$-parameter space for six different choices of $\frac{r_2}{r_1}$ taken from Mcfadden (1986) (see Fig. 1). It can then be clearly seen that the invasion of a resident by a mutant does not depend solely on the size of the mutant refuge but also on the value or magnitude of the specificity γ.

The regions below the curves correspond to the subset of mutant characteristics, in terms of the relative hunting availability and of the degree of specificity, for which a mutant can invade. As shown in Figure 1, for high relative hunting availability (>1), the sharpness of the transition decreases with the increase of the relative growth rate, while for low relative hunting availability (<1), the sharpness increases with the increase of the relative growth rate. In other words, the transition is even more sudden as the growth rate of the mutant gets closer to the resident growth rate. These results suggest that a mutant with a high growth rate can invade even if it has a smaller size refuge,

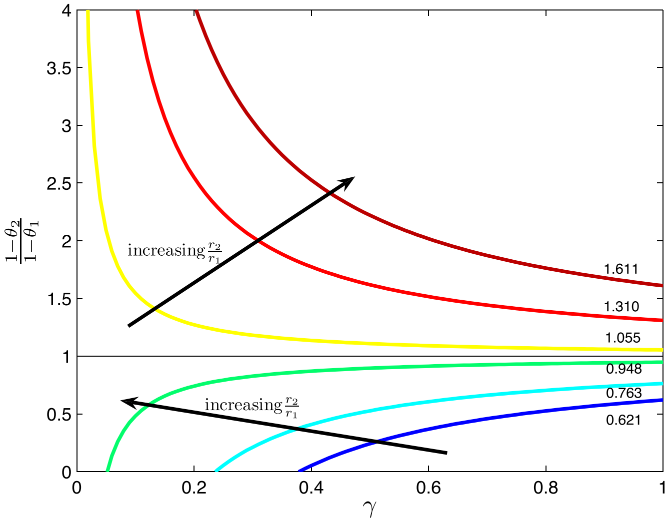

Fig. 1. Ability to invade as a function of the specificity γ. Four genotypes of *Podocoryne carnea* ($P1$–$P4$) were used in a laboratory competition experiment. It was observed that the growth rates of $P1$, $P2$, $P3$ and $P4$ were $1.007\,\frac{\log mm}{\log day}$, $1.319\,\frac{\log mm}{\log day}$, $1.662\,\frac{\log mm}{\log day}$ and $1.062\,\frac{\log mm}{\log day}$. The different curves correspond to the relative growth rate $\frac{r_2}{r_1} \in \{0.621, 0.763, 0.948, 1.055, 1.310, 1.611\}$.

Table 1
Schematic representation of our analytical findings.

Invasion of	Invasion condition	Possible evolutionary outcomes	Stability condition
x_2	$S(\gamma) > 0, \theta_1 < \theta^*$	Only x_2 evolves without y	Appendix I
x_2	$S(\gamma) > 0, \theta_1 < \theta^*$	x_1 and x_2 stably evolve without y	Appendix II
x_2	$S(\gamma) > 0, \theta_1 < \theta^*$	Only x_2 evolves with y	Appendix III
x_2	$S(\gamma) > 0, \theta_1 < \theta^*$	x_1 and x_2 stably evolve with y	Appendix IV

Table 2
The definitions of the system parameters and default values chosen for numerical simulations.

Parameter	Description	Default values
r_1	Growth rate of the resident prey	1.602
r_2	Growth rate of the mutant prey	$0.93r_1$, $1.1r_1$
K	Carrying capacity of the prey	10^5
γ	Degree of specificity	[0, 1]
θ_1	Proportion of protected residents	0.2
θ_2	Proportion of protected mutants	0.3117, 0.6, 0.8,0.9
p	Predation rate without size refuge	0.001, 0.002, 0.008
q	Conversion rate	0.01
δ	Predator death rate	0.1, 0.13, 0.3

while a mutant with a large size refuge can not invade for smaller values of γ, which implies that evolutionary outcomes are strongly determined by the degree of specificity of the size refuge.

As expected, different genotypes of the prey showed a size-specific response to the presence of the predator that reflected their respective difference in mortality risk. Such size-specific responses to predation risk are well identified by experimental research (Bystrom et al., 2003; Sih, 1982). Our results presented herein underline the importance of taking specificity parameter into account when attempting to explain the evolution of the prey can limit the recruitment rate of the predator by stunting the predator's growth rate or let the predator starve to death (Persson, 1988; Persson and Greenberg, 1990), and also, from the mathematical viewpoint, demonstrate the theory that size refuges in the prey can facilitate the coexistence of the predator and prey but only to a small extent (Briggs, 1993; Rudolf, 2007).

2.3. Outcomes of selection

Intuitively, the biological system described by the model (4) could experience different evolutionary outcomes (see Table 1). In order to test this hypothesis, we further investigate the model (4) to account for its evolutionary dynamics.

To this purpose, we consider a resident prey population with $r_1 = 1.602$, $K = 10^5$ and $x_1(0) = 400$. The system is solved numerically with time step $\Delta t = 0.01$, a new mutant being introduced with probability $1,25 \times 10^{-2} x_T \Delta t$ at each time step (see Gerlee and Anderson, 2015). For simplicity, the growth rate and carrying capacity of the prey species and the predation and conversion rates are assumed to be independent of the resident population, but sufficient for our purposes (see Table 2).

Suppose that a rare mutant species appears in the resident population. Natural selection may cause mutants not only to invade, but also to replace the former resident and thus become the new resident (Doebeli and Dieckmann, 2000). As shown in Fig. 2, it is observed that there is an initial increase in both prey populations, resident and mutant. However, the initial growth of the mutant population is much slower, which suggests that the mutants may only gradually take over the resident population. That is, the mutant population invade all genotypes of the residents and, even though the total prey population finally increases (see Fig. 3), this results in lack of available food

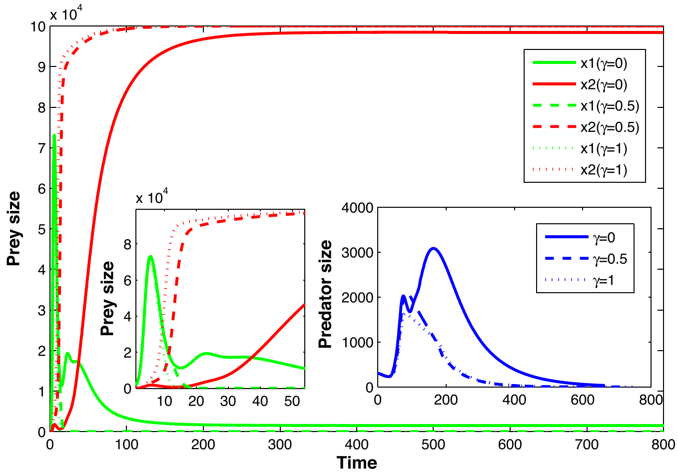

Fig. 2. Evolutionary dynamics of the resident, mutant prey species and predator species for different values of the specificity γ. Here, $r_1 = 1.602$, $r_2 = 1.1r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.9$, $p = 0.001$, $q = 0.01$, $\delta = 0.13$ and $K = 10^5$.

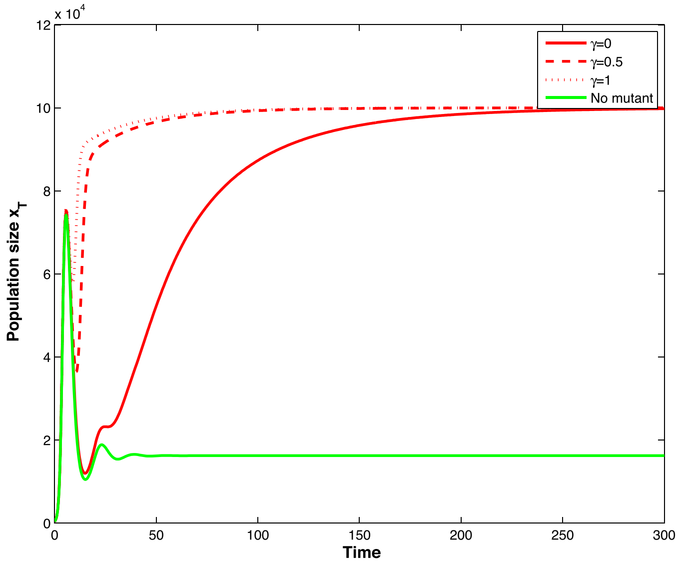

Fig. 3. Total population size of the prey species for different values of the specificity γ. Here, $r_1 = 1.602$, $r_2 = 1.1r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.9$, $p = 0.001$, $q = 0.01$, $\delta = 0.13$ and $K = 10^5$.

for the predators (note that in our simulations θ_2 is several times larger than θ_1). Hence, the size of the predator population falls sharply and the predators are condemned to extinction. Particularly, in the intermediate ($\gamma = 0.5$) and local ($\gamma = 1$) cases, the ability to replace the former resident depends not only on the mutant growth rate, but also on the hunting availability.

In Fig. 2, it is obvious that if the size refuge is global ($\gamma = 0$) and determined by all genotypes, then there is a selection for mutants with a higher protecting proportion. As shown in Fig. 4, once the mutant can invade the resident genotype, then co-evolution is assured if the predator species experiences an increased death rate. We thereby observe the mutant and resident species can coexist in mild environments with the extinction of predator species (see Figs. 2 and 4).

From a practical viewpoint, Fig. 4 highlights the coexistence of mutants and residents as more and more predators die, leading to predator extinction. For $\gamma = 0$, all three populations initially grow, and in time both mutants and residents continue to grow at a constant rate, while the predator population declines drastically. At $\gamma = 0.5$, there is a sharp decline in the predator population, which further decreases until the predator population goes extinct. As a result of the sharp decline in the predator population, the mutant population grows with a sharply increased rate at first and tends to grow at a constant rate afterwards. Also, the resident population declines sharply from a higher height and tends to grow at a constant rate afterwards. However, as more and more mutants invade the resident population, there is a decrease in food supply for the predators and this causes a sharp decline in the predators population. This scenario makes possible the coexistence of mutants and residents. The same scenario is observed for $\gamma = 1$, but occurring at a faster rate compared to what happens when $\gamma = 0$ and $\gamma = 0.5$.

On the other hand, if the predator species has a low death rate and the mutant prey has a low relative hunting availability, then the mutant species can not only invade but also replace the former resident and thus become the new resident as the former prey population gradually die out. Further, the new resident can co-exist with the predator population. This is clearly observed as γ takes values between 0 and 1 (see Fig. 5). Specifically, in the global case ($\gamma = 0$) the evolutionary outcome depends only on the mutant growth rate, whereas in the

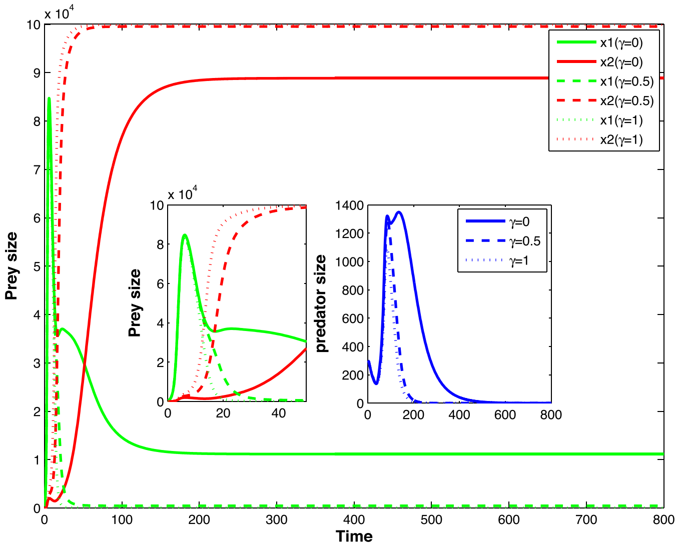

Fig. 4. Evolutionary dynamics of the resident and mutant prey species and of the predator species for different values of the specificity γ (prey coexistence with extinction of the predators). Here, $r_1 = 1.602$, $r_2 = 1.1r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.8$, $p = 0.001$, $q = 0.01$, $\delta = 0.3$ and $K = 10^5$.

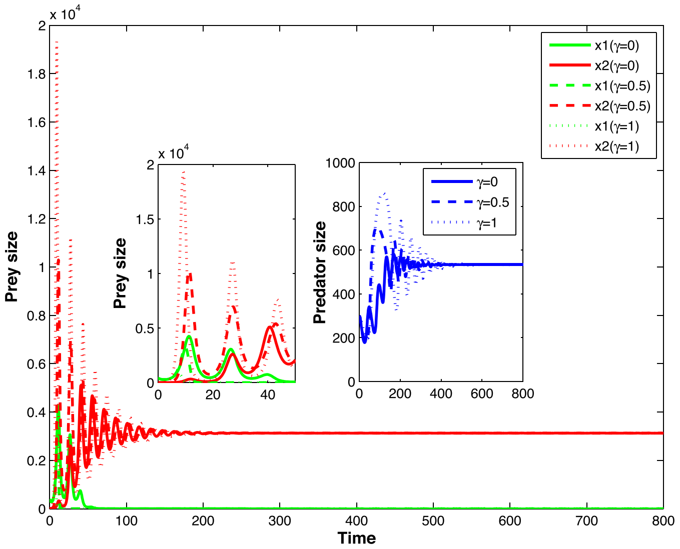

Fig. 5. Evolutionary dynamics of the resident, mutant prey species and predator species for different values of the specificity γ (new resident prey with predator coexistence). Here, $r_1 = 1.602$, $r_2 = 1.1r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.6$, $p = 0.008$, $q = 0.01$, $\delta = 0.1$ and $K = 10^5$.

local case ($\gamma = 1$) the dependence is almost exclusively in the θ-direction. The replacement of the resident population and the coexistence with the predator happen if

$$\theta_2 < \theta^* \quad \text{and} \quad \tilde{S}(\gamma) < 0,$$

in which

$$\tilde{S}(\gamma) = \frac{r_1}{r_2} - \left[\gamma\left(\frac{1-\theta_1}{1-\theta_2} - 1\right) + 1\right],$$

which is illustrated in Fig. 6.

The impact of the degree of specificity γ on the transition from the local to the global dynamics is further examined in Fig. 7. At $\gamma = 0$, all three populations grow freely as in their natural habitats, but as γ is varied from 0 to 1 there is a sharp decline in the resident prey population and a sharp increase in both mutant prey and predator population.

This clearly indicates the impact of the degree of specificity on the transition from the local to global evolution dynamics. Also, the panel shows that at the two extremes of size refuge specificity, the mutant may not need to have a growth rate that exceeds the one of resident in order to spread in the population, which does not resemble the situation pictured in Fig. 5, because of the higher growth rate of the mutants. Since the predator species has a higher death rate, the mutant has a chance of replacing the former resident provided that it is offered protection by the size refuge mechanism. Moving between the two extremes by varying the specificity parameter γ shows the fact that mutant and resident prey species may evolve and co-exist with the predator species, which could ensure the preservation of community diversity and structure.

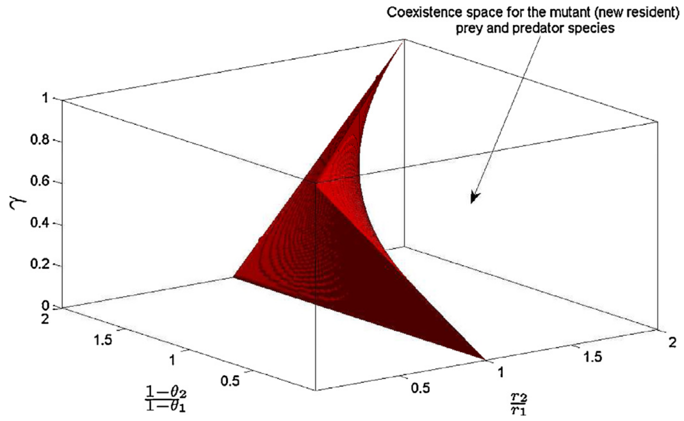

Fig. 6. Coexistence space (on the right hand side of the red surface) of the mutant (new resident) prey species and predator species for different values of the specificity γ, the relative growth rate ($\frac{r_2}{r_1}$) and the relative hunting availability $\frac{1-\theta_2}{1-\theta_1}$.

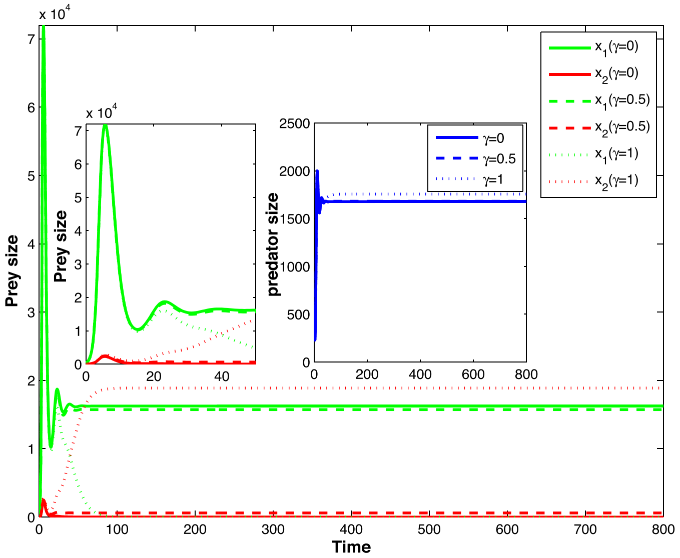

Fig. 7. Evolutionary dynamics of the resident, mutant prey species and predator species for different values of the specificity γ. Here, $r_1 = 1.602$, $r_2 = 0.93r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.3117$, $p = 0.002$, $q = 0.01$, $\delta = 0.3$ and $K = 10^5$.

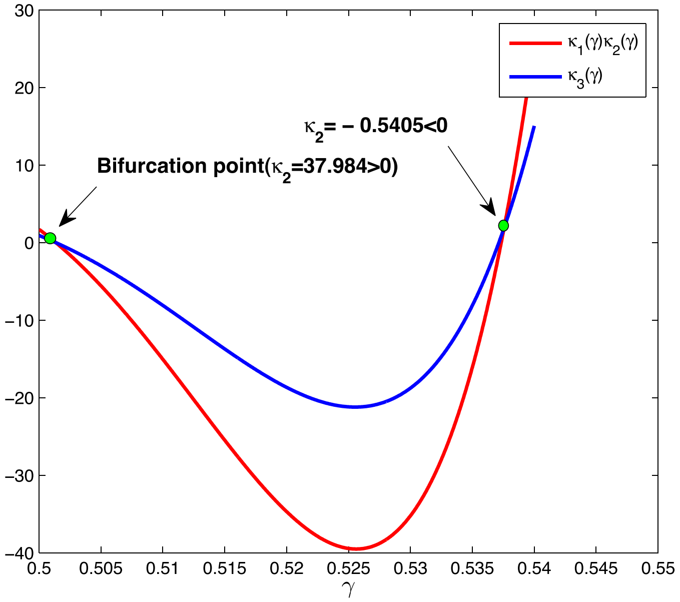

Fig. 8. Sufficient conditions for the existence of a Hopf bifurcation, with γ taken as a bifurcation parameter. Here, $r_1 = 1.602$, $r_2 = 0.93r_1$, $\theta_1 = 0.2$, $\theta_2 = 0.3117$, $p = 0.002$, $q = 0.01$, $\delta = 0.3$ and $K = 10^5$.

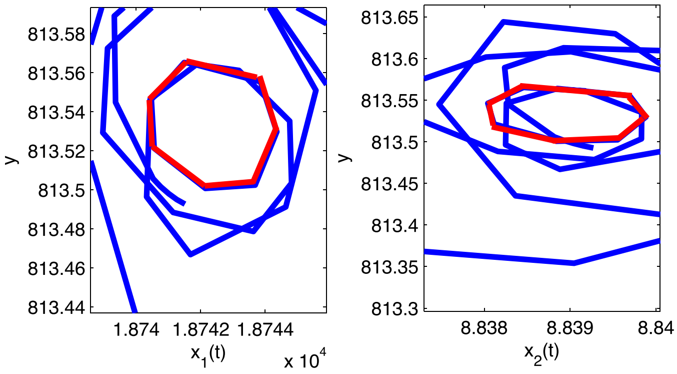

Fig. 9. Projections of the limit cycle on the x_1–y plane and the x_2–y plane, respectively.

2.4. Bifurcation analysis

In this section, we characterize from a numerical viewpoint the occurrence of a Hopf bifurcation, with γ taken as a bifurcation parameter. The characteristic equation of the Jacobian matrix evaluated at the equilibrium $E_4^* = (x_1^*, x_2^*, y^*)$ is given by

$$\Delta(\lambda) = \lambda^3 + \kappa_1\lambda^2 + \kappa_2\lambda + \kappa_3 = 0,$$

κ_1, κ_2, κ_3 being defined as in Subsection 2.2. The sufficient condition for a Hopf bifurcation to occur is that there exists a value γ_0 of γ such that $\kappa_1(\gamma_0)\kappa_2(\gamma_0) - \kappa_3(\gamma_0) = 0$, with $\kappa_2 > 0$ and $\frac{d}{d\gamma}(Re(\lambda(\gamma)))|_{\gamma=\gamma_0} \neq 0$, in which λ is given by the characteristic equation $\Delta(\lambda) = 0$. In our settings, this condition is met with $\gamma_0 \approx 0.501342882721575$, fact illustrated in Fig. 8. One notes that there is a unique stable limit cycle in our system, as shown in Fig. 9.

3. Concluding remarks

In this paper, we model the effect of size refuge formation on predator–prey interactions by using a modified Lotka-Volterra model consisting of three populations: resident prey, x_1, predators, y and an invading prey, x_2. Of concern is the impact of specificity γ, characterizing the trade-off between the intrinsic (local) and combinational (global) size refuge structures, upon the dynamics of the system.

First of all, a criterion establishing the ability of the mutant to invade the equilibria of the system, namely the equilibrium with resident prey and no mutants or predators and the equilibrium with resident prey and predators, but no mutants, is derived by ensuring the instability of these equilibria.

After investigating the stability of a resident population with respect to an invading mutant, we find out that under the invasibility condition

$$S(\gamma) > 0, \quad \theta_1 < \theta^*,$$

we can observe four different outcomes:

(i) Only mutants evolve without predators.
(ii) Residents and mutants both evolve and are stable without predators.
(iii) Only mutants evolve with predators.
(iv) Residents and mutants are stable with predators.

Further investigation is done on the impact of specificity γ, being observed that at higher values of γ, the rate of invasion and takeover by the mutants are very high and the dynamics of the system is fast compared to what happens for lower values of γ. Also, at higher values of γ, once there is a major takeover by the mutants, the predator population dies at a faster rate and this creates a state of co-existence between the remaining prey and predator (mutants which serve as new residents).

Moving between the two extremes, by varying the specificity parameter between zero and one, results in the mutant and resident prey species evolving in a stable co-existence with the predator species, which may play an important role in the preservation of community structures and diversity. Also, it becomes clear that the different degrees of specificity have great impact on the transition from the local to the global dynamics of evolution.

Acknowledgments

The work of P. Georgescu was supported by a grant of the Romanian National Authority for Scientific Research, CNCS UEFISCDI, project number PN-II-ID-PCE-2011-3-0557.

Appendix A. Stability condition for $E_1^* = (0, K, 0)$

The Jacobian at $E_1^* = (0, K, 0)$ is given by

$$J(E_1^*) = \begin{pmatrix} 0 & 0 & 0 \\ -r_2 & -r_2 & -p(1-\theta_2)K \\ 0 & 0 & qp(1-\theta_2)K - \delta \end{pmatrix}.$$

Then,

$$\det(\lambda I_3 - J(E_1^*)) = \lambda(\lambda + r_2)\{\lambda - [qp(1-\theta_2)K - \delta]\},$$

which implies that the condition for the stability of E_1^* is

$$\theta_2 > \theta^*.$$

Appendix B. Stability condition for $E_2^* = (x_1^*, x_2^*, 0)$

The Jacobian at $E_2^* = (x_1^*, x_2^*, 0)$ is given by:

$$J(E_2^*) = \begin{pmatrix} b_{11} & b_{12} & b_{13} \\ b_{21} & b_{22} & b_{23} \\ b_{31} & b_{32} & b_{33} \end{pmatrix},$$

with

$$\begin{aligned}
b_{11} &= -\frac{r_1 x_1^*}{K}, \\
b_{12} &= -\frac{r_1 x_1^*}{K} - \frac{p(1-\gamma)(\theta_1 - \theta_2){x_1^*}^2}{K^2}, \\
b_{13} &= -p x_1^* R_1(x_1^*, x_2^*), \\
b_{21} &= -\frac{r_2 x_2^*}{K} - \frac{p(1-\gamma)(\theta_2 - \theta_1){x_2^*}^2}{K^2}, \\
b_{22} &= -\frac{r_2 x_2^*}{K}, \\
b_{23} &= -p x_2^* R_2(x_1^*, x_2^*), \\
b_{31} &= 0, \\
b_{32} &= 0, \\
b_{33} &= qp x_1^* R_1(x_1^*, x_2^*) + qp x_2^* R_2(x_1^*, x_2^*) - \delta.
\end{aligned}$$

Then,

$$\begin{aligned}
\det(\lambda I_3 - J(E_2^*)) = {} & \left\{ \lambda^2 + \frac{r_1 x_1^* + r_2 x_2^*}{K}\lambda + \frac{p(1-\gamma)x_1^* x_2^*}{K^3} \cdot \left[\frac{p(\theta_1 - \theta_2)^2 (1-\gamma) x_1^* x_2^*}{K} - r_1 x_1^*(\theta_1 - \theta_2) - r_2 x_2^*(\theta_2 - \theta_1) \right] \right\} \\
& \cdot \left\{ \lambda - \left[qp x_1^* R_1(x_1^*, x_2^*) + qp x_2^* R_2(x_1^*, x_2^*) - \delta \right] \right\}.
\end{aligned}$$

It is then seen that E_2^* is stable provided that

$$\begin{aligned}
\frac{p(\theta_1 - \theta_2)^2 (1-\gamma) x_1^* x_2^*}{K} &> r_1 x_1^*(\theta_1 - \theta_2) + r_2 x_2^*(\theta_2 - \theta_1) \\
qp x_1^* R_1(x_1^*, x_2^*) + qp x_2^* R_2(x_1^*, x_2^*) &< \delta.
\end{aligned}$$

Appendix C. Stability condition for $E_3^* = (0, x_2^*, y^*)$

The Jacobian at

$$E_3^* = (0, x_2^*, y^*) = \left(0, \frac{\delta}{qp(1-\theta_2)}, \frac{r_2}{p(1-\theta_2)}\left[1 - \frac{\delta}{qp(1-\theta_2)K}\right]\right)$$

is given by

$$J(E_3^*)=\begin{pmatrix} \tilde{S}(\gamma)r_2[1-\dfrac{\delta}{qp(1-\theta_2)K}] & 0 & 0\\ -\dfrac{r_2\delta}{qp(1-\theta_2)K}-p(1-\gamma)(\theta_2-\theta_1) & -\dfrac{r_2\delta}{qp(1-\theta_2)K} & -\dfrac{\delta}{q}\\ \dfrac{qr_2(1-\theta_1)}{1-\theta_2}[1-\dfrac{\delta}{qp(1-\theta_2)K}] & qr_2[1-\dfrac{\delta}{qp(1-\theta_2)K}] & 0 \end{pmatrix},$$

in which

$$\tilde{S}(\gamma)=\frac{r_1}{r_2}-\left[\gamma\left(\frac{1-\theta_1}{1-\theta_2}-1\right)+1\right].$$

Then

$$\det(\lambda I_3-J(E_3^*))=\left\{\lambda-\tilde{S}(\gamma)r_2\left[1-\frac{\delta}{qp(1-\theta_2)K}\right]\right\}\cdot\left\{\lambda^2+\frac{r_2\delta}{qp(1-\theta_2)K}\lambda+r_2\delta\left[1-\frac{\delta}{qp(1-\theta_2)K}\right]\right\}. \tag{11}$$

Let us consider the following algebraic equation

$$\lambda^2+\frac{r_2\delta}{qp(1-\theta_2)K}\lambda+r_2\delta\left[1-\frac{\delta}{qp(1-\theta_2)K}\right]=0.$$

One sees that

$$\begin{aligned}\lambda_1+\lambda_2 &= -\frac{r_2\delta}{qp(1-\theta_2)K}<0\\ \lambda_1\lambda_2 &= r_2\delta[1-\frac{\delta}{qp(1-\theta_2)K}]>0\end{aligned}$$

if $\theta_2<\theta^*$. Consequently, E_3^* is stable if

$$\theta_2<\theta^* \quad \text{and} \quad \tilde{S}(\gamma)<0.$$

Appendix D. Stability condition for $E_4^*=(x_1^*,x_2^*,y^*)$

Here, $E_4^*=(x_1^*,x_2^*,y^*)$, with

$$\begin{aligned} x_1^* &= \frac{\delta}{qp\gamma}\frac{\gamma r_2(\theta_2-\theta_1)+(r_2-r_1)(1-\theta_2)}{(\theta_1-\theta_2)[r_1(1-\theta_2)-r_2(1-\theta_1)]},\\ x_2^* &= \frac{\delta}{qp\gamma}\frac{\gamma r_1(\theta_1-\theta_2)+(r_1-r_2)(1-\theta_1)}{(\theta_1-\theta_2)[r_1(1-\theta_2)-r_2(1-\theta_1)]},\\ y^* &= \frac{r_2-r_1}{p(\theta_1-\theta_2)}\left\{1-\frac{\delta}{qp\gamma K}\frac{(1-\gamma)(r_2-r_1)}{r_1(1-\theta_2)-r_2(1-\theta_1}\right\}.\end{aligned}$$

Note also that the following relations need to be satisfied

$$x_1^*+x_2^* = \frac{\delta}{qp\gamma}\frac{(1-\gamma)(r_2-r_1)}{r_1(1-\theta_2)-r_2(1-\theta_1)}, \quad R_1 = \frac{\gamma r_1(\theta_1-\theta_2)}{r_2-r_1}, \quad R_2=\frac{\gamma r_2(\theta_1-\theta_2)}{r_2-r_1}.$$

It then follows that in order to ensure the existence of E_4^* one should assume one of the following sets of conditions

(i)
$$\begin{gathered} r_1>r_2, \quad \theta_2>\theta_1, \quad \gamma<\frac{1-\theta_1}{\theta_2-\theta_1}\\ \frac{1}{1-\dfrac{\gamma(\theta_2-\theta_1)}{1-\theta_1}}<\frac{r_1}{r_2}<1+\frac{\gamma(\theta_2-\theta_1)}{1-\theta_2}, \quad \frac{r_1}{r_2}<\frac{Kqp\gamma(1-\theta_1)+\delta(1-\gamma)}{Kqp\gamma(1-\theta_2)+\delta(1-\gamma)}\end{gathered}$$

(ii)
$$\begin{gathered} r_2>r_1, \quad \theta_1>\theta_2, \quad \gamma<\frac{1-\theta_2}{\theta_1-\theta_2}\\ \frac{1}{1-\dfrac{\gamma(\theta_1-\theta_2)}{1-\theta_2}}<\frac{r_2}{r_1}<1+\frac{\gamma(\theta_1-\theta_2)}{1-\theta_1}, \quad \frac{r_2}{r_1}<\frac{Kqp\gamma(1-\theta_2)+\delta(1-\gamma)}{Kqp\gamma(1-\theta_1)+\delta(1-\gamma)}\end{gathered}$$

Note that E_4^* may not exist for certain parameter ranges. For instance, for the first set of conditions, E_4^* does not exist if

$$\frac{Kqp\gamma(1-\theta_1)+\delta(1-\gamma)}{Kqp\gamma(1-\theta_2)+\delta(1-\gamma)} < \frac{1}{1-\frac{\gamma(\theta_2-\theta_1)}{1-\theta_1}},$$

while for the second set of conditions, it does not exist if

$$\frac{Kqp\gamma(1-\theta_2)+\delta(1-\gamma)}{Kqp\gamma(1-\theta_1)+\delta(1-\gamma)} < \frac{1}{1-\frac{\gamma(\theta_1-\theta_2)}{1-\theta_2}}$$

Then the Jacobian $J(E_4^*)$ is of the form

$$J(E_4^*) = \begin{pmatrix} a & b & c \\ d & e & f \\ g & h & l \\ & & \end{pmatrix},$$

where

$$\begin{aligned}
a &= r_1\left(1-\frac{x_1^*+x_2*}{K}\right)-\frac{r_1x_1^*}{K}-py^*\left(\gamma(1-\theta_1)+(1-\gamma)[\frac{(1-\theta_1)x_1^*+(1-\theta_2)x_2^*}{x_1^*+x_2^*}]\right)\\
&\quad -px_1^*y^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)^2}+\frac{(1-\gamma)(1-\theta_1)}{x_1^*+x_2^*}\right),\\
b &= -\frac{r_1x_1^*}{K}-px_1^*y^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)^2}+\frac{(1-\gamma)(1-\theta_2)}{x_1^*+x_2^*}\right),\\
c &= -px_1^*\left(\gamma(1-\theta_1)+\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{x_1^*+x_2^*}\right), d=-\frac{r_2x_2^*}{K}-px_2^*y^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)^2}+\frac{(1-\gamma)(1-\theta_1)}{x_1^*+x_2^*}\right),\\
e &= r_2(1-\frac{x_1^*+x_2*}{K})-\frac{r_2x_2^*}{K}-py^*\left(\gamma(1-\theta_2)+(1-\gamma)[\frac{(1-\theta_1)x_1^*+(1-\theta_2)x_2^*}{x_1^*+x_2^*}]\right)\\
&\quad -px_2^*y^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)^2}+\frac{(1-\gamma)(1-\theta_2)}{x_1^*+x_2^*}\right), f=-px_2^*\left(\gamma(1-\theta_2)+\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{x_1^*+x_2^*}\right),\\
g &= qpy^*\left(\gamma(1-\theta_1)+(1-\gamma)[\frac{(1-\theta_1)x_1^*+(1-\theta_2)x_2^*}{x_1^*+x_2^*}]\right)+qpy^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)}+(1-\gamma)(1-\theta_1)\right),\\
h &= qpy^*\left(\gamma(1-\theta_2)+(1-\gamma)[\frac{(1-\theta_1)x_1^*+(1-\theta_2)x_2^*}{x_1^*+x_2^*}]\right)+qpy^*\left(-\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{(x_1^*+x_2^*)}+(1-\gamma)(1-\theta_2)\right),\\
l &= qpx_1^*\left(\gamma(1-\theta_1)+\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{x_1^*+x_2^*}\right)+qpx_2^*\left(\gamma(1-\theta_2)+\frac{(1-\gamma)[(1-\theta_1)x_1^*+(1-\theta_2)x_2^*]}{x_1^*+x_2^*}\right)-\delta.
\end{aligned}$$

We then obtain the characteristic equation

$$\lambda^3+a_2\lambda^2+a_1\lambda+a_0=0,$$

in which

$$\begin{aligned}
a_2 &= -(a+e+l),\\
a_1 &= ae+al+el-(cg+fh+bd),\\
a_0 &= afh+bdl+ceg-(ael+cdh+bfg).
\end{aligned}$$

It follows from the Routh-Hurwitz criterion that E_4^* is stable if and only if

$$a_0, a_1, a_2 > 0 \quad \text{and} \quad a_1a_2 > a_0.$$

As a side remark, note that the model without prey refuge does not exhibit stability properties for the positive equilibrium, not even of a local nature.

For $r_1 \neq r_2$, the model without prey refuge does not have a positive equilibrium to begin with, since the first two equilibrium equations are incompatible.

For $r_1 = r_2$, one sees that the boundary equilibrium $(\frac{\delta}{qp}, 0, \frac{r}{p}\left(1-\frac{\delta}{qpK}\right))$ attracts all solutions whose (x_1, x_2)-components start above the line which bisects the first (x_1, x_2)-quadrant, while the boundary equilibrium $(0, \frac{\delta}{qp}, \frac{r}{p}\left(1-\frac{\delta}{qpK}\right))$ attracts all solutions whose (x_1, x_2)-components start below the line which bisects the first (x_1, x_2)-quadrant, the (non-unique) positive equilibria being unstable. Consequently, whatever stability properties E_4^* may have, they are induced by the prey refuge structure and there may be situations in which E_4^* is unstable, inheriting its (in)stability properties from the model without prey refuge. However, we have been unable to obtain a more precise analytic characterization of the stability properties of E_4^*, apart from the above one.

References

Almeida, M.J., González-Gordillo, J.I., Flores, A.A.V., Queiroga, H., 2011. Cannibalism, post-settlement growth rate and size refuge in a recruitment-limited population of the shore crab Carcinus maenas. J. Exp. Mar. Biol. Ecol. 410, 72–79.

Anderson, T.W., 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82, 245–257.

Birkeland, C., 1974. Interactions between a sea pen and seven of its predators. Ecol. Monogr. 44, 211–232.

Briggs, C.J., 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. Am. Nat. 141, 372–397.

Bystrom, P., Persson, L., Wahlstrom, E., Westman, E., 2003. Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. J. Anim. Ecol. 72, 156–168.

Collings, J.B., 1995. Bifurcation and stability analysis of temperature-dependent mite predator–prey interaction model incorporating a prey refuge. J. Math. Biol. 57, 63–76.

Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Syst. 3, 169–192.

Cressman, R., Garay, J., 2009. A predator–prey refuge system: evolutionary stability in ecological systems. Theor. Popul. Biol. 76, 248–257.

Doebeli, M., Dieckmann, U., 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. Am. Nat. 156, 77–101.

Ebling, F.J., Kitching, J.A., Muntz, L., Taylor, C.M., 1964. The ecology of Lough Ine XIII. Experimental observations of the destruction of Mytilus edulis and Nucella lapillus by crabs. J. Anim. Ecol. 33, 73–82.

Ferrière, R., 2000. Adaptive responses to environmental threats: evolutionary suicide, insurance, and rescue. In: in Options Spring 2000, Laxenburg, Austria: IIASA, pp. 12–16.

Gerlee, P., Anderson, A.R., 2015. The evolution of carrying capacity in constrained and expanding tumour cell populations. Phys. Biol. 12 (5), article id. 056001.

Gonzalez-Olivares, E., Ramos-Jiliberto, R., 2003. Dynamics consequences of prey refuge in a simple model system: more prey and few predators and enhanced stability. Ecol. Model 166, 135–146.

Gyllenberg, M., Parvinen, K., 2001. Necessary and sufficient conditions for evolutionary suicide. Bull. Math. Biol. 63, 981–993.

Hochberg, M.E., Holt, R.D., 1995. Refuge evolution and the population dynamics of coupled of host-parasitoid associations. J. Evol. Ecol. 9, 633–661.

Huang, Y., Chen, F., Zhong, L., 2006. Stability analysis of prey-predator model with Holling type III response function incorporating a prey refuge. Appl. Math. Comput. 182, 672–683.

Kar, T.K., 2005. Stability analysis of a prey-predator model incorporating a prey refuge. Commun. Nonlinear Sci. Numer. Simul. 10, 681–691.

Ma, Z., Li, W., Zhao, Y., Wang, W., Zhang, H., Li, Z., 2009. Effects of prey refuges on a predator–prey model with a class of functional responses: the role of refuges. Math. Biosci. 218, 73–79.

Magalhaes, S., van Rijn, P.C.J., Montserrat, M., Pallini, A., Sabelis, M.W., 2007. Population dynamics of thrips prey and their mite predators in a refuge. Oecologia 150, 557–568.

Mcfadden, C.S., 1986. Laboratory evidence for a size refuge in competitive interactions between the hydroids hydractinia echinata (flemming) and podocoryne carnea (SARS). Biol. Bull. 171, 161–174.

McNair, J.N., 1986. The effect of refuge on prey-predator interactions: a reconsideration. Theor. Popul. Biol. 29, 38–63.

Mukherjee, D., 2016. The effect of refuge and immigration in a predator–prey system in the presence of a competitor for the prey. Nonlinear Anal. Real World Appl. 31, 277–287.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Adv. Ecol. Res. 9, 1–31.

Olson, M.H., Mittelbach, G.G., Osenberg, C.W., 1995. Competition between Predator and Prey: Resource-Based Mechanisms and Implications for Stage-Structured Dynamics. Ecology 76, 1758–1771.

Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the Mytilus Pisaster interaction. Ecology 57, 858–873.

Paine, R.T., 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Acad. Nat. Sci. Special Publ. 12, 245–270.

Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations. In: Ebenman, B., Persson, L. (Eds.), Size-structured populations-ecology and evolution. Springer, Berlin, pp. 203–218.

Persson, L., Greenberg, L.A., 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-Roach (*Rutilus rutilus*) interaction. Ecology 71, 44–56.

Rudolf, V.H.W., 2006. The influence of size-specific indirect interactions in predator–prey systems. Ecology 87, 362–371.

Rudolf, V.H.W., 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88, 2697–2705.

Rudolf, V.H.W., Armstrong, J., 2008. Emergent impacts of cannibalism and size refuges in prey on intraguild predation systems. Oecologia 157, 675–686.

Ruxton, G.D., 1995. Short term refuge use and stability of predator–prey model. Theor. Popul. Biol. 47, 1–17.

Sarwardi, S., Mandal, P.K., Ray, S., 2012. Analysis of a competitive prey-predator system with a prey refuge. Biosystems 110, 133–148.

Sarwardi, S., Mandal, P.K., Ray, S., 2013. Dynamical behaviour of a two-predator model with prey refuge. J. Biol. Phys. 39, 701–722.

Sih, A., 1982. Foraging strategies and the avoidance of predation by an aquatic insect, Notonecta hoffmanni. Ecology 63, 786–796.

Sih, A., 1987. Prey refuge and predator–prey stability. Theor. Popul. Biol. 31, 1–12.

Tripathi, J.P., Abbas, S., Thakur, M., 2015. A density dependent delayed predator–prey model with Beddington–DeAngelis type function response incorporating a prey refuge. Commun. Nonlinear Sci. Numer. Simul. 22, 427–450.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15, 393–426.

Wissinger, S.A., 1992. Niche overlap and the potential for competition between intraguild predation between size-structured populations. Ecology 74, 207–218.