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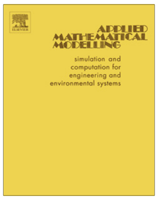

Evolutionary analysis of a predator–prey community under natural and artificial selections ☆

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ABSTRACT

This paper investigates the evolutionary impacts of size-selective harvesting and size-dependent competition in predators on an evolving trait of predator individuals (e.g. body size and maturation age) in a predator–prey model. By using population dynamics and adaptive dynamics, we obtain the evolutionary conditions allowing for evolutionary branching and continuously stable strategy under asymmetric competition in predators for natural selection and size-dependent harvesting for artificial selection. The evolution of polymorphism is explored by numerical analysis and simulations. It is shown that high levels of sequence polymorphism may work up during adaptive evolution that leads to biological diversity. First, increase in competition among predators can result in rapid evolution towards larger body size or maturation age, but harvesting has an opposite effect. Second, competition can make for evolutionary branching, while harvesting can go against evolutionary branching and promote evolutionary stability. Last, from an evolutionary point of view, that competition can promote species diversity among predator populations, however, harvesting has an opposite effect.

1. Introduction

We know that, in recent years, great changes have taken place in the phenotype traits of many species, such as small body size and earlier maturation [1–3], and we are also aware that natural selection and artificial selection play an important role in phenotype traits' evolution processes. However, they have different consequences of the phenotype traits [4].

Natural selection is good for improving individuals' adaptability, and individuals which have high fitness values survive. Thus it is not surprising that the mutant with a lager body size is easier to survive under natural selection. When competing for limited resources, the larger individuals have competition advantage to survive relative to its small contestant [5], which is a phenomenon known as asymmetric competition, for example, the bigger predator can catch more prey. The natural selection due to the asymmetric competition is a persistent and continuing phenomenon in nature [6].

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Artificial selection happens all the time nowadays, for example, size-dependent harvesting where large individuals of a particular species are preferentially taken, as a consequence a rapid evolution of smaller body mass occurs in both terrestrial and marine resources [7,8]. Therefore, as a phenotype trait, body size will be taken as an object of study. Human-induced evolution due to the artificial selection can be fast and harmful, which has been confirmed by both theoretical and empirical studies [9,10].

The aim of this paper is to explore the influence of size-selective harvesting predators and competition in predators on evolutionary changes in adaptive dynamics of a predator–prey system. In particular, we will seek the conditions, under which evolutionary branches in predator phenotype and the mutant predator stably coexists with the resident predator at a much longer timescale of evolution. Moreover, after the primary branching in predator phenotype, we further investigate the final evolutionary state of such a dimorphic predator population and show an attractive dimorphism can proceed to undergo a secondary branching which leads to a polymorphic population.

The rest of the paper is organised as follows. Next section, a predator–prey type of model is proposed. Population dynamics and evolutionary dynamics are investigated and the invasion fitness for the mutant predators is derived in Section 3. We then study the influence of competition for natural selection and harvesting for artificial selection on evolution changes in the phenotype traits in Section 4. Moreover, Section 4 also discusses the dimorphic coexistence and the coevolution of population model with two resident predators. Finally, we conclude the paper in Section 5 with discussions.

2. The mathematical model

Well known facts are that

- individuals with large body size (maturation age) have not only the higher probability to win the competition but also the higher capture rates;
- it is common in nature that the large individuals of a particular species are preferentially taken.

In virtue of the importance of body size (maturation age) in size-selective harvesting and in determining interactions between competing species, we regard body size (maturation age) as the phenotype trait. And in this study, we consider effects of the trait on (a) the capital capture rate, (b) the harvesting rate and (c) the competition coefficient in the predator population. Then, we reach a model governed by

$$\begin{cases} N'(t) = rN\left(1 - \frac{N}{k}\right) - \sum_{i=1}^{n} \beta(x_i)NP_i, \\ P_i'(t) = \theta\beta(x_i)NP_i - dP_i - h(x_i)P_i - \sum_{j=1}^{n} a(x_i - x_j)P_iP_j, \end{cases} \tag{1}$$

where $N(t)$ is the prey density and $P_i(t), i = 1, 2, \ldots, n$ denote the population densities of the predators at time t; x_i is the phenotype trait of the predator population P_i; n is the number of strategies which present in the population; r is the intrinsic growth rate of $N(t)$; k denotes the biggest environmental intake capacity; $\beta(x_i)$ and θ stand for the capital capture rate and the transform rate, respectively; d is the death rate of the predator population; $h(x_i)$ is the harvest rate of the predator population $P_i(t)$; the competition coefficient, $a(x_i - x_j)$, indicates the effect of strategy x_j on strategy x_i.

3. Adaptive dynamics

In this section, we shall derive the invasion fitness of a rare mutant predator in a resident-settled environment and seek the general conditions for evolutionary branching and evolutionary stable strategy. We start with a singe resident population and then proceed with higher level dimorphic populations. It assumes that the mutation occurs infrequently when the resident populations are settling on their demographic attractor [11]. In addition, when a mutant with a slightly different strategy appears in a resident system, its population density is assumed to be so rare that it has a negligible effect on the resident populations. Thus the invasion fitness of the mutant is entirely determined by the demographic attractor of the resident strategies.

3.1. Monomorphic adaptive dynamics

In this subsection, we first develop the population dynamics with a prey and a resident predator that has a trait x; then we seek the invasion fitness that to be used to explore the evolutionary dynamics; and at last, we seek the conditions under which the resident predator undergoes evolution branching.

For a predator population of a single resident strategy x, population model (1) becomes

$$\begin{cases} N'(t) = rN\left(1 - \frac{N}{k}\right) - \beta(x)NP, \\ P'(t) = \theta\beta(x)NP - dP - h(x)P - a(0)P^2. \end{cases} \tag{2}$$

Obviously, if

$$\theta k\beta(x) > d + h(x), \tag{3}$$

(2) has a positive equilibrium $E_1(N^*(x), P^*(x))$ with

$$N^*(x) = \frac{k[d\beta(x) + h(x)\beta(x) + ra(0)]}{\theta k\beta^2(x) + ra(0)}, \quad P^*(x) = \frac{r[-d + \theta k\beta(x) - h(x)]}{\theta k\beta^2(x) + ra(0)} \tag{4}$$

and it is globally asymptotically stable. Therefore, condition (3) ensures the global asymptotical stability of $E_1(N^*(x), P^*(x))$ before the mutant predators appear. To know how and why predators evolve, we first need to derive the invasion fitness for a mutant predator population.

Suppose that mutant predators with a slightly different trait are rare when they appear in the resident populations. From [11–14], also assume that mutations occur infrequently and the populations have reached their equilibria by the time the next mutants come along. Thus, mutant predators can encounter the resident predator–prey community at $E_1(N^*(x), P^*(x))$.

When rare mutant predators with a slightly different trait y appear in the resident predator–prey model at a low density, the population dynamical model (1) becomes

$$\begin{cases} N'(t) = rN\left(1 - \frac{N}{k}\right) - \beta(x)NP - \beta(y)NP_y, \\ P'(t) = \theta\beta(x)NP - dP - h(x)P - a(0)P^2 - a(x-y)PP_y, \\ P'_y(t) = \theta\beta(y)NP_y - dP_y - h(y)P_y - a(y-x)P_yP - a(0)P_y^2, \end{cases} \tag{5}$$

where $P_y(t)$ is the population density of mutant predators at time t. Before the mutation occurs, the resident populations are at $E_1(N^*(x), P^*(x))$ or close to it. This implies that the mutant and resident populations are close to the equilibrium $(N^*(x), P^*(x), 0)$ which is one of the equilibria of system (5) after the rare and slight mutations encounter the resident populations. Thus, the stability of the equilibrium $(N^*(x), P^*(x), 0)$ determines whether mutant predators can invade resident predator population. That is, mutant predators can not invade if $(N^*(x), P^*(x), 0)$ is stable, otherwise they can.

We now analyze the stability of the equilibrium $(N^*(x), P^*(x), 0)$ of system (5). Notice that the Jacobian is given by

$$J_1 = \begin{bmatrix} -\frac{rN^*}{k} & -\beta(x)N^* & -\beta(y)N^* \\ \theta\beta(x)P^* & -a(0)P^* & -a(x-y)P^* \\ 0 & 0 & \theta\beta(y)N^* - d - h(y) - a(y-x)P^* \end{bmatrix} = \begin{bmatrix} J_{\text{res}} & J_2 \\ \mathbf{0} & J_{\text{mut}} \end{bmatrix},$$

where

$$J_{\text{res}} = \begin{bmatrix} -\frac{rN^*}{k} & -\beta(x)N^* \\ \theta\beta(x)P^* & -a(0)P^* \end{bmatrix}, \quad J_2 = \begin{bmatrix} -\beta(y)N^* \\ -a(x-y)P^* \end{bmatrix},$$

$$\mathbf{0} = (0,0), J_{\text{mut}} = \theta\beta(y)N^* - d - h(y) - a(y-x)P^*$$

and is a block upper triangular matrix. So the eigenvalues of the diagonal blocks, J_{res} and J_{mut} are the eigenvalues of J_1. When (3) holds, $(N^*(x), P^*(x))$ is globally asymptotically stable before mutant predators appear, that is, the eigenvalues of J_{res} have negative real parts. Therefore, if $J_{\text{mut}} < 0$, then all eigenvalues of J_1 have negative real parts, which means that the equilibrium $(N^*(x), P^*(x), 0)$ of system (5) is stable, and mutant predators can not invade. Otherwise, they can invade. In view of the property of J_{mut}, we define a function by

$$s_x(y) = \theta\beta(y)N^*(x) - d - h(y) - a(y-x)P^*(x), \tag{6}$$

where $s_x(x) = 0$. Please notice that $s_x(y)$ is just a long-term exponential growth rate of the mutant predator population. Therefore, if $s_x(y) > 0$, the population density of mutant predators will initial increase, that is, mutant predators can invade; while if $s_x(y) < 0$, mutant predators can not invade, and they are doomed to extinct. Thus, function $s_x(y)$ is called the invasion fitness [15,16], which determines the fate of mutant predators. References [11,12] suggest that the direction of gradual evolutionary changes is determined by a quantity, $D(x)$, which is known as the local fitness gradient. Straightforward calculation yields

$$D(x) = \left.\frac{\partial s_x(y)}{\partial y}\right|_{y=x} = \theta\beta'(x)N^*(x) - h'(x) - a'(0)P^*(x), \tag{7}$$

where $a'(0) = \left.\frac{\partial a(y-x)}{\partial y}\right|_{y=x}$. Since when mutations are very small, traits y is similar to x, then from [11] the linear approximation of the mutant's fitness is given by

$$s_x(y) = s_x(x) + D(x)(y - x).$$

Notice that $s_x(x) = 0$, we know if the fitness gradient is positive, the mutant strategy y which is slightly larger than x can invade and take over the resident, and if the fitness gradient is negative, smaller mutant strategy can invade and take over the resident population.

Since mutations are random and very small, the evolutionary adaptive dynamics of trait x can be approximated as [12]:

$$\frac{dx}{dt} = \frac{1}{2}\mu\sigma^2 P^*(x)D(x), \tag{8}$$

where μ is the probability of individual mutation which is born in resident predator population; σ^2 is the variance of mutation distribution of predator population; $\frac{1}{2}\mu\sigma^2$ is mutational rate of the predators; $P^*(x)$ is the population density of resident predator at positive equilibrium. Furthermore, from [11] we know that a trait x^* is called evolutionary singular strategy if

$$D(x^*) = \frac{\partial s_x(y)}{\partial y}\bigg|_{y=x^*} = 0. \tag{9}$$

Obviously, x^* is the intersection of $s_x(y) = 0$ and $y = x$, and it is easy to verify that when x^* is an evolutionary singular strategy, we have

$$h'(x^*) = \theta\beta'(x^*)N^*(x^*) - a'(0)P^*(x^*). \tag{10}$$

The resident predator population is subjected to repeated invasions and substitutions, which results in directional evolution until it reaches an evolutionary singular strategy x^*, where directional evolution may come to a halt [11].

Next, we discuss the conditions under which the population of resident predator may undergo evolutionary branching. It depends on the following two stability criteria [11]:

- First, singular strategy must lack evolutionary stability (ES) [17] so that x^* can be invaded by nearby mutant predator if

$$\frac{\partial^2 s_x(y)}{\partial y^2}\bigg|_{y=x=x^*} > 0. \tag{11}$$

- Second, directional evolution of resident predator population can approach singular strategy. So the singularity must be convergence stable [18,19] when

$$\frac{dD(x)}{dx}\bigg|_{x=x^*} = \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2}\bigg|_{y=x=x^*} < 0. \tag{12}$$

From the above criteria, we can classify the singular strategy. The singular strategy is called continuously stable strategy (CSS) if it is both evolutionary stable and convergence stable[18]; while it is called evolutionary repeller if it is not convergence stable [11].

Then in our case, we have

$$\frac{\partial^2 s_x(y)}{\partial y^2}\bigg|_{y=x=x^*} = \theta\beta''(x^*)N^*(x^*) - a''(0)P^*(x^*) - h''(x^*) \tag{13}$$

and

$$\frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2}\bigg|_{y=x=x^*} = \theta\beta''(x^*)N^*(x^*) + \theta\beta'(x^*)[N^*]'(x^*) - a'(0)[P^*]'(x^*) - h''(x^*), \tag{14}$$

where $[N^*]'(x^*) = \frac{dN^*(x)}{dx}\Big|_{x=x^*}$, $[P^*]'(x^*) = \frac{dP^*(x)}{dx}\Big|_{x=x^*}$, $a''(0) = \frac{\partial^2 a(y-x)}{\partial y^2}\Big|_{y=x}$.

We now obtain:

Proposition 3.1. *Assume that (3) holds, which allows for stable equilibrium $(N^*(x), P^*(x))$ of (2). Then if the singularity x^* of (8) satisfies that*

(i) *(13) is positive and (14) is negative, it is an evolutionary branching point;*
(ii) *both (13) and (14) are negative, it is a continuously stable strategy (CSS).*

Please notice that if x^* is a branching point, predator population evolves to a fitness minimum trait, therefore, predator population undergoes evolutionary branching, monomorphic predator population may split into two different predator subpopulations.

3.2. Dimorphic adaptive dynamics

When singular strategy reaches a branching point, resident predator population splits into two different resident predator populations. Let one predator population be denoted by P_1 with phenotype strategy x_1 and the other P_2 with phenotype strategy x_2. In the rest of this section, we will investigate the evolution of these two resident predator populations with traits x_1 and x_2 and also study whether further evolutionary branching or evolutionary stable coexistence occurs.

Evolutionary branching causes a monomorphic predator population of a singular trait to a dimorphism of two substantially different strategies. Thus, the subsequent coevolution of the coexisting strategies can be modeled by

$$\begin{cases} N'(t) = rN\left(1-\frac{N}{k}\right) - \beta(x_1)NP_1 - \beta(x_2)NP_2, \\ P_1'(t) = \theta\beta(x_1)NP_1 - dP_1 - h(x_1)P_1 - a(0)P_1^2 - a(x_1-x_2)P_1P_2, \\ P_2'(t) = \theta\beta(x_2)NP_2 - dP_2 - h(x_2)P_2 - a(x_2-x_1)P_2P_1 - a(0)P_2^2, \end{cases} \tag{15}$$

which has an equilibrium $E_2(N^*(x_1,x_2), P_1^*(x_1,x_2), P_2^*(x_1,x_2))$ with

$$N^*(x_1,x_2) = k\frac{[\omega\beta(x_1) - \beta(x_2)a(x_2-x_1)]A_1 + [\omega\beta(x_2) - \beta(x_1)a(x_1-x_2)]A_2 + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)]}{\theta k\omega[\beta^2(x_1)+\beta^2(x_2)] - \theta k\beta(x_1)\beta(x_2)[a(x_1-x_2)+a(x_2-x_1)] + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)]},$$

$$P_1^*(x_1,x_2) = \frac{[\theta k\beta(x_1)\beta(x_2) + ra(x_1-x_2)]A_2 - [\theta k\beta^2(x_2) + r\omega]A_1 + \theta kr[\omega\beta(x_1) - \beta(x_2)a(x_1-x_2)]}{\theta k\omega[\beta^2(x_1)+\beta^2(x_2)] - \theta k\beta(x_1)\beta(x_2)[a(x_1-x_2)+a(x_2-x_1)] + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)]},$$

$$P_2^*(x_1,x_2) = \frac{[\theta k\beta(x_1)\beta(x_2) + ra(x_2-x_1)]A_1 - [\theta k\beta^2(x_1) + r\omega]A_2 + \theta kr[\omega\beta(x_2) - \beta(x_1)a(x_2-x_1)]}{\theta k\omega[\beta^2(x_1)+\beta^2(x_2)] - \theta k\beta(x_1)\beta(x_2)[a(x_1-x_2)+a(x_2-x_1)] + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)]},$$

where $d + h(x_1) = A_1,\ d + h(x_2) = A_2$ and $\omega = a(0)$. Then it is easy to verify that when either

$$\begin{cases} \theta k\omega[\beta^2(x_1)+\beta^2(x_2)] - \theta k\beta(x_1)\beta(x_2)[a(x_1-x_2)+a(x_2-x_1)] + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)] > 0, \\ [\omega\beta(x_1) - \beta(x_2)a(x_2-x_1)]A_1 + [\omega\beta(x_2) - \beta(x_1)a(x_1-x_2)]A_2 + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)] > 0, \\ [\theta k\beta(x_1)\beta(x_2) + ra(x_1-x_2)]A_2 - [\theta k\beta^2(x_2) + r\omega]A_1 + \theta kr[\omega\beta(x_1) - \beta(x_2)a(x_1-x_2)] > 0, \\ [\theta k\beta(x_1)\beta(x_2) + ra(x_2-x_1)]A_1 - [\theta k\beta^2(x_1) + r\omega]A_2 + \theta kr[\omega\beta(x_2) - \beta(x_1)a(x_2-x_1)] > 0 \end{cases} \tag{16}$$

or

$$\begin{cases} \theta k\omega[\beta^2(x_1)+\beta^2(x_2)] - \theta k\beta(x_1)\beta(x_2)[a(x_1-x_2)+a(x_2-x_1)] + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)] < 0, \\ [\omega\beta(x_1) - \beta(x_2)a(x_2-x_1)]A_1 + [\omega\beta(x_2) - \beta(x_1)a(x_1-x_2)]A_2 + r[\omega^2 - a(x_2-x_1)a(x_1-x_2)] < 0, \\ [\theta k\beta(x_1)\beta(x_2) + ra(x_1-x_2)]A_2 - [\theta k\beta^2(x_2) + r\omega]A_1 + \theta kr[\omega\beta(x_1) - \beta(x_2)a(x_1-x_2)] < 0, \\ [\theta k\beta(x_1)\beta(x_2) + ra(x_2-x_1)]A_1 - [\theta k\beta^2(x_1) + r\omega]A_2 + \theta kr[\omega\beta(x_2) - \beta(x_1)a(x_2-x_1)] < 0 \end{cases} \tag{17}$$

holds, $E_2(N^*(x_1,x_2), P_1^*(x_1,x_2), P_2^*(x_1,x_2))$ is a strictly positive ecological equilibrium. Furthermore, it is globally asymptotically stable if

$$2a(0) - [a(x_1-x_2) + a(x_2-x_1)] > 0. \tag{18}$$

A mathematically rigorous proof of global asymptotical stability of the positive equilibrium E_2 is presented in Appendix A.

If mutant population of predator with a rare and slightly different trait y appears at a low density in the dimorphic predator populations, the model (15) can be modified into the following form.

$$\begin{cases} N'(t) = rN\left(1-\frac{N}{k}\right) - \beta(x_1)NP_1 - \beta(x_2)NP_2 - \beta(y)NP_y, \\ P_1'(t) = \theta\beta(x_1)NP_1 - dP_1 - h(x_1)P_1 - a(0)P_1^2 - a(x_1-x_2)P_1P_2 - a(x_1-y)P_1P_y, \\ P_2'(t) = \theta\beta(x_2)NP_2 - dP_2 - h(x_2)P_2 - a(x_2-x_1)P_2P_1 - a(0)P_2^2 - a(x_2-y)P_2P_y, \\ P_y'(t) = \theta\beta(y)NP_y - dP_y - h(y)P_y - a(y-x_1)P_yP_1 - a(y-x_2)P_yP_2 - a(0)P_y^2, \end{cases} \tag{19}$$

where $P_y(t)$ is the population density of mutant predator at time t. By the same arguments as (6), we get invasion fitness

$$s_{x_1,x_2}(y) = \theta\beta(y)N^*(x_1,x_2) - d - h(y) - a(y-x_1)P_1^*(x_1,x_2) - a(y-x_2)P_2^*(x_1,x_2), \tag{20}$$

which determines whether mutants can invade. Similarly, the directions of evolutionary change of x_1 and x_2 are given by

$$\begin{cases} D_1(x_1,x_2) = \left.\frac{\partial S_{x_1,x_2}(y)}{\partial y}\right|_{y=x_1} = \theta\beta'(x_1)N^*(x_1,x_2) - h'(x_1) - a'(0)P_1^*(x_1,x_2) - a'(x_1-x_2)P_2^*(x_1,x_2), \\ D_2(x_1,x_2) = \left.\frac{\partial S_{x_1,x_2}(y)}{\partial y}\right|_{y=x_2} = \theta\beta'(x_2)N^*(x_1,x_2) - h'(x_2) - a'(0)P_2^*(x_1,x_2) - a'(x_2-x_1)P_1^*(x_1,x_2), \end{cases} \tag{21}$$

respectively. From [11,12], when individual mutations are random and sufficiently small, the evolutionary adaptive dynamics of trait x_1 and x_2 can be approximated as

$$\begin{cases} \frac{dx_1}{dt} = \frac{1}{2}\mu_1\sigma_1^2P_1^*(x_1,x_2)D_1(x_1,x_2) \triangleq m_1(x_1,x_2)D_1(x_1,x_2), \\ \frac{dx_2}{dt} = \frac{1}{2}\mu_2\sigma_2^2P_2^*(x_1,x_2)D_2(x_1,x_2) \triangleq m_2(x_1,x_2)D_2(x_1,x_2), \end{cases} \tag{22}$$

where $P_i^*(x_1,x_2)$ is the equilibrium population density of predator P_i; $m_i(x_1,x_2) = \frac{1}{2}\mu_i\sigma_i^2P_i^*(x_1,x_2)$ is evolutionary rate of the resident predator population; μ_i is the probability of individual mutation which is born in predator population P_i; σ_i^2 is the mutation distribution variance of predator population P_i.

Now, we are ready to discuss whether there exists a CSS or branching point of evolutionary dynamics (22). We mainly analyse evolution dynamics of dimorphic predator populations numerically as a general condition for convergence stability is not straightforward in polymorphic populations.

As we know that the evolutionary singular coalitions is point (x_1^*, x_2^*) at which fitness gradients vanish, namely

$$D_1(x_1^*, x_2^*) = 0, \quad D_2(x_1^*, x_2^*) = 0.$$

Then the point (x_1^*, x_2^*) is an evolutionary stable strategy if

$$\left.\frac{\partial^2 s_{x_1^*,x_2^*}(y)}{\partial y^2}\right|_{y=x_1^*} < 0, \quad \left.\frac{\partial^2 s_{x_1^*,x_2^*}(y)}{\partial y^2}\right|_{y=x_2^*} < 0. \tag{23}$$

By the straightforward calculation, we have

$$\begin{cases} \left.\frac{\partial^2 s_{x_1^*,x_2^*}(y)}{\partial y^2}\right|_{y=x_1^*} = \theta\beta''(x_1)N^*(x_1,x_2) - h''(x_1^*) - a''(0)P_1^*(x_1^*,x_2^*) - a''(x_1^* - x_2^*)P_2^*(x_1^*,x_2^*) < 0, \\ \left.\frac{\partial^2 s_{x_1^*,x_2^*}(y)}{\partial y^2}\right|_{y=x_2^*} = \theta\beta''(x_2)N^*(x_1,x_2) - h''(x_2^*) - a''(x_2^* - x_1^*)P_1^*(x_1^*,x_2^*) - a''(0)P_2^*(x_1^*,x_2^*) < 0. \end{cases} \tag{24}$$

From previous analysis, the local convergence stability of the interior singular dimorphism (x_1^*, x_2^*) can be gotten from the eigenvalues of the Jacobian matrix of evolutionary dynamics (22) at this point

$$J = \left.\begin{bmatrix} m_1(x_1,x_2)\frac{\partial D_1(x_1,x_2)}{\partial x_1} & m_1(x_1,x_2)\frac{\partial D_1(x_1,x_2)}{\partial x_2} \\ m_2(x_1,x_2)\frac{\partial D_2(x_1,x_2)}{\partial x_1} & m_2(x_1,x_2)\frac{\partial D_2(x_1,x_2)}{\partial x_2} \end{bmatrix}\right|_{\substack{x_1 = x_1^* \\ x_2 = x_2^*}}.$$

Thus, the strong convergence stability of (x_1^*, x_2^*) is determined by $\det(J) > 0$, $\operatorname{tr}(J) < 0$ [20], which implies, in our case, that

$$\left.\frac{\partial D_i(x_1,x_2)}{\partial x_i}\right|_{\substack{x_1 = x_1^* \\ x_2 = x_2^*}} < 0 \tag{25}$$

for $i = 1,\ 2$ and

$$\left.\left[\frac{\partial D_1(x_1,x_2)}{\partial x_1}\frac{\partial D_2(x_1,x_2)}{\partial x_2}\right]\right|_{\substack{x_1 = x_1^* \\ x_2 = x_2^*}} > \left.\left[\frac{\partial D_1(x_1,x_2)}{\partial x_2}\frac{\partial D_2(x_1,x_2)}{\partial x_1}\right]\right|_{\substack{x_1 = x_1^* \\ x_2 = x_2^*}}. \tag{26}$$

Then we can conclude the following.

Proposition 3.2. *Assume that the conditions (16) and (18) are satisfied. For the evolutionary singular point (x_1^*, x_2^*) of system (22),*

(i) *if conditions (23), (25) and (26) are satisfied, then it is a continuously stable strategy; however,*
(ii) *if conditions (25) and (26) are satisfied and condition (23) is not satisfied, then it is a evolutionary branching point.*

4. Application for size-selective harvesting

In this section, we apply our theoretic results to a size-selective harvesting model. First, we assume that the capital capture rate is trait-independent to concentrate on the role of harvesting disturbance. Then we consider asymmetric competition among predator individuals and use the concave–convex function for the asymmetric competition [21],

$$a(x_i - x_j) = c\left(1 - \frac{1}{1 + q\exp(-\delta(x_i - x_j))}\right), \tag{27}$$

where $c,\ q$, and δ are positive constants. We let parameter q donate the strength of competition, that is, the higher the value of q, the more competitiveness between resident predator population and mutant predator population. Such competition coefficient implies that individuals with big body size have competitive advantage to survival relative to its small contestant. Mathematically, we have $a(x) > 0$ for any x and $a'(0) < 0$.

For the harvesting disturbance $h(x)$, biological considerations dictate the following properties:

(i) $h(x)$ should be a continuous and increasing function, because big individuals generally mean great harvesting rates.
(ii) $h(0) = 0$ because no individuals can be harvested when body size is equal to zero.

By which, the harvesting function $h(x)$ can be modeled using a Chi square distribution function (Fig. 1)

$$h(x) = \alpha - (\alpha + px)e^{-px}, \tag{28}$$

where the non-negative p governs the strength of harvesting effort.

4.1. Adaptive dynamics with size-selective harvesting and size-dependent competition

The singular strategy is sitting at a fitness maxima, i.e., an evolutionarily stable strategy (or ESS) if

$$\frac{a''(0)}{a'(0)}h'(x^*) - h''(x^*) < 0. \tag{29}$$

The singular strategy is convergence stable, i.e., it can be approached by gradual evolution, if

$$\frac{a'(0)}{\theta k\beta^2/r + a(0)}h'(x^*) - h''(x^*) < 0. \tag{30}$$

Then if the singular strategy x^* is both evolutionarily stable and convergence stable, x^* is a CSS such that selection drives the evolving trait toward x^* and ceases there, i.e., x^* is the endpoint of the evolutionary process. As shown in Fig. 2(a), x^* is a CSS. If a singular strategy x^* is convergence stable but evolutionarily stable, then the evolutionary branching occurs, and x^* is called the evolutionary branching point. As shown in Fig. 2(b), where at x^*, the resident is actually located at a fitness minima, and any nearby mutant can invade.

It follows from inequality (30) that the singularity is always convergence stable if $h(x)$ is convex or linear, and may be convergence stable if $h(x)$ is concave. However, the singularity may be not convergence stable, i.e., an evolutionary repeller when $h(x)$ is concave. It can be seen from inequality (29) that evolutionary stability of the singularity is decided by the concave–convex shapes of $h(x)$ at x^* and $a(y-x)$ near $y-x=0$. It is easy to see that the evolutionary outcome, regarding the stability of evolutionarily singular strategy, is the most sensitive to the chosen parameters when a concave disturbance function is employed in combination of a concave asymmetric competition function. In contrast, a convex disturbance function combined with a convex asymmetric competition gives rise to a singular strategy that is both evolutionarily and convergence stable. Hence in the latter situation there is no evolutionary branching.

4.2. The influence of natural selection and artificial selection

The objective of this section is to investigate the impacts of competition for natural selection and harvesting for artificial selection on evolution changes in the phenotype trait which is related to body size. Natural selection is always displayed by competition coefficient, while artificial selection is displayed by size-selective harvesting.

Competitive interaction are ubiquitous in nature, and is likely to be an important force of natural selection. So in this subsection, we mainly discuss the effect of competition for natural selection in the evolutionary process using the trade-off function $a(x_i - x_j)$ which is given in (27). Again, we use parameter q to donate the strength of competition. From the bifurcation diagram for trade-off function $a(x_i - x_j)$, namely Fig. 3(a), we see that a small increase in competitiveness may result in an increase in the singular strategy value. However, intense competition can lead to a decrease in the singular strategy value. So natural selection causes rapid stable evolution towards larger body size. In addition, we also know the evolutionary stability of singular strategy will alter once the strength of competition goes beyond a threshold value.

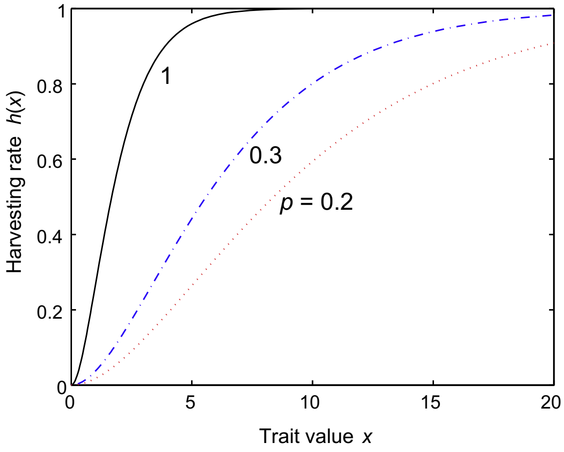

Fig. 1. Convex–concave shape of harvesting rate $h(x)$ given by Eq. (28) when $\alpha = 1$.

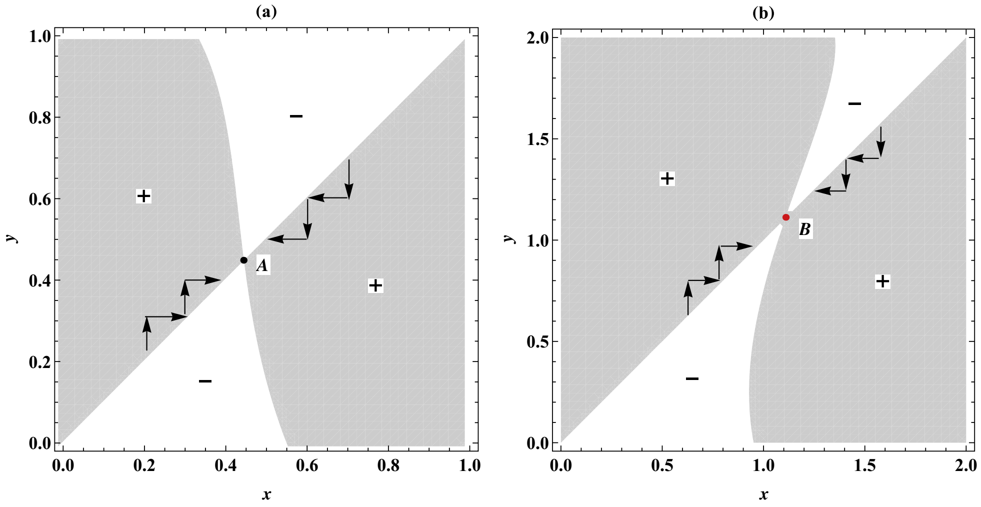

Fig. 2. Pairwise invasibility plots. The shaded areas marked with '+' mean that mutants have positive invasion fitness, whereas the white areas means the opposite. Arrows indicate the direction of disruptive selection which ceases at the evolutionarily stable singular strategy *A*. The singular point *B* is a branching point. (a) Only the generalist singular strategy is a CSS when $p = 0.3$; (b) The singular strategy is an evolutionary branching point when $p = 0.2$; Other parameter values: $d = 0.2,\ \theta = 0.5,\ \beta = 1.5,\ r = 2,\ k = 2,\ c = 0.08,\ \delta = 2.5,\ q = 3.8,\ \alpha = 1$.

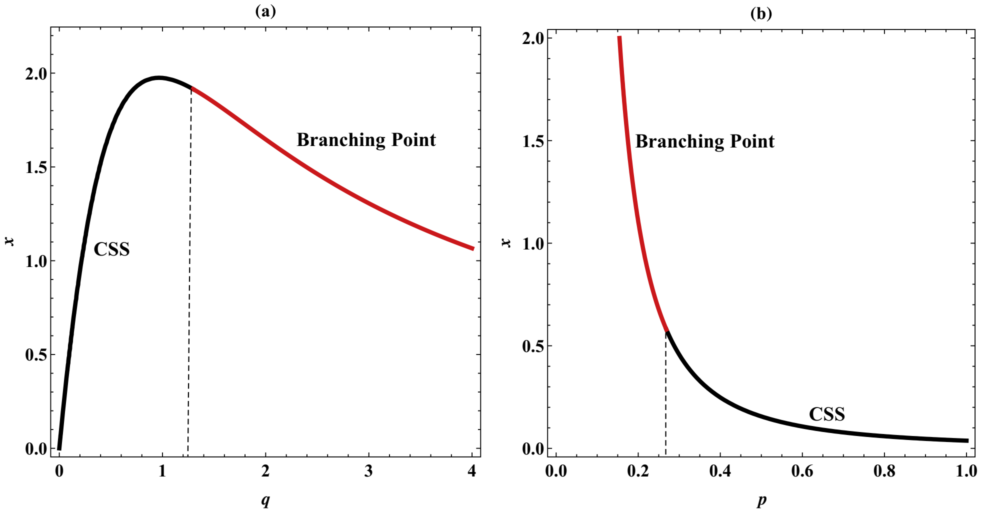

Fig. 3. Red dashed lines indicate unstable singular strategy *x* (i.e. evolutionary branching point) while black solid lines the CSS. (a) Bifurcation diagram for competition function (27) when $p = 0.2$. (b) Bifurcation diagram for selective harvesting under the trade-off disturbance function (28) when $q = 3.8$. Non-varying parameter values are: $d = 0.2,\ \theta = 0.5,\ \beta = 1.5,\ r = 2,\ k = 2,\ c = 0.08,\ \delta = 2.5,\ \alpha = 1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Thus it is clearly to know that a small competitiveness can lead to evolutionary stable while a large competitiveness can undergo evolutionary branching. This condition means that natural selection promotes predator population undergoing evolution branching.

Artificial selection can also be aware of making an important influence except natural selection. So in this subsection, we use the similar way to investigate the effect of harvest for artificial selection by considering trade-off function $h(x)$ which is given in (28). Assume p donates the strength of harvesting, that is, the high value of p, the more harvest of predator population. A bifurcation diagram for trade-off function $h(x)$ is carried out in Fig. 3(b). We can see that increase in harvesting on predators can lead to quick stable evolution towards smaller body size. Moreover, we also know the evolutionary stability of singular strategy will alter once the strength of harvesting goes beyond a threshold value. A small harvest in predators can undergo evolutionary branching, but a large harvest can prevent branching to reach evolutionary stable. This condition means that artificial selection can reduce evolutionary branching and promote evolutionary stable.

4.3. Dimorphic coexistence and coevolution

A singular coalition represents a final evolutionary endpoint, that is, after branching in original predator phenotype, monomorphic predator population evolves to an evolutionary stable dimorphism in which they have maximum fitness and continue to coexist. A singular coalition that is convergence-stable but for which at least one strategy lacks evolutionary stability will cause further evolutionary branching. At last, monomorphic predator population evolves to a polymorphism population. After the first evolutionary branching, the resident predator population may reach an evolutionary stable coalition of strategies $x_1,\ x_2$ which is showed in Fig. 4(f); the resident predator population also may continue to undergo evolutionary branching, and there are two conditions of branching. The first condition is that one strategy undergoes branching; another strategy reaches an evolutionary stable state which is showed in Fig. 4(e). Fig. 4(d) shows both strategies undergo evolutionary branching.

This can also be derived from the geometrical argument presented in Fig. 4(a)–(c). We draw the red dashed straight line $s(y, x_1, x_2) = 0$, where $x_1,\ x_2$ are evolutionarily singular coalition so that the invasibility condition $s(y, x_1, x_2) > 0$ and the opposite condition $s(y, x_1, x_2) < 0$, which determines whether the mutant predator can invade, are easily seen. In panel (a), mutants near strategies either x_1^* or x_2^* have positive fitness. Therefore, both of the two strategies can undergo evolutionary branching. In panel (b), mutants near strategy x_2^* have positive fitness so can invade, while mutants near x_1^* have negative fitness and as a consequence not invade. So the phenotype trait x_1^* is evolutionarily stable, but phenotype trait x_2^* continues to undergo evolutionary branching. However, in panel (c), mutants near strategies both x_1^* and x_2^* are below the line $s(y, x_1, x_2) = 0$, so can not invade successfully. Thus they are CSS.

Corresponding to Fig. 2(b), the Fig. 5(a) is a simulative evolutionary tree which starts with a monomorphic population, evolution first converges to $x = 1.108$ where it undergoes evolutionary branching and becomes two strategies; then two strategies evolve to $x_1 = 0.4604,\ x_2 = 1.285$, where the strategies are evolutionary stable and come to a halt. Fig. 5(b) starts with a monomorphic predator population, repeated invasions and substitutions lead to an evolutionary stable strategy at $x = 0.4568$ which can not undergo evolutionary branching and attain a evolutionary halt (corresponding to Fig. 2(a)).

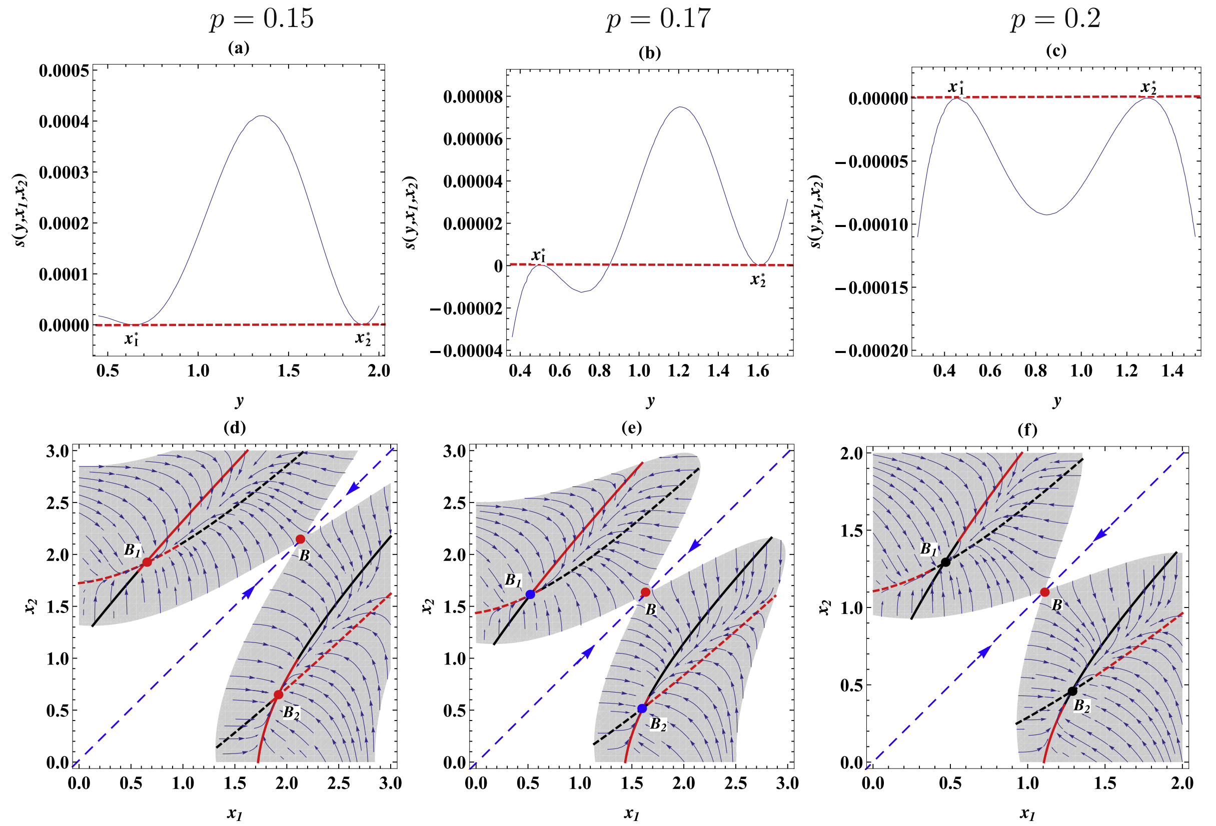

Fig. 4. Fitness landscape (a,b,c) at the singular coalition $B_1 = (x_1^*, x_2^*)$, trait coevolution (d,e,f) for different harvesting efforts $p = 0.15$ (a,d), 0.17 (b,e) and 0.2 (c,f). The second row: shaded areas indicating protected dimorphism are separated by stable (black) and unstable (red) isoclines at which selection gradient vanishes in either x_1-direction (solid) or x_2-direction (dash). Red '●' B = initial branching point, red '●' B_i = branching singular coalition and black '●' B_i= evolutionarily stable singular coalition, blue '●' B_i = one evolutionarily stable and another branching singular coalition. Arrows on the main diagonal show the evolutionary directions in a monomorphic environment. The vector fields obtained from the deterministic model (22) denote the directions of evolutionary change of traits x_1 and x_2. Parameter values: $d = 0.2,\ \theta = 0.5,\ \beta = 1.5,\ r = 2,\ k = 2,\ c = 0.08,\ \delta = 2.5,\ q = 3.8,\ \alpha = 1$.

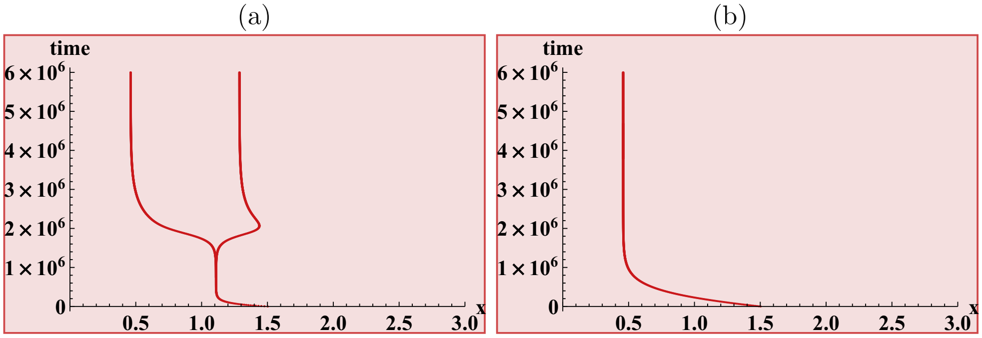

Fig. 5. Simulated evolutionary tree. (a) Evolutionary branch when $p = 0.2$; (b) CSS when $p = 0.3$; Other parameter values: $d = 0.2,\ \theta = 0.5,\ \beta = 1.5,\ r = 2,\ k = 2,\ c = 0.08,\ \delta = 2.5,\ q = 3.8,\ \alpha = 1$.

5. Discussion and conclusion

In a classic model based on the predator–prey community, we have considered the evolution of phenotype trait and acquired the invade fitness which is the key to investigate evolution. The conditions that predator phenotype trait will undergo evolutionary branching, and the mutant predator and the resident predator can stably coexist have been obtained, please see Propositions 3.1 and 3.2. Our study shows that repeated evolutionary branching can lead to high levels of polymorphism. Moreover, our analysis reveals a resident predator population can undergo branching, then evolution towards the singular coalition leads to further branching and become an evolutionary tree, that is, an attractive dimorphism can further undergoes secondary branching giving rise to a polymorphic population. This benefits the biological diversity.

Next we have demonstrated the different effect of competition for natural selection and harvesting for artificial selection by considering different trade-off function $a(x_i - x_j)$ and $h(x)$. Our analysis results show that (i) A small increase in the strength of the $a(x_i - x_j)$ increases evidently in the singular strategy, and eventually turns the continuously stable strategy into branching point. Natural selection is advantageous to which predator population evolves to large values of phenotype trait, this becomes people's common understanding. However, large values of the trait come to a halt at last because the cost of large trait values increase and eventually outweighs the advantage, or because population density decreases so that competition is relaxed. (ii) However, any increase in the strength of the $h(x)$ decreases evidently in the singular strategy, and eventually turns the branching point into continuously stable strategy. This has been also confirmed by [22]. Artificial selection is disadvantageous to which predator population evolves to small values of the phenotype trait, which also agrees well with general knowledge. In short, as seen from the above analysis, natural selection can promote species diversity and spatial differentiation of populations; whereas artificial selection is apparently opposite.

Appendix A

The system of the monomorphic population (15) has eight equilibria. Besides $E_2^*(N^*, P_1^*, P_2^*)$, they are

$$O_0(0,0,0),\quad O_1(k,0,0),\quad O_2\left(0,-\frac{d+h(x_1)}{a(0)},0\right),\quad O_3\left(0,0,-\frac{d+h(x_2)}{a(0)}\right),$$

$$O_4\left(\frac{k[d\beta(x_1)+h(x_1)\beta(x_1)+ra(0)]}{\theta k\beta^2(x_1)+ra(0)},\frac{r[-d+\theta k\beta(x_1)-h(x_1)]}{\theta k\beta^2(x_1)+ra(0)},0\right),$$

$$O_5\left(\frac{k[d\beta(x_2)+h(x_2)\beta(x_2)+ra(0)]}{\theta k\beta^2(x_2)+ra(0)},0,\frac{r[-d+\theta k\beta(x_2)-h(x_2)]}{\theta k\beta^2(x_2)+ra(0)}\right),$$

$$O_6\left(0,\frac{a(x_1-x_2)d+a(x_1-x_2)h(x_2)-a(0)d-a(0)h(x_1)}{a^2(0)-a(x_1-x_2)a(x_2-x_1)},\frac{a(x_2-x_1)d+a(x_2-x_1)h(x_1)-a(0)d-a(0)h(x_2)}{a^2(0)-a(x_1-x_2)a(x_2-x_1)}\right).$$

From (16) or (17), we can see that the system has a positive equilibrium. The Jacobian matrix of system (15) at $E_2^*(N^*, P_1^*, P_2^*)$ is

$$J_2=\begin{bmatrix} -\frac{rN^*}{k} & -\beta(x_1)N^* & -\beta(x_2)N^* \\ \theta\beta(x_1)P_1^* & -a(0)P_1^* & -a(x_1-x_2)P_1^* \\ \theta\beta(x_2)P_2^* & -a(x_2-x_1)P_2^* & -a(0)P_2^* \end{bmatrix}.$$

The associated characteristic equation is

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{31}$$

where

$$a_1 = \frac{rN^*}{k} + a(0)P_1^* + a(0)P_2^* > 0,$$

$$a_2 = \theta\beta^2(x_1)N^*P_1^* + \theta\beta^2(x_2)N^*P_2^* - a(x_1 - x_2)a(x_2 - x_1)P_1^*P_2^* + \frac{ra(0)}{k}N^*P_1^* + \frac{ra(0)}{k}N^*P_2^* + a^2(0)P_1^*P_2^*,$$

$$a_3 = \left[\frac{ra^2(0)}{k} - [a(x_1 - x_2) + a(x_2 - x_1)]\theta\beta(x_1)\beta(x_2) + [\beta^2(x_1) + \beta^2(x_2)]\theta a(0) - \frac{r}{k}a(x_1 - x_2)a(x_2 - x_1)\right]N^*P_1^*P_2^*.$$

Let

$$H_2 = a_1a_2 - a_3, \quad H_3 = (a_1a_2 - a_3)a_3. \tag{32}$$

Then by the Routh–Hurwitz criteria, we know that if the signs of H_2 and H_3 are positive then $E_2^*(N^*, P_1^*, P_2^*)$ is asymptotically stable. By direct calculations, we have

$$\begin{aligned} H_2 = {} & \left[\frac{r}{k}N^* + a(0)P_1^*\right]N^*P_1^*\left[\theta\beta^2(x_1) + \frac{r}{k}a(0)\right] + \left[\frac{r}{k}N^* + a(0)P_2^*\right]N^*P_2^*\left[\theta\beta^2(x_2) + \frac{r}{k}a(0)\right] + a(0)P_1^*P_2^*(P_1^* \\ & + P_2^*)\left[a^2(0) - a(x_1 - x_2)a(x_2 - x_1)\right] + \left[\frac{2r}{k}a^2(0) + \theta\beta(x_1)\beta(x_2)(a(x_1 - x_2) + a(x_2 - x_1))\right]N^*P_1^*P_2^*, \end{aligned}$$

$$H_3 = \frac{r}{k}\left[a^2(0) - a(x_1 - x_2)a(x_2 - x_1)\right] + \theta a(0)\left[\beta^2(x_1) + \beta^2(x_2)\right] - \theta\beta(x_1)\beta(x_2)[a(x_1 - x_2) + a(x_2 - x_1)].$$

We can easily see that H_3 is positive is equivalent to the first equation of (16). So when (16) and (32) hold, $E_2^*(N^*, P_1^*, P_2^*)$ is asymptotically stable. Next, we investigate whether it is globally asymptotically stable. To this end, define

$$V(N, P_1, P_2) = \theta\left(N - N^* - N^*\ln\frac{N}{N^*}\right) + \left(P_1 - P_1^* - P_1^*\ln\frac{P_1}{P_1^*}\right) + \left(P_2 - P_2^* - P_2^*\ln\frac{P_2}{P_2^*}\right).$$

Obviously $V(N, P_1, P_2)$ is positive definite, its total derivative along the system (15) is

$$\begin{aligned} \dot{V}(t) & = \theta(N - N^*)\left[r\left(1 - \frac{N}{k}\right) - \sum_{i=1}^{2}\beta(x_i)P_i\right] + \sum_{i,j=1, i\neq j}^{2}(P_i - P_i^*)[\theta\beta(x_i)N - d - h(x_i) - a(0)P_i - a(x_i - x_j)P_j] \\ & = -\frac{\theta r}{k}(N - N^*)^2 - \left\{a(0)(P_1 - P_1^*)^2 + a(0)(P_2 - P_2^*)^2 + [a(x_1 - x_2) + a(x_2 - x_1)](P_1 - P_1^*)(P_2 - P_2^*)\right\}. \end{aligned}$$

Then when

$$\Delta = -[4a^2(0) - [a(x_1 - x_2) + a(x_2 - x_1)]^2] < 0,$$

that is

$$2a(0) > a(x_1 - x_2) + a(x_2 - x_1),$$

we have $\dot{V}(t)$ is negative definite. According to the above discussion, if (16) and (18) hold, $E_2(N^*(x_1, x_2), P_1^*(x_1, x_2), P_2^*(x_1, x_2))$ is globally asymptotically stable.

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