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Effects of Trade-off Specificity and Harvesting on a Consumer-Resource Model

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Abstract: The maintenance of species diversity depends on the sum of each species responses to the environment and on the interactions among them. Little is known about the overall distribution of the proportion of consumers and resources in real ecosystems which is systematically changing between habitats or extensive taxonomic groups together with resource harvesting activity. We research the relationship between resources and consumers together with harvesting by using a modified Rosenzweig-MacArthur model, in which the proportion of each genotype available for consumption consists of two components: an intrinsic part and a combination from all genotypes present in the resource. 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 resource strongly depends on the values of this parameter. Finally, we illustrate the possible evolutionary outcomes via numerical simulations.

Keywords: consumer; resource; trade-off; harvesting

1 Introduction

A major challenge in population ecology is to explain the persistence of species. On one hand, in the ever-changing, uncertain, and sometimes catastrophic natural world, species extinction is natural process. From the fossil record, one notes that all species have a finite lifespan and that the large majority of species that have ever existed are now extinct. A substantial body of theoretical literature has shown that temporal variability can allow the coexistence of competing species that would not coexist under constant conditions [1–4]. On the other hand, the maintenance of species diversity depends on the sum of each species responses to the environment and on the interactions among them. Also, these species-specific responses can arise from factors related to evolutionary history, intraspecific variation, and so on. Therefore, one of the main purposes of this study of consumer-resource dynamics is an exploration of the regulatory mechanisms and their impacts [5], which provide the fundamental mechanisms of species extinction or coexistence.

It has been suggested that differences in the size and degree of genetic connectedness of consumers and resource species may have important implications for interaction intensity, population dynamics, and the structure, function, and evolution of the final food web. However, little is known about the overall distribution of the proportion of consumers and resources in real ecosystems which is systematically changing between habitats or extensive taxonomic groups [6] together with resource harvesting activity. Cross found large elemental imbalances between consumers and food resources compared with living plant-based systems, particularly in regard to phosphorus content, which were reduced with enrichment [7]. Traditional resource management is largely based on local ecological knowledge. Strauch and Almedom examined traditional resources among the Sonjo in rural Northern Tanzania, with particular reference to catchment forest protection and water quality [8]. By examining past, present and future human-environmental interactions, traditional resource and environmental management could be considered as the application of traditional ecological knowledge to maintain or enhance the productivity, diversity, availability, or other desired qualities of natural resources or ecosystems [9]. Nakazawa

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explored a consumer-resource model including reproductive and non-reproductive subpopulations of the consumer to consider whether resource-dependent reproductive adjustment by the consumer would stabilize consumer-resource dynamics [10].

The structure of the remainder of the paper is as follows. In Section 2, we propose a modified Rosenzweig-MacArthur model to understand the relationship between resources and consumers together with harvesting. In addition, an invading mutant may outcompete the former resident and become the new resident. We then find the invasibility criterion of invading mutant and possible outcomes of selection. Subsequently, We illustrate our theoretical results via numerical simulations in Section 3. Finally, we give several concluding remarks in Section 4.

2 Evolutionary results

2.1 The model

In order to understand the relationship between resources and consumers together with harvesting, we use a modified Rosenzweig-MacArthur model. For $i = 1, 2, \cdots, n$,

$$\begin{aligned} \frac{dx_i}{dt} &= r_i x_i (1 - \frac{x_T}{K}) - pR_i(x) x_i y - (1-\theta_i) x_i E_i, \\ \frac{dy}{dt} &= qp\Sigma_{i=1}^n R_i(x) x_i y - \delta y, \end{aligned} \tag{1}$$

in which x_i represents the value of the concentration resource of genotype i, $x_T = \Sigma_{i=1}^n x_i$ is the total value of the concentration of all resources, y represents the value of the concentration of the consumer, $r_i > 0$ is the resource growth rate, the stock level K is the total carrying capacity, p is the consumption rate without the trade-off structure on resources, E_i describes the harvesting effort, q and δ are the conversion and removal rates for consumers, respectively.

We define the following form of the trade-off structure on resource consumption,

$$R_i(x) = \gamma(1-\theta_i) + \frac{1-\gamma}{x_T} \Sigma_{j=1}^n (1-\theta_j) x_j. \tag{2}$$

Here the term 1-θ_i represents the removal proportion of the i-th genotype in the resource population, $\theta_i \in (0, 1)$, $\gamma = 1$ corresponds to the local case in which each genotype has its own quantity for consumption, $\gamma = 0$ corresponds to the global case in which each genotype use the same quantity for consumption.

In this work, for the sake of simplicity, we let $n = 2$ and then the system (1) is simplified to

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 (1 - \frac{x_1 + x_2}{K}) - p x_1 R_1(x_1, x_2) y - (1-\theta_1) x_1 E_1, \\ \frac{dx_2}{dt} &= r_2 x_2 (1 - \frac{x_1 + x_2}{K}) - p x_2 R_2(x_1, x_2) y - (1-\theta_2) x_2 E_2, \\ \frac{dy}{dt} &= qp\big[x_1 R_1(x_1, x_2) + x_2 R_2(x_1, x_2)\big] y - \delta y, \end{aligned} \tag{3}$$

where

$$\begin{aligned} R_1(x_1, x_2) &= \gamma(1-\theta_1) + \frac{1-\gamma}{x_1 + x_2}[(1-\theta_1)x_1 + (1-\theta_2)x_2], \\ R_2(x_1, x_2) &= \gamma(1-\theta_2) + \frac{1-\gamma}{x_1 + x_2}[(1-\theta_1)x_1 + (1-\theta_2)x_2]. \end{aligned}$$

2.2 Invasibility criterion

The Jacobian of (3) at an arbitrary equilibrium point $(\hat{x}_1, \hat{x}_2, \hat{y})$ is given by

$$J = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}, \tag{4}$$

where

$$\begin{aligned}
a_{11} &= r_1\Big(1-\frac{2\hat{x}_1+\hat{x}_2}{K}\Big)-p\hat{y}\Big(R_1+\hat{x}_1\frac{\partial R_1}{\partial x_1}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}\Big)-(1-\theta_1)E_1,\\
a_{12} &= -\frac{r_1\hat{x}_1}{K}-p\hat{y}\hat{x}_1\frac{\partial R_1}{\partial x_2}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2},\\
a_{13} &= -p\hat{x_1}R_1,\\
a_{21} &= -\frac{r_2\hat{x}_2}{K}-p\hat{y}\hat{x}_2\frac{\partial R_2}{\partial x_1}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2},\\
a_{22} &= r_2\Big(1-\frac{\hat{x}_1+2\hat{x}_2}{K}\Big)-p\hat{y}\Big(R_2+\hat{x}_2\frac{\partial R_2}{\partial x_2}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}\Big)-(1-\theta_2)E_2,\\
a_{23} &= -p\hat{x_2}R_2,\\
a_{31} &= qp\Big(R_1+\hat{x}_1\frac{\partial R_1}{\partial x_1}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}+\hat{x}_2\frac{\partial R_2}{\partial x_1}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}\Big)\hat{y},\\
a_{32} &= qp\Big(R_2+\hat{x}_2\frac{\partial R_2}{\partial x_2}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}+\hat{x}_1\frac{\partial R_1}{\partial x_2}\Big|_{x_1=\hat{x}_1,x_2=\hat{x}_2}\Big)\hat{y},\\
a_{33} &= qp(\hat{x}_1R_1+\hat{x}_2R_2)-\delta,
\end{aligned} \tag{5}$$

where $R_i = R_i(\hat{x}_1, \hat{x}_2)$ for $i = 1, 2$ and

$$\begin{aligned}
\frac{\partial R_1}{\partial x_1} = \frac{\partial R_2}{\partial x_1} &= \frac{(1-\gamma)(\theta_2-\theta_1)\hat{x}_2}{(\hat{x}_1+\hat{x}_2)^2},\\
\frac{\partial R_1}{\partial x_2} = \frac{\partial R_2}{\partial x_2} &= \frac{(1-\gamma)(\theta_1-\theta_2)\hat{x}_1}{(\hat{x}_1+\hat{x}_2)^2}.
\end{aligned} \tag{6}$$

Without lose of generality, we assume that x_1 represents resident resources and x_2 represents mutant resources. One notes that the mutants can invade the residents if at least one of the eigenvalues of the Jacobian evaluated at the monomorphic resident resource steady states of the system (3)

$$M_1^* = (K, 0, 0) \text{ and } M_2^* = (x_1^*, 0, y^*) = \Big(\frac{\delta}{qp(1-\theta_1)}, 0, \frac{A-E_1}{p}\Big),$$

has a positive real part under the assumption that

$$E_1 < A,$$

in which

$$A = \frac{r_1}{1-\theta_1}[1-\frac{\delta}{Kqp(1-\theta_1)}].$$

From (4) and (5), we then get that $J(M_1^*)$ has always two negative eigenvalues $\lambda_1 = -r_1-(1-\theta_1)E_1$, $\lambda_2 = -(1-\theta_2)E_2$ and λ_3 is determined by

$$\lambda_3 = qpK(1-\theta_1)-\delta.$$

One notes that M_1^* is unstable if

$$A > 0 \Longleftrightarrow \theta_1 < 1-\frac{\delta}{qpK}. \tag{7}$$

Similarly, it follows from (4) and (5) that

$$det(\lambda I_3 - J(M_2^*)) = [\lambda - S(\gamma, E_1, E_2)]\Big[\lambda^2+\frac{r_1\delta}{Kqp(1-\theta_1)}\lambda+\delta(1-\theta_1)(A-E_1)\Big],$$

in which

$$S(\gamma, E_1, E_2) = \Big\{\frac{r_1}{r_2} - \Big[\gamma\Big(\frac{1-\theta_2}{1-\theta_1} - 1\Big) + 1\Big]\Big\}(1-\theta_1)A + E_1[\gamma(1-\theta_2) + (1-\gamma)(1-\theta_1)] - (1-\theta_2)E_2. \quad (8)$$

Also, we consider the following quadratic equation

$$\lambda^2 + \frac{r_1\delta}{Kqp(1-\theta_1)}\lambda + \delta(1-\theta_1)(A-E_1) = 0.$$

Since

$$\lambda_1 + \lambda_2 = -\frac{r_1\delta}{Kqp(1-\theta_1)} < 0$$
$$\lambda_1\lambda_2 = \delta(1-\theta_1)(A-E_1) > 0,$$

which imply that $J(M_2^*)$ has always two negative eigenvalues. Thus M_2^* is unstable if

$$E_1 < A \text{ and } \mathrm{S}(\gamma, \mathrm{E}_1, \mathrm{E}_2) > 0. \quad (9)$$

Consequently, we obtain the following result.

Theorem 1 *The mutant can invade if the invasion condition* (9) *holds.*

2.3 Possible outcomes of selection

2.3.1 Only mutants evolve without consumers

From (4) and (5), one notes that $J\big(M_3^* = (0, K, 0)\big)$ has always two negative eigenvalues $\lambda_1 = -(1-\theta_1)E_1$, $\lambda_2 = -r_2 - (1-\theta_2)E_2$ and λ_3 is determined by

$$\lambda_3 = qpK(1-\theta_2) - \delta.$$

Obviously, we may get the following result

Theorem 2 *Only mutants can evolve without consumers if the invasion condition* (9) *and the following conditon hold,*

$$\theta_2 > 1 - \frac{\delta}{qpK}.$$

2.3.2 Residents and mutants stably evolve without consumers

We shall consider the stability condition for $M_4^* = (x_1^*, x_2^*, 0)$. The characteristic equation of the Jacobian at M_4^* can be obtained by

$$det(\lambda I_3 - J(M_4^*)) = \lambda(\lambda + \frac{r_1x_1^* + r_2x_2^*}{K})\left\{\lambda - [qpx_1^*R_1(x_1^*, x_2^*) + qpx_2^*R_2(x_1^*, x_2^*) - \delta]\right\}.$$

It is then seen that M_4^* is stable provided that

$$qpx_1^*R_1(x_1^*, x_2^*) + qpx_2^*R_2(x_1^*, x_2^*) < \delta. \quad (10)$$

Theorem 3 *Resident and mutant resources stably evolve without consumers provided that the conditions* (9) *and* (10) *are satisfied.*

2.3.3 Only mutants evolve with consumers

The steady state for $M_5^* = (0, x_2^*, y^*)$ is given by

$$M_5^* = (0, x_2^*, y^*) = \Big(0, \frac{\delta}{qp(1-\theta_2)}, \frac{\tilde{A} - E_2}{p}\Big),$$

in which

$$\tilde{A} = \frac{r_2}{1-\theta_2}[1 - \frac{\delta}{Kqp(1-\theta_2)}].$$

To guarantee the existence of the steady state above, we need the following precondition

$$E_2 < \tilde{A}. \tag{11}$$

Subsequently,

$$det(\lambda I_3 - J(M_5^*)) = [\lambda - \tilde{S}(\gamma, E_1, E_2)]\Big[\lambda^2 + \frac{r_2\delta}{Kqp(1-\theta_2)}\lambda + \delta(1-\theta_2)(\tilde{A} - E_2)\Big],$$

in which

$$\begin{aligned}\tilde{S}(\gamma, E_1, E_2) \quad = \quad & \Big\{\frac{r_1}{r_2} - [\gamma(\frac{1-\theta_1}{1-\theta_2} - 1) + 1]\Big\}(1-\theta_2)\tilde{A} \\ & + E_2[\gamma(1-\theta_1) + (1-\gamma)(1-\theta_2)] - (1-\theta_1)E_1. \end{aligned} \tag{12}$$

Consequently, if the precondition (11) holds, then it is obvious that the ability of the mutant resource to invade and then make the resident resource extinct depends only on the sign of $\tilde{S}(\gamma, E_1, E_2)$.

Theorem 4 *If the invasion condition* (9)*, the precondition* (11) *and the following condition hold*

$$\tilde{S}(\gamma, E_1, E_2) < 0,$$

then the invading mutant succeeds under the pressure of consumption and the residents will be extinct.

2.3.4 Residents and mutants stably coevolve with consumers

In order to ensure the existence of $M_6^* = (x_1^*, x_2^*, y^*)$, one of the following relations need to be satisfied

(Existence condition i) $\theta_1 > \theta_2$, $\frac{r_2}{1-\theta_2} - \frac{r_1}{1-\theta_1} > E_2 - E_1$, $\frac{r_2}{1-\theta_2} > \frac{r_1}{1-\theta_1}$,

$$\frac{1-\theta_2}{1-\theta_1} > \frac{\gamma(r_1+r_2)(\theta_1+\theta_2) - (r_1-r_2)(\theta_1-\theta_2)}{2\gamma r_1},$$

$$\frac{r_1 - r_2 + (1-\theta_2)E_2 - (1-\theta_1)E_1 + \gamma(\theta_1-\theta_2)(\frac{r_1}{1-\theta_1} - E_1)}{\gamma r_1(\theta_1-\theta_2) - (r_2-r_1)(1-\theta_1)} < \frac{\delta}{Kqp(1-\theta_1)^2};$$

(Existence condition ii) $\theta_1 > \theta_2$, $\frac{r_2}{1-\theta_2} - \frac{r_1}{1-\theta_1} > E_2 - E_1$, $\frac{r_2}{1-\theta_2} < \frac{r_1}{1-\theta_1}$,

$$\frac{1-\theta_2}{1-\theta_1} > \frac{\gamma(r_1+r_2)(\theta_1+\theta_2) - (r_1-r_2)(\theta_1-\theta_2)}{2\gamma r_1},$$

$$\frac{r_1 - r_2 + (1-\theta_2)E_2 - (1-\theta_1)E_1 + \gamma(\theta_1-\theta_2)(\frac{r_1}{1-\theta_1} - E_1)}{\gamma r_1(\theta_1-\theta_2) - (r_2-r_1)(1-\theta_1)} > \frac{\delta}{Kqp(1-\theta_1)^2};$$

(Existence condition iii) $\theta_1 < \theta_2$, $\frac{r_2}{1-\theta_2} - \frac{r_1}{1-\theta_1} < E_2 - E_1$, $\frac{r_2}{1-\theta_2} > \frac{r_1}{1-\theta_1}$,

$$\frac{1-\theta_2}{1-\theta_1} > \frac{\gamma(r_1+r_2)(\theta_1+\theta_2) - (r_1-r_2)(\theta_1-\theta_2)}{2\gamma r_1},$$

$$\frac{r_1 - r_2 + (1-\theta_2)E_2 - (1-\theta_1)E_1 + \gamma(\theta_1-\theta_2)(\frac{r_1}{1-\theta_1} - E_1)}{\gamma r_1(\theta_1-\theta_2) - (r_2-r_1)(1-\theta_1)} < \frac{\delta}{Kqp(1-\theta_1)^2};$$

(Existence condition iv) $\theta_1 < \theta_2$, $\frac{r_2}{1-\theta_2} - \frac{r_1}{1-\theta_1} < E_2 - E_1$, $\frac{r_2}{1-\theta_2} < \frac{r_1}{1-\theta_1}$,

$$\frac{1-\theta_2}{1-\theta_1} > \frac{\gamma(r_1+r_2)(\theta_1+\theta_2)-(r_1-r_2)(\theta_1-\theta_2)}{2\gamma r_1},$$

$$\frac{r_1-r_2+(1-\theta_2)E_2-(1-\theta_1)E_1+\gamma(\theta_1-\theta_2)(\frac{r_1}{1-\theta_1}-E_1)}{\gamma r_1(\theta_1-\theta_2)-(r_2-r_1)(1-\theta_1)} > \frac{\delta}{Kqp(1-\theta_1)^2}.$$

The Jacobian $J(M_6^*)$ at M_6^* is of the form

$$J(M_6^*) = \begin{pmatrix} a & b & c \\ d & e & f \\ g & h & l \end{pmatrix},$$

in which a, b, c, d, e, f, g, h, and l are obtained from (5) by replacing $(\hat{x}_1, \hat{x}_2, \hat{y})$ with (x_1^*, x_2^*, y^*). We then obtain the characteristic equation

$$\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0, \tag{13}$$

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 M_6^* is stable if and only if

$$a_0, a_1, a_2 > 0 \text{ and } a_1a_2 > a_0. \tag{14}$$

Theorem 5 *Residents and mutants stably evolve with consumers provided that the invasion condition* (9)*, the existence condition (i) or (ii) and the stability condition* (14) *hold.*

3 Numerical simulations

In this section, we shall illustrate our mathematical results by some numerical examples. All values of parameters of the system (3) are chosen from Table 1. If we choose $r_1 = 1.62$, $r_2 = 1.49$, $K = 10^5$, $\gamma = 0.5$, $\theta_1 = 0.2$, $\theta_2 = 0.91$, $E_1 = 1.252$, $E_2 = 1.221$, $p = 0.001$, $q = 0.01$ and $\delta = 0.1$, as shown in Figure 1, then we note only mutants evolve without consumer population.

If we choose $r_1 = 1.6$, $r_2 = 0.6$, $K = 10^5$, $\gamma = 0.5$, $\theta_1 = 0.2$, $\theta_2 = 0.6$, $E_1 = 1.2$, $E_2 = 0.9$, $p = 0.001$, $q = 0.01$ and $\delta = 0.1$, as shown in Figure 2, then we observe that residents and mutants can coevolve without consumer population.

If we choose $r_1 = 1.602$, $r_2 = 1.32$, $K = 10^5$, $\gamma = 0.5$, $\theta_1 = 0.2$, $\theta_2 = 0.4$, $E_1 = 1.24$, $E_2 = 0.51$, $p = 0.004$, $q = 0.01$ and $\delta = 0.3$, as shown in Figure 3, then we observe that mutants coevolve with consumer population. However, the resident resources lose their habitats and go extinct.

If we choose $r_1 = 1.2$, $r_2 = 1.02$, $K = 10^5$, $\gamma = 0$, $\theta_1 = 0.2$, $\theta_2 = 0.3$, $E_1 = 1.1$, $E_2 = 1.06$, $p = 0.008$, $q = 0.01$ and $\delta = 0.4$, as shown in Figure 4, then we observe that residents and mutants stably coevolve with consumers.

4 Conclusions

In this paper, we model the effect of trade-off specificity and harvesting on consumer-resource interactions by using a modified Rosenzweig-MacArthur model consisting of three populations: resident resources, x_1, mutant resources, x_2 and consumer y. First of all, a criterion establishing the ability of the mutant to invade the equilibria of system. After investigating the stability of resident resources with respect to invading mutant, we find out that under the invasibility condition we can observe four different outcomes: (i) Only mutant resources evolve without consumers. (ii) Resident resources and mutant resources stably evolve without consumers. (iii) Only mutant resouces evolve with consumers. (iv) Resident resources and mutants stably coevolve with consumers.

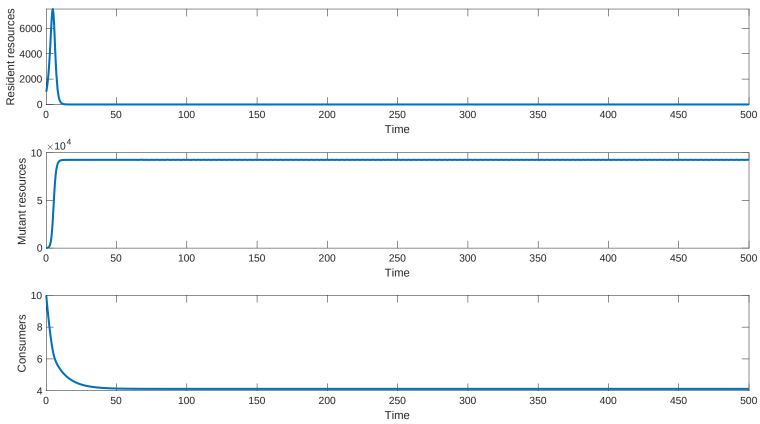

Figure 1: Only mutants evolve without consumers.

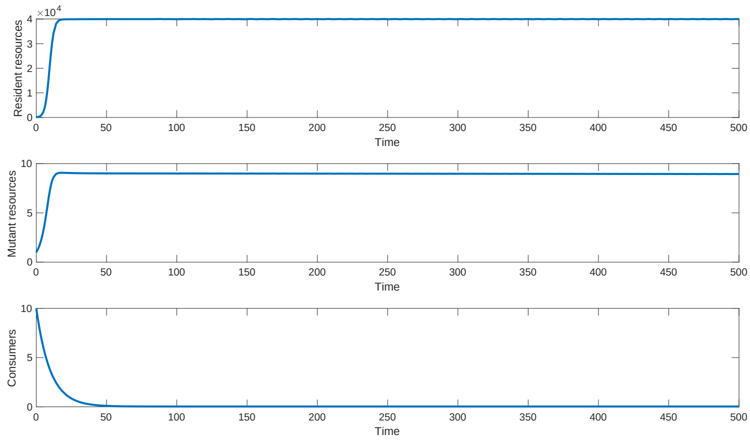

Figure 2: Residents and mutants coevolve without consumers.

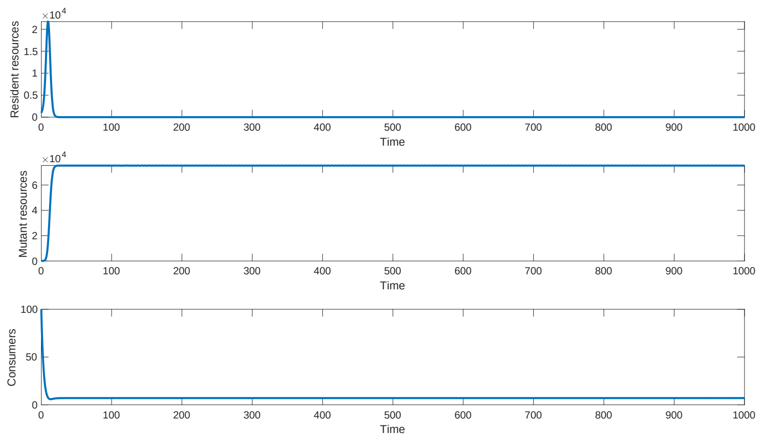

Figure 3: Only mutants evolve with consumers.

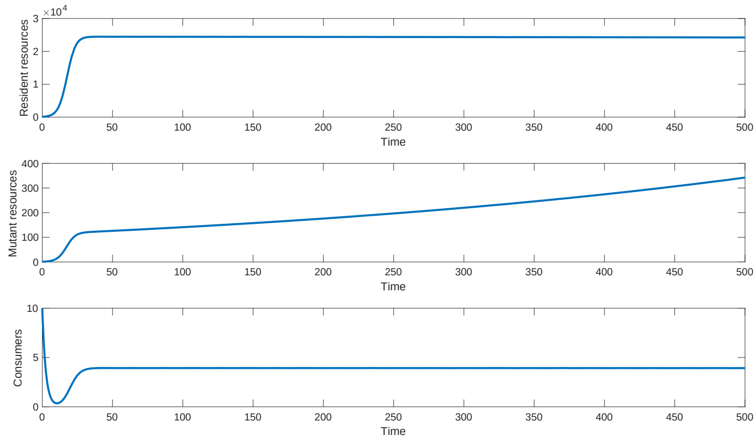

Figure 4: Residents and mutants stably coevolve with consumers.

Table 1: The definitions of the system parameters and default values chosen for numerical simulations.

Parameter	Description	Default value
r_1	Growth rate of the resident resources	1.2, 1.6, 1.602, 1.62
r_2	Growth rate of the mutant resources	0.6, 1.02, 1.32, 1.49
K	Total carrying capacity of the resources	10^5
γ	Degree of specificity	[0, 1]
θ_1	Proportion of residents	0.2
θ_2	Proportion of mutants	0.3, 0.4, 0.6, 0.91
E_1	Harvesting effort of the resident resources	1.1, 1.2, 1.24, 1.252
E_2	Harvesting effort of the mutant resources	0.51, 0.9, 1.06, 1.221
p	Consumption rate without trade-off structure	0.001, 0.002, 0.004, 0.008
q	Conversion rate	0.01
δ	Removal rate	0.1, 0.13, 0.3, 0.4

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