ON PREDATION EFFORT ALLOCATION STRATEGY OVER TWO PATCHES

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ABSTRACT. In this paper, we formulate an ODE model to describe the population dynamics of one non-dispersing prey and two dispersing predators in a two-patch environment with spatial heterogeneity. The dispersals of the predators are implicitly reflected by the allocation of their presence (foraging time) in each patch. We analyze the dynamics of the model and discuss some biological implications of the theoretical results on the dynamics of the model. Particularly, we relate the results to the evolution of the allocation strategy and explore the impact of the spatial heterogeneity and the difference in fitness of the two predators on the allocation strategy. Under certain range of other parameters, we observe the existence of an evolutionarily stable strategy (ESS) while in some other ranges, the ESS disappears. We also discuss some possible extensions of the model. Particularly, when the model is modified to allow distinct preys in the two patches, we find that the heterogeneity in predation rates and biomass transfer rates in the two patches caused by such a modification may lead to otherwise impossible bi-stability for some pairs of equilibria.

1. **Introduction.** Biological invasion has been a big concern in agriculture, fishery and forest. Possible consequences of an exotic species invading a habitat of a native species include competing for the limited resources, predating on native species to extinction, expelling native species, acquiring the ecological status of native species, carrying new diseases that cause large-scale epidemics, and changing native species' genetic composition [34]. A biological invasion often leads to, sooner or later, some significant negative effects on agriculture, fishery and forestry, with unpredictable economic losses [30]. As mentioned above, species invasion may lead to resource competition between a native species and an exotic species or multiple species,

and thus, predicting the results of competition is of both theoretical and practical significance.

Among all types of interactions between biological species, predator-prey (P-P) type of interactions is the richest and yet most challenging to explore. Here a prey could either be a plant species or a animal species or some other resources on which the predator lives on. As far as predator-prey interactions are concerned, [23] is a pioneering work that considered the populations of *two* predator species competing for the same resource (prey). Subsequent research on models for two-consumers and one resource has extensively investigated possibilities of competitive exclusion and coexistence for two predators with various functional responses including linear [20], Holling type II [13, 14] and Beddington-DeAngelis [3].

In the case of two predators competing for one prey (recourse), competition exclusion is a common phenomenon. This is explained by the principle of competitive exclusion which conclude that two species competing for the same limited resource cannot coexist in an environment, and the one with certain advantage will dominate its rival in the long term [19, 26]. However, due to biological complexity, competition between two predators for the same prey (resource) many not always lead to exclusion, and coexistence is also possible [13, 14]. See, also [29] two organisms in a chemostat competing for nutrients and light, and [25] for two diseases competing for the same pool of susceptible individuals. As such, distinguishing the two competition outcomes is a critical problem in relevant research fields.

It is known that spatial heterogeneity plays an important role in shaping a stable ecological system. When considering populations in a spatially continuum environment, partial differential equations models are typically used with the resource related terms dependent on the location in the habitat. It is amazing to find that when accounting for the effects of the diffusion and spatial distribution of the resources for *one consumer*, spatially heterogeneous resources can actually support a total population that is *larger* than the environment's total carrying capacity [21]. In the case of two consumers competing for the same resource modelled by a Lotka-Volterra competition-diffusion system where the resource is spatially heterogeneous and has the same benefit to both consumers, it has been shown that the slower diffuser always prevails; that is, the consumer with slower dispersal rate always wins the competition [9]. When the environment has distinct spatially heterogeneous carrying capacities for different consumers, but with the same total resources, the two consumers are more comparable and the likelihood of coexistence increases [12]. These results reveal that spatial heterogeneity may have significant and complicated impact on the consequence of competition between two or more species for the same resource(s).

When considering discrete spatial heterogeneity, patch models are used with dispersion of populations between patches. Spatially heterogeneity is typically reflected by patch-wise resources which can engender different predator populations in different patches. In such an environment, the fate of a dispersing individual is markedly influenced by its strategy in selecting a target patch [4, 28]. Patch models with individual dispersal have been extensively studied, see e.g., [2, 8, 17] and the references therein. Recent studies [15, 27] considered an immobile prey species and two competitive predators with density-dependent dispersal according to two mechanisms of prey-predator interaction, with predation strength measured by a combination of conspecific blue attraction and prey population density, and with the passive dispersal driven by the local density of predators to avoid overcrowding.

In many predator-prey interactions, foraging of predators needs to be involved and has been reported in studies on the behaviour of various creatures, including insects (coccinellids [18]), amphibians (snakes [33]), and mammals (wild dogs [5]). Foraging movement typically depend on the spatial abundance of resources, intra-species competition, and inter-species interaction both in a local patch and among different patches and, hence, is a key factor in studying patch models. A recent study [32] proposed a patch model to describe population dynamics for a dispersing specialist predator and a non-dispersing prey in two different patches with the predator distributing its presence (foraging time) in each patch in an adaptive way. In addition to analyzing the persistence and extinction of the predator, they also observed that torus bifurcation may occur because of the adaptive behaviour of predators.

The model in [32] only considered one predator capable of allocate its presence in two different patches foraging and predating one non-dispersing prey species. Due to its importance, biological invasion can be incorporated along this line. As mentioned above, biological invasion may threaten the survival prospects of native species and even destroy the regional ecological balance. Examples of predator invaders include Procambarus clarkii (aquatic invertebrate), Vespula vulgaris (terrestrial invertebrate), Sturnus vulgaris (Aves), and Capra hircus (Mammalia) [22]. All these exotic species are mobile predators that feed on their immobile prey resources (which may be mobile in a local patch). Accordingly, it is of both theoretical and practical significance to explore how an invading predator species will allocate its presence (or foraging time) in heterogeneous patches to compete with the resident predator species, and what are the possible consequences of competition between the invading predator species and resident predator species. Understanding the mechanisms underlying this would facilitate biologically managing an imbalanced ecosystem. This constitute the goal of this paper.

The rest of the paper is organized as follows. In Section 2, we formulate a two patch predator-prey model along the line of [32] and address its well-poseness. In Section 3, we analyze the dynamics of the model including the existence of equilibria with various biological meanings, as well as their stability. In Section 4, we discuss some biological implications of the mathematical results obtained in Section 3 for some special but biologically meaningful cases, including a discussion on evolutionary implications reflecting the impact of spatial heterogeneity and fitnesses of the two predator species. We conclude the paper by some further discussions on more general cases of the model and possible extensions of the model and future work.

2. **Model formulation and its well-posedness.** As in [32], we consider a prey species that live in two patches with the populations u_1 and u_2 in each patch being governed by a logistic ODE. This prey species is assumed to be unable to disperse between the two patches, and it is assumed to be the sole food source of a predator species v (hence, a specialist predator) that can choose to forage, hunt and predate in both patches. Then there arises the natural question of how the predator should allocate their presence foraging and predating in each patch.

In [32], the authors considered this problem in light of the adaptive dynamics by introducing an *allocation variable* $\alpha(t)$ which is governed by the replicator equation. Here in this paper, we explore this problem by an alternative approach, that is, the approach of evolutional dynamics. More specifically, instead of considering an allocation variable $\alpha(t)$, we consider two *constant parameters* α_1 and α_2 accounting for *two different allocation strategies* on patch 1 (hence $\beta_1 = 1 - \alpha_1$ and $\beta_2 = 1 - \alpha_2$

on patch 2) played by two subpopulations or strains of the predator. Of course, we can also consider two different specialist predators predating on this prey by adopting the allocation strategies α_1 and α_2 respectively. Also, unlike in [32] where Holling Type II functional responses are adopted, here in this paper, we use the Holling Type I (e.g. linear, to make things a bit easier) functional response for the predation in each patch. The above considerations and assumptions lead to the following model system of ordinary differential equations:

$$\begin{cases} \dfrac{du_1(t)}{dt} = ru_1\left(1 - \dfrac{u_1}{K_1}\right) - p_1 u_1[\alpha_1 v_1] - p_2 u_1[\alpha_2 v_2], \\[2mm] \dfrac{du_2(t)}{dt} = ru_2\left(1 - \dfrac{u_2}{K_2}\right) - p_1 u_2[\beta_1 v_1] - p_2 u_2[\beta_2 v_2], \\[2mm] \dfrac{dv_1(t)}{dt} = -\mu_1 v_1 + p_1 e_1 u_1[\alpha_1 v_1] + p_1 e_1 u_2[\beta_1 v_1], \\[2mm] \dfrac{dv_2(t)}{dt} = -\mu_2 v_2 + p_2 e_2 u_1[\alpha_2 v_2] + p_2 e_2 u_2[\beta_2 v_2]. \end{cases} \tag{1}$$

Here for $i, j = 1, 2$, u_i represents the population of prey in patch-i, v_j denotes the population of the predator playing allocation strategy (α_j, β_j), where $\alpha_j \in [0, 1]$ is the proportion that predator j allocates its presence in patch 1 and $\beta_j = 1 - \alpha_j$ is thus the proportion that predator j allocates its presence in patch 2. Since u_1 and u_2 are population of the same prey species in two habitats that may have different resources, it is natural to assume intrinsic growth rates of the prey in both patches are same, denoted by r; yet carrying capacities for the prey in the two patches may be different, reflected by K_1 and K_2. For other parameters, p_j denotes the attacking rate of species-j predator, e_j is the efficiency of biomass conversion from the prey to the species-j predator after predation, and μ_j is the per capita morality rate of species-j predators.

By the background of the model system (1), the following non-negative initial condition is needed to be associated to it:

$$(u_1(0), u_2(0), v_1(0), v_2(0)) \in \mathbb{R}^4_+ \tag{2}$$

The right hand side of model (1) are all polynomial functions, and hence, the local existence of a unique solution to (1)-(2) is guaranteed. Since system (1) is of Gauss type, the solution to (1)-(2) will remain in $\mathbb{R}^4_+$ whenever it exists.

Next, we show the boundedness of solutions. Let $B(t) = \hat{e}u_1(t) + \hat{e}u_2(t) + v_1(t) + v_2(t)$, where $\hat{e} = \max\{e_1, e_2\}$ and denote $\check{\mu} = \min\{\mu_1, \mu_2\}$. Then

$$\begin{aligned} \frac{dB(t)}{dt} &\leq \hat{e}r(u_1 + u_2) - \frac{\hat{e}r}{K_1}u_1^2 - \frac{\hat{e}r}{K_2}u_2^2 - \mu_1 v_1 - \mu_2 v_2 \\ &= -\check{\mu}B + (r + \check{\mu})\hat{e}(u_1 + u_2) - \frac{\hat{e}r}{K_1}u_1^2 - \frac{\hat{e}r}{K_2}u_2^2 \\ &\leq -\check{\mu}B + \frac{(r + \check{\mu})^2 \hat{e}}{4r}(K_1 + K_2) =: -\check{\mu}B + \tilde{K}. \end{aligned}$$

It follows from the comparison principle that

$$\limsup_{t \to \infty} B(t) \leq \frac{\tilde{K}}{\check{\mu}}.$$

Hence a solution to (1) is eventually bounded, which in term also implies the unique solution to (1)-(2) actually exists globally for $t \in (0, \infty)$.

3. **Dynamics of the model.** It is obvious that (1) has four unconditional equilibria:

$$E_0^0 = (0,0,0,0), \ E_1^0 = (K_1,0,0,0), \ E_2^0 = (0,K_2,0,0), \ E_3^0 = (K_1,K_2,0,0).$$

In addition, there may exist the conditional equilibria E_1^1, E_2^1, E_3^1 and E_1^2, E_2^2, E_3^2 in the boundary subspaces with $v_1 = 0$ and $v_2 = 0$ respectively, and possibly a positive (co-persistent) equilibrium E^*, where

$$E_1^1 \left(\frac{K_1}{\mathcal{R}_1^1}, 0, \frac{r}{p_1 \alpha_1} \left(1 - \frac{1}{\mathcal{R}_1^1} \right), 0 \right) \ \text{and} \ E_1^2 \left(\frac{K_1}{\mathcal{R}_1^2}, 0, 0, \frac{r}{p_2 \alpha_2} \left(1 - \frac{1}{\mathcal{R}_1^2} \right) \right),$$

$$E_2^1 \left(0, \frac{K_2}{\mathcal{R}_2^1}, \frac{r}{p_1 \beta_1} \left(1 - \frac{1}{\mathcal{R}_2^1} \right), 0 \right) \ \text{and} \ E_2^2 \left(0, \frac{K_2}{\mathcal{R}_2^2}, 0, \frac{r}{p_2 \beta_2} \left(1 - \frac{1}{\mathcal{R}_2^2} \right) \right),$$

$$E_3^1 \left(K_1 \left(1 - \frac{p_1 \alpha_1 \bar{v}_1}{r} \right), K_2 \left(1 - \frac{p_1 \beta_1 \bar{v}_1}{r} \right), \bar{v}_1, 0 \right),$$

$$E_3^2 \left(K_1 \left(1 - \frac{p_2 \alpha_2 \bar{v}_2}{r} \right), K_2 \left(1 - \frac{p_2 \beta_2 \bar{v}_2}{r} \right), 0, \bar{v}_2 \right),$$

where

$$\bar{v}_j = \frac{r \mu_j (\mathcal{R}_0^j - 1)}{p_j^2 e_j (\alpha_j^2 K_1 + \beta_j^2 K_2)}, \ j = 1, 2,$$

$$\mathcal{R}_1^j = \frac{p_j e_j \alpha_j K_1}{\mu_j}, \ \mathcal{R}_2^j = \frac{p_j e_j \beta_j K_2}{\mu_j}, \ \mathcal{R}_0^j = \mathcal{R}_1^j + \mathcal{R}_2^j, \ j = 1, 2.$$

For convenience of discussion, we denote

$$\hat{\mathcal{R}}_1^j = \mathcal{R}_1^j \left(1 - \frac{\alpha_j}{1 - \alpha_j} \right), \ \hat{\mathcal{R}}_2^j = \mathcal{R}_2^j \left(1 - \frac{1 - \alpha_j}{\alpha_j} \right), \ j = 1, 2.$$

Note that

$$\hat{\mathcal{R}}_1^j > 0 \ \left(\hat{\mathcal{R}}_2^j > 0 \right) \ \text{if and only if} \ 0 \le \alpha_j < \frac{1}{2} \ \left(\frac{1}{2} < \alpha_j \le 1 \right). \tag{3}$$

Then, the condition(s) for each of the above equilibria to be biologically meaningful is reflected directly by its formula and the positivity requirement. For example, by straightforward verifications, we observe the following equivalences:

$$\bar{v}_1 > 0 \Longleftrightarrow R_0^1 > 0,$$

$$1 - \frac{p_1 \alpha_1 \bar{v}_1}{r} > 0 \Longleftrightarrow \hat{\mathcal{R}}_2^1 < 1,$$

$$1 - \frac{p_1 \beta_1 \bar{v}_1}{r} > 0 \Longleftrightarrow \hat{\mathcal{R}}_1^1 < 1.$$

Parallelly, there hold

$$\bar{v}_2 > 0 \Longleftrightarrow R_0^2 > 0,$$

$$1 - \frac{p_2 \alpha_2 \bar{v}_2}{r} > 0 \Longleftrightarrow \hat{\mathcal{R}}_2^2 < 1,$$

$$1 - \frac{p_2 \beta_2 \bar{v}_2}{r} > 0 \Longleftrightarrow \hat{\mathcal{R}}_1^2 < 1.$$

Note that $\mathcal{R}_1^j$ and $\mathcal{R}_2^j$ represent the basic reproduction ratios of predator j in patches 1 and 2 respectively when playing the allocation strategy (α_j, β_j) in the absence of predator k $(k \ne j)$, and hence, $\mathcal{R}_0^j = \mathcal{R}_1^j + \mathcal{R}_2^j$ is the total reproduction ratio of predator j on both patches in the absence of predator i.

Among the four unconditional equilibria, by standard stability analysis, it is easy (trivial) to show that E_0^0, E_1^0 and E_2^0 are always unstable; while the stability of the predator-free equilibrium E_3^0 depends on the composite parameters $\mathcal{R}_0^1$ and $\mathcal{R}_0^2$. By their biological meanings, we expect that if $\mathcal{R}_0^j < 1$, then the predator j will go to extinction, and this is confirmed in the following theorem.

Theorem 3.1. *The species j of predators in system* (1) *go to extinction if* $\mathcal{R}_0^j < 1$.

Proof. Since $\mathcal{R}_0^j < 1$, there is a constant $\epsilon > 0$ such that

$$\mu_j > p_j e_j \alpha_1 (K_1 + \epsilon) + p_j e_j \beta_1 (K_2 + \epsilon). \tag{4}$$

Consider the u_i equation in (1). By applying the comparison principle, it yields that

$$\limsup_{t \to \infty} u_i(t) \le K_i.$$

Hence, for ϵ in (4), there exists $t_0 > 0$ such that $u_i(t) \le K_i + \epsilon$ for $t \ge t_0$. This leads to

$$\frac{dv_j}{dt} \le [-\mu_j + p_j e_j \alpha_1 (K_1 + \epsilon) + p_j e_j \beta_1 (K_2 + \epsilon)] v_1 =: a_0 v_1.$$

Since $a_0 < 0$, it yields that $v_1(t) \to 0$ as $t \to \infty$. $\qquad\square$

Applying this theorem to both predators, we then obtain the global convergence to the predatory-free equilibrium E_3^0, as stated in the following theorem.

Theorem 3.2. *When* $\max\{\mathcal{R}_0^1, \mathcal{R}_0^2\} < 1$, *the equilibrium* E_3^0 *in system* (1) *is globally asymptotically stable in* $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2 > 0\}$.

In order to explore the situation when $\max\{\mathcal{R}_0^1, \mathcal{R}_0^2\} > 1$, it is helpful to first look at the case when there is only one predator j (either $j = 1$ or $j = 2$), represented by the following reduced 3-d system:

$$\begin{cases} \dfrac{du_1(t)}{dt} = ru_1 \left(1 - \dfrac{u_1}{K_1}\right) - p_j u_1 [\alpha_j v_j], \\[2mm] \dfrac{du_2(t)}{dt} = ru_2 \left(1 - \dfrac{u_2}{K_2}\right) - p_j u_2 [\beta_j v_j], \\[2mm] \dfrac{dv_j(t)}{dt} = -\mu v_j + p_j e_j u_1 [\alpha_j v_j] + p_j e_j u_2 [\beta_j v_j]. \end{cases} \tag{5}$$

Several literatures had studied single-species predator-prey models which can disperse between two or more patches, see [17] and references therein. Assuming bidirectional dispersal among a two patches environment, there exists a threshold which determines the extinction or persistence of both predator and prey populations. In contrast to the dichotomy, prey can persist in a single patch of the system (5) and extinct in the other patch.

By standard analyses on local stability and applying the Lyapunov method, the convergent dynamics of (5) can be summarized in the following lemma.

Lemma 3.3. *The system* (5) *has the threshold dynamics of global convergence to an equilibrium, in terms of the* $\mathcal{R}_0^j$, $\hat{\mathcal{R}}_1^j$ *and* $\hat{\mathcal{R}}_2^j$, *described in the following lemma.*

(i) *when* $\mathcal{R}_0^j < 1$, *the equilibrium* $\hat{E}_3^0 (K_1, K_2, 0)$ *is globally asymptotically stable (GAS) in* $\{(u_1, u_2, v_j) \in \mathbb{R}_+^3 | u_1, u_2 > 0\}$.

(ii) *when* $\mathcal{R}_0^j > 1$, $\hat{\mathcal{R}}_1^j < 1$ *and* $\hat{\mathcal{R}}_2^j < 1$, *the equilibrium* $\hat{E}_3^j \left(K_1 \left(1 - \frac{p_j \alpha_j \bar{v}_j}{r}\right),\right.$ $\left. K_2 \left(1 - \frac{p_j \beta_j \bar{v}_j}{r}\right), \bar{v}_j\right)$ *is GAS in* $\{(u_1, u_2, v_j) \in \mathbb{R}_+^3 | u_1, u_2, v_j > 0\}$.

(iii) when $\hat{\mathcal{R}}_1^j > 1$ (then $\mathcal{R}_0^j > 1$), the equilibrium $\hat{E}_1^j \left(\frac{K_1}{\mathcal{R}_1^j}, 0, \frac{r}{p_j \alpha_j} \left(1 - \frac{1}{\mathcal{R}_1^j} \right) \right)$ is GAS in $\{(u_1, u_2, v_j) \in \mathbb{R}_+^3 | u_1, v_j > 0\}$.

(iv) when $\hat{\mathcal{R}}_2^j > 1$ (then $\mathcal{R}_0^j > 1$), the equilibrium $\hat{E}_2^j \left(0, \frac{K_2}{\mathcal{R}_2^j}, \frac{r}{p_j \beta_j} \left(1 - \frac{1}{\mathcal{R}_2^j} \right) \right)$ is GAS in $\{(u_1, u_2, v_j) \in \mathbb{R}_+^3 | u_2, v_j > 0\}$.

From this lemma, we see that when $\mathcal{R}_0^j < 1$, the v_j in (5) goes to extinction. However, when $\mathcal{R}_0^j > 1$, then there are there possibilities (a) $\hat{\mathcal{R}}_1^j > 1$, corresponding to the scenario that allocation strategy α_j enable v_j to persist only in patch 1; (b) $\hat{\mathcal{R}}_2^j > 1$, corresponding to the scenario that allocation strategy α_j enable v_j to persist only in patch 2; (c) both $\hat{\mathcal{R}}_a^j < 1$ and $\hat{\mathcal{R}}_2^j < 1$ corresponding to the scenario that the persistence of v_j is achieved in both patches.

Remark 1. For a clear picture of how the allocation strategy (related to the value of α_j) of v_j impact its survival in the environment, we have the following observations.

(i) The condition $\hat{\mathcal{R}}_1^j < 1$ holds true for $\alpha_j \in [0, 1)$ if $\frac{\mu_j}{p_j e_j K_1} > m_0 := 3 - 2\sqrt{2}$, and holds true for $\alpha_j \in [0, \alpha_{j1}^*) \cup (\alpha_{j2}^*, 1)$ for some α_{j1}^* and α_{j2}^* with $0 < \alpha_{j1}^* \leq \alpha_{j2}^* < 1$, if $\frac{\mu}{p_j e_j K_1} \leq m_0$.

(ii) The condition $\hat{\mathcal{R}}_2^j < 1$ holds true for $\alpha_j \in (0, 1]$ if $\frac{\mu_j}{p_j e_j K_2} > m_0$, and holds true for $\alpha_j \in (0, \alpha_{j3}^*) \cup (\alpha_{j4}^*, 1]$ for some α_{j3}^* and α_{j4}^* with $0 < \alpha_{j3}^* \leq \alpha_{j4}^* < 1$, if $\frac{\mu}{p_j e_j K_2} \leq m_0$.

(iii) The conditions $\hat{\mathcal{R}}_1^j < 1$ and $\hat{\mathcal{R}}_2^j < 1$ hold true for the following α_j in variant conditions:

(a) $\alpha_j \in (0, 1)$, if $\min\{\frac{\mu_j}{p_j e_j K_1}, \frac{\mu_j}{p_j e_j K_2}\} > m_0$;

(b) $\alpha_j \in (0, \alpha_{j1}^*) \cup (\alpha_{j2}^*, 1)$ for some α_{j1}^* and α_{j2}^* with $0 < \alpha_{j1}^* \leq \alpha_{j2}^* < 1$, if $\frac{\mu_j}{p_j e_j K_1} \leq m_0 < \frac{\mu_j}{p_j e_j K_2}$;

(c) $\alpha_j \in (0, \alpha_{j3}^*) \cup (\alpha_{j4}^*, 1)$ for some α_{j3}^* and α_{j4}^* with $0 < \alpha_{j3}^* \leq \alpha_{j4}^* < 1$, if $\frac{\mu_j}{p_j e_j K_2} \leq m_0 < \frac{\mu_j}{p_j e_j K_1}$;

(d) $\alpha_j \in (0, \alpha_{j1}^*) \cup (\alpha_{j2}^*, \alpha_{j3}^*) \cup (\alpha_{j4}^*, 1)$ for some α_{j1}^*, α_{j2}^*, α_{j3}^* and α_{j4}^* with $0 < \alpha_{j1}^* \leq \alpha_{j2}^* \leq \alpha_{j3}^* \leq \alpha_{j4}^* < 1$, if $\max\{\frac{\mu_j}{p_j e_j K_1}, \frac{\mu_j}{p_j e_j K_2}\} \leq m_0$.

Now, we go back to the full model (1) to explore its dynamics when E_3^0 is unstable, implying that at least one of the predators can persist. First, we have the following theorem for the scenario that a predator species is persistent.

Theorem 3.4. *The following statements hold.*

(i) *Assume that $\mathcal{R}_0^1 > 1$, $\hat{\mathcal{R}}_1^1 < 1$ and $\hat{\mathcal{R}}_2^1 < 1$ so that the equilibrium E_3^1 exists. Then it is locally asymptotically stable if and only if*

$$\frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2 e_2(\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2)} < \frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1 e_1(\alpha_1^2 K_1 + \beta_1^2 K_2)}$$

(ii) *Assume that $\mathcal{R}_0^2 > 1$, $\hat{\mathcal{R}}_1^2 < 1$ and $\hat{\mathcal{R}}_2^2 < 1$ so that the equilibrium E_3^2 exists. Then it is locally asymptotically stable if and only if*

$$\frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1 e_1(\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2)} < \frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2 e_2(\alpha_2^2 K_1 + \beta_2^2 K_2)}$$

Proof. We just need to prove (i) as (ii) is just symmetric to (i). The Jacobian matrix of (1) is

$$J(u_1, u_2, v_1, v_2) = \begin{bmatrix} J_{11} & 0 & -p_1\alpha_1 u_1 & -p_2\alpha_2 u_1 \\ 0 & J_{22} & -p_1\beta_1 u_2 & -p_2\beta_2 u_2 \\ p_1 e_1 \alpha_1 v_1 & p_1 e_1 \beta_1 v_1 & J_{33} & 0 \\ p_2 e_2 \alpha_2 v_2 & p_2 e_2 \beta_2 v_2 & 0 & J_{44} \end{bmatrix},$$

where

$$\begin{aligned} J_{11} &= r - \frac{2r}{K_1}u_1 - p_1\alpha_1 v_1 - p_2\alpha_2 v_2, \\ J_{22} &= r - \frac{2r}{K_2}u_2 - p_1\beta_1 v_1 - p_2\beta_2 v_2, \\ J_{33} &= -\mu_1 + p_1 e_1 \alpha_1 u_1 + p_1 e_1 \beta_1 u_1, \\ J_{44} &= -\mu_2 + p_2 e_2 \alpha_2 u_1 + p_2 e_2 \beta_2 u_1. \end{aligned}$$

For convenience, we rewrite E_3^1 as $E_3^1 = (\bar{u}_1, \bar{u}_2, \bar{v}_1, 0)$. By a direct calculation, we obtain the characteristic equation at E_3^1 as

$$(\lambda - \hat{J}_{44})(\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0) = 0,$$

where

$$\begin{aligned} a_2 &= -(\hat{J}_{11} + \hat{J}_{22} + \hat{J}_{33}), \\ a_1 &= \hat{J}_{11}\hat{J}_{22} + \hat{J}_{11}\hat{J}_{33} + \hat{J}_{22}\hat{J}_{33} + p_1^2 e_1 \alpha_1^2 \bar{u}_1 \bar{v}_1 + p_1^2 e_1 \beta_1^2 \bar{u}_2 \bar{v}_1, \\ a_0 &= \hat{J}_{11}\hat{J}_{22}\hat{J}_{33} - p_1^2 e_1 \beta_1^2 \bar{u}_2 \bar{v}_1 \hat{J}_{11} - p_1^2 e_1 \alpha_1^2 \bar{u}_1 \bar{v}_1 \hat{J}_{22}, \end{aligned}$$

and

$$\begin{aligned} &\hat{J}_{11} = -r + p_1\alpha_1 \bar{v}_1 < 0, \\ &\hat{J}_{22} = -r + p_1\beta_1 \bar{v}_1 < 0, \\ &\hat{J}_{33} = -\mu_1 + p_1 e_1 \alpha_1 K_1 + p_1 e_1 \beta_1 K_2 - p_1^2 e_1 (\alpha_1^2 K_1/r + \beta_1^2 K_2/r)\bar{v}_1, \\ &\hat{J}_{44} = -\mu_2 + p_2 e_2 \alpha_2 K_1 + p_2 e_2 \beta_2 K_2 - p_1 p_2 e_2 (\alpha_1\alpha_2 K_1/r + \beta_1\beta_2 K_2/r)\bar{v}_1. \end{aligned} \tag{6}$$

Substituting the equilibrium into (6) reveals that $\hat{J}_{33} = 0$. Hence $a_0, a_1, a_2 > 0$, and direct calculation gives

$$\begin{aligned} &a_1 a_2 - a_0 \\ &= -(\hat{J}_{11} + \hat{J}_{22})(\hat{J}_{11}\hat{J}_{22} + p_1^2 e_1 \alpha_1^2 \bar{u}_1 \bar{v}_1 + p_1^2 e_1 \beta_1^2 \bar{u}_2 \bar{v}_1) \\ &\quad + p_1^2 e_1 \beta_1^2 \bar{u}_2 \bar{v}_1 \hat{J}_{11} + p_1^2 e_1 \alpha_1^2 \bar{u}_1 \bar{v}_1 \hat{J}_{22} \\ &= -\hat{J}_{11}(\hat{J}_{11}\hat{J}_{22} + p_1^2 e_1 \alpha_1^2 \bar{u}_1 \bar{v}_1) - \hat{J}_{22}(\hat{J}_{11}\hat{J}_{22} + p_1^2 e_1 \beta_1^2 \bar{u}_2 \bar{v}_1) \\ &> 0. \end{aligned}$$

By Routh-Hurwitz criterion, the equation $\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0$ has all roots with negative real parts. Accordingly, the local stability of E_3^1 is determined by the sign of $\hat{J}_{44}$. Note that

$$\hat{J}_{44} = \mu_2(\mathcal{R}_0^2 - 1) - \mu_1(\mathcal{R}_0^1 - 1)\frac{p_2 e_2(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2)}{p_1 e_1(\alpha_1^2 K_1 + \beta_1^2 K_2)}.$$

Therefore, the assertion is proved.   □

Equilibrium	Existence	Stability	Condition for stability
E_0^0, E_1^0, E_2^0	always exists	unstable	
E_3^0	always exists	LS	$\mathcal{R}_0^1 < 1, \mathcal{R}_0^2 < 1$
E_1^1	$\mathcal{R}_1^1 > 1$	LS	$\hat{\mathcal{R}}_1^1 > 1, \mathcal{R}_1^2 < \mathcal{R}_1^1$
E_2^1	$\mathcal{R}_2^1 > 1$	LS	$\hat{\mathcal{R}}_2^1 > 1, \mathcal{R}_2^2 < \mathcal{R}_2^1$
E_3^1	$\mathcal{R}_0^1 > 1, \hat{\mathcal{R}}_1^1 < 1, \hat{\mathcal{R}}_2^1 < 1$	LS	Cond-1
E_1^2	$\mathcal{R}_1^2 > 1$	LS	$\hat{\mathcal{R}}_1^2 > 1, \mathcal{R}_1^1 < \mathcal{R}_1^2$
E_2^2	$\mathcal{R}_2^2 > 1$	LS	$\hat{\mathcal{R}}_2^2 > 1, \mathcal{R}_2^1 < \mathcal{R}_2^2$
E_3^2	$\mathcal{R}_0^2 > 1, \hat{\mathcal{R}}_1^2 < 1, \hat{\mathcal{R}}_2^2 < 1$	LS	Cond-2
E^*	Theorem 3.8		

TABLE 1. Existence and stability of boundary equilibria for system (1). Cond-1: $\frac{\mu_2(\mathcal{R}_0^2-1)}{p_2 e_2(\alpha_1\alpha_2 K_1+\beta_1\beta_2 K_2)} < \frac{\mu_1(\mathcal{R}_0^1-1)}{p_1 e_1(\alpha_1^2 K_1+\beta_1^2 K_2)}$; Cond-2: $\frac{\mu_1(\mathcal{R}_0^1-1)}{p_1 e_1(\alpha_1\alpha_2 K_1+\beta_1\beta_2 K_2)} < \frac{\mu_2(\mathcal{R}_0^2-1)}{p_2 e_2(\alpha_2^2 K_1+\beta_2^2 K_2)}$; LS: locally stable.

The stability of other boundary equilibria can be similarly investigated. To save space, we omit these proofs, but just summarize the results in Table 1.

We have seen that when $\mathcal{R}_0^j < 1$, species-j predator goes to extinction. Thus, in order for predator j to be able to persist, $\mathcal{R}_0^j > 1$ is necessary. Next, we explore sufficient conditions for the persistence of species-j predator.

Theorem 3.5. *The species-j predator population in system (1) is uniformly persistent if one of the following holds:*

(i) $\mathcal{R}_0^j > 1$ and $\mathcal{R}_0^k < 1$, $k \neq j$;
(ii) $\mathcal{R}_0^k > 1$, $k \neq j$, and
   (H_1^k) $\hat{\mathcal{R}}_1^k > 1$, $\mathcal{R}_1^j > \mathcal{R}_1^k$, or
   (H_2^k) $\hat{\mathcal{R}}_2^k > 1$, $\mathcal{R}_2^j > \mathcal{R}_2^k$, or
   (H_3^k) $\hat{\mathcal{R}}_1^k < 1$, $\hat{\mathcal{R}}_2^k < 1$ and

$$\frac{\mu_k(\mathcal{R}_0^k - 1)}{p_k e_k(\alpha_k^2 K_1 + \beta_k^2 K_2)} < \frac{\mu_j(\mathcal{R}_0^j - 1)}{p_j e_j(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2)}.$$

Proof. We prove the theorem with $j = 1$ and $k = 2$. Define

$$\begin{aligned}
X &= \{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4\}, \\
X_0 &= \{(u_1, u_2, v_1, v_2) \in X | v_1 > 0\}, \\
\partial X_0 &= X \setminus X_0 = \{(u_1, u_2, v_1, v_2) \in X | v_1 = 0\}.
\end{aligned}$$

There exist at most seven equilibria in ∂X_0. Explicitly, E_0^0, E_1^0, E_2^0, E_3^0 always exist and at least one of E_1^2, E_2^2, E_3^2 exists if and only if $\mathcal{R}_0^2 > 1$ (see Table 1). It is easy to see that the spaces X_0 and ∂X_0 are positively invariant under the solution flow of (1). From the boundedness of the solution, there exists a global attractor in ∂X_0, say A_∂^0.

When (i) $\mathcal{R}_0^1 > 1$ and $\mathcal{R}_0^2 < 1$ hold, there are four equilibria, E_0^0, E_1^0, E_2^0 and E_3^0, in ∂X_0. From Lemma 3.3-(i) and $\mathcal{R}_0^2 < 1$, E_3^0 is globally asymptotically stable in set $\partial X_0 \setminus \{u_1 = 0 \text{ or } u_2 = 0\}$. It is clear that E_0^0, E_1^0, E_2^0 and E_3^0 are isolated and acyclic in set ∂X_0. Next, we show that $W^s(E_3^0) \cap X_0 = \emptyset$, and the cases for E_0^0, E_1^0, E_2^0 can be similarly treated. Suppose for the sake of contradiction that there

exists a solution of (1) with $v_1(t)$ positive for all $t \geq 0$ such that

$$\lim_{t \to \infty} (u_1(t), u_2(t), v_1(t), v_2(t)) = (K_1, K_2, 0, 0).$$

Denote the function

$$A(t) = -\mu_1 + p_1 e_1 \alpha_1 u_1(t) + p_1 e_1 \beta_1 u_2(t).$$

Then it satisfies that $A(t) \to \mu_1(\mathcal{R}_0^1 - 1) > 0$ as $t \to \infty$. Hence, there is a $t_1 > 0$ such that $A(t) > \frac{\mu_1}{2}(\mathcal{R}_0^1 - 1)$ for $t \geq t_1$, and then

$$\frac{dv_1(t)}{dt} = A(t)v_1(t) \geq \frac{\mu_1}{2}\left(\mathcal{R}_0^1 - 1\right)v_1(t), \text{ for } t \geq t_1.$$

By the comparison principle, v_1 grows unboundedly and it contradicts to the boundedness of the solution. Therefore, $W^s(E_3^0) \cap X_0 = \emptyset$ whenever $\mathcal{R}_0^1 > 1$. By the persistence theory in [11, 31], it concludes that the population of species-1 predator, v_1, uniformly persists in (1).

When (ii) $\mathcal{R}_0^2 > 1$, at least one of equilibria E_1^2, E_2^2, E_3^2 exists in (1). If, in addition, $\hat{\mathcal{R}}_1^2 > 1$ and $\mathcal{R}_1^1 > \mathcal{R}_1^2$, then E_1^2 exists, E_3^2 does not exist, and E_2^2 possibly exists in the system. We show that $W^s(E_1^2) \cap X_0 = \emptyset$. Suppose for the sake of contradiction that there exists a solution of (1) with $v_1(t)$ positive for all $t \geq 0$ such that

$$\lim_{t \to \infty} (u_1(t), u_2(t), v_1(t), v_2(t)) = \left(\frac{K_1}{\mathcal{R}_1^2}, 0, 0, \frac{r}{p_2 \alpha_2}\left(1 - \frac{1}{\mathcal{R}_1^2}\right)\right).$$

Then it satisfies that $A(t) \to \mu_1\left(\frac{\mathcal{R}_1^1}{\mathcal{R}_1^2} - 1\right)$ as $t \to \infty$. Since $\mathcal{R}_1^1 > \mathcal{R}_1^2$, it holds that $\mu_1(\mathcal{R}_1^1/\mathcal{R}_1^2 - 1) > 0$. Hence, there is a $t_2 > 0$ such that $A(t) > \frac{\mu_1}{2}(\mathcal{R}_1^1/\mathcal{R}_1^2 - 1)$ for $t \geq t_2$, and then

$$\frac{dv_1(t)}{dt} = A(t)v_1(t) \geq \frac{\mu_1}{2}\left(\frac{\mathcal{R}_1^1}{\mathcal{R}_1^2} - 1\right)v_1(t), \text{ for } t \geq t_2.$$

By the comparison principle, v_1 grows unboundedly and it contradicts to the boundedness of the solution. Therefore, $W^s(E_1^2) \cap X_0 = \emptyset$. Next, we show that $W^s(E_2^2) \cap X_0 = \emptyset$ if the equilibrium E_2^2 exists (when $\mathcal{R}_2^2 > 1$). Suppose for the sake of contradiction that there exists a solution of (1) with $v_1(t)$ positive for all $t \geq 0$ such that

$$\lim_{t \to \infty} (u_1(t), u_2(t), v_1(t), v_2(t)) = \left(0, \frac{K_2}{\mathcal{R}_2^2}, 0, \frac{r}{p_2 \beta_2}\left(1 - \frac{1}{\mathcal{R}_2^2}\right)\right).$$

Denote the function

$$B(t) = r\left(1 - \frac{u_1(t)}{K_1}\right) - p_1 \alpha_1 v_1(t) - p_2 \alpha_2 v_2(t).$$

Then it satisfies that

$$B(t) \to r\left(1 - \frac{\alpha_2}{\beta_2}\left(1 - \frac{1}{\mathcal{R}_2^2}\right)\right) = \frac{r\alpha_2}{\beta_2}\frac{1}{\mathcal{R}_2^2}\left(1 - \hat{\mathcal{R}}_2^2\right) =: b_0.$$

Note, from (3) and $\hat{\mathcal{R}}_1^2 > 1$, that $b_0 > 0$. Hence, there is a $t_3 > 0$ such that $B(t) > b_0/2$ for $t \geq t_3$, and then

$$\frac{du_1(t)}{dt} = B(t)u_1(t) \geq \frac{b_0}{2}u_1(t), \text{ for } t \geq t_3.$$

By the comparison principle, u_1 grows unboundedly and it contradicts to the boundedness of the solution. Therefore, $W^s(E_2^2) \cap X_0 = \emptyset$. By the persistence theory

in [11, 31], it concludes that the population of species-1 predator, v_1, uniformly persists in (1).

When $\mathcal{R}_0^2 > 1$, $\hat{\mathcal{R}}_1^2 < 1$ and $\hat{\mathcal{R}}_2^2 < 1$, E_3^2 exists, and E_1^2, E_2^2 possibly exists in the system. Considering the u_1 equation in (1) and applying the same method in last argument, we can show that, when E_2^2 exists, $W^s(E_2^2) \cap X_0 = \emptyset$ because of the assumption $\hat{\mathcal{R}}_2^2 < 1$. Similarly, when E_1^2 exists, $W^s(E_1^2) \cap X_0 = \emptyset$ since $\hat{\mathcal{R}}_2^2 < 1$. Next, we show that $W^s(E_3^2) \cap X_0 = \emptyset$ when the condition in (H_3^2) holds true. Suppose for the sake of contradiction that there exists a solution of (1) with $v_1(t)$ positive for all $t \geq 0$ such that

$$\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = \left(K_1\left(1 - \frac{p_2\alpha_2\bar{v}_2}{r}\right), K_2\left(1 - \frac{p_2\beta_2\bar{v}_2}{r}\right), 0, \bar{v}_2\right).$$

Then it satisfies that

$$\begin{aligned}A(t) \quad &\to \quad -\mu_1 + p_1e_1\alpha_1 K_1\left(1 - \frac{p_2\alpha_2\bar{v}_2}{r}\right) + p_1e_1\beta_1 K_2\left(1 - \frac{p_2\beta_2\bar{v}_2}{r}\right)\\ &= \quad p_1e_1(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2) \times\\ &\qquad \left(\frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1e_1(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2)} - \frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2e_2(\alpha_2^2 K_1 + \beta_2^2 K_2)}\right) =: b_1\end{aligned}$$

as $t \to \infty$. From the assumption (H_3^2), we have $b_1 > 0$. Hence, there is a $t_4 > 0$ such that $A(t) > b_1/2$ for $t \geq t_4$, and then

$$\frac{dv_1(t)}{dt} = A(t)v_1(t) \geq \frac{b_1}{2}v_1(t), \text{ for } t \geq t_4.$$

By the comparison principle, v_1 grows unboundedly and it contradicts to the boundedness of the solution. Therefore, $W^s(E_3^2) \cap X_0 = \emptyset$. By the persistence theory in [11, 31], it concludes that the population of species-1 predator, v_1, uniformly persists in (1). It completes the proof. □

Remark 2. We would like to remark the following.

(i) It holds that $\mathcal{R}_0^j > 1$ in each case of Theorem 3.5 (ii). For example, when $\hat{\mathcal{R}}_1^k > 1$ holds true, it yields $\mathcal{R}_1^k > 1$ and then $\mathcal{R}_0^j > 1$ due to $\mathcal{R}_1^j > \mathcal{R}_1^k$.

(ii) The criteria in the cases (ii) (H_1^k), (H_2^k) and (H_3^k) enforce the local *instability* of E_1^k, E_2^k and E_3^k respectively whenever one exists.

(iii) Obviously, the combinatorial criteria (H_1^1) and (H_1^2) (resp. (H_2^1) and (H_2^2)) cannot hold simultaneously.

(iv) In order to explore the global convergence to the positive equilibrium in next section, we note that (H_3^k) does not hold when $\alpha_1 = \alpha_2$ and $p_1e_1/\mu_1 = p_2e_2/\mu_2$.

From Theorem 3.5, uniform persistence of both predators is possible for system (1) only if $\mathcal{R}_0^1 > 1$ and $\mathcal{R}_0^2 > 1$ (necessary conditions for co-persistence). Indeed, by Theorem 3.5, one can obtain the following theorem which summarizes further conditions ensuring co-persistence of both predators for variant biological scenarios, according to the existence of the equilibria E_k^j for $j = 1, 2$ and $k = 1, 2, 3$.

Theorem 3.6. *Both predator species uniformly persist in system* (1) *if* $\mathcal{R}_0^1 > 1$, $\mathcal{R}_0^2 > 1$ *and one of the following combinations holds:*

$$\left\{\begin{array}{c}(H_1^1)\\(H_2^2),\end{array}\right. \left\{\begin{array}{c}(H_2^1)\\(H_1^2),\end{array}\right. \left\{\begin{array}{c}(H_1^1)\\(H_3^2),\end{array}\right. \left\{\begin{array}{c}(H_2^1)\\(H_3^2),\end{array}\right. \left\{\begin{array}{c}(H_3^1)\\(H_1^2),\end{array}\right. \left\{\begin{array}{c}(H_3^1)\\(H_2^2),\end{array}\right. \left\{\begin{array}{c}(H_3^1)\\(H_3^2).\end{array}\right. \tag{7}$$

For some special cases, the above combinations can be more explicitly presented. For example, if consider a scenario that two species of predators are two strains of the same predator only differing in the allocation strategies, we would have $p_1 = p_2$ and $e_1 = e_2$ then we have the following theorem with more explicit conditions.

Theorem 3.7. *When $p_1 = p_2$ and $e_1 = e_2$, both predator species uniformly persist in system* (1) *if $\mathcal{R}_0^1 > 1$, $\mathcal{R}_0^2 > 1$ and one of the following holds:*

  (i) $\hat{\mathcal{R}}_1^1 > 1$ and $\hat{\mathcal{R}}_2^2 > 1$ (ensuring (H_1^1) and (H_2^2));
  (ii) $\hat{\mathcal{R}}_2^1 > 1$ and $\hat{\mathcal{R}}_1^2 > 1$ (ensuring (H_2^1) and (H_1^2));
 (iii) $\hat{\mathcal{R}}_1^1 > 1$, $\hat{\mathcal{R}}_1^2 < 1$, $\hat{\mathcal{R}}_2^2 < 1$, $\frac{\alpha_1}{\mu_1} < \frac{\alpha_2}{\mu_2}$ and $\mathcal{P}_1$ holds (ensuring (H_1^1) and (H_3^2));
  (iv) $\hat{\mathcal{R}}_2^1 > 1$, $\hat{\mathcal{R}}_1^2 < 1$, $\hat{\mathcal{R}}_2^2 < 1$, $\frac{\beta_1}{\mu_1} < \frac{\beta_2}{\mu_2}$ and $\mathcal{P}_1$ holds (ensuring (H_2^1) and (H_3^2));
   (v) $\hat{\mathcal{R}}_1^1 < 1$, $\hat{\mathcal{R}}_2^1 < 1$, $\hat{\mathcal{R}}_1^2 > 1$, $\frac{\alpha_2}{\mu_2} < \frac{\alpha_1}{\mu_1}$ and $\mathcal{P}_2$ holds (ensuring (H_3^1) and (H_1^2));
  (vi) $\hat{\mathcal{R}}_1^1 < 1$, $\hat{\mathcal{R}}_2^1 < 1$, $\hat{\mathcal{R}}_2^2 > 1$, $\frac{\beta_2}{\mu_2} < \frac{\beta_1}{\mu_1}$ and $\mathcal{P}_2$ holds (ensuring (H_3^1) and (H_2^2));
 (vii) $\hat{\mathcal{R}}_k^j < 1$ for $j, k = 1, 2$, $\mathcal{P}_1$ and $\mathcal{P}_2$ hold (ensuring (H_3^1) and (H_3^2)),

where

$$\mathcal{P}_1 \quad : \quad \frac{\mu_2(\mathcal{R}_0^2 - 1)}{\alpha_2^2 K_1 + \beta_2^2 K_2} < \frac{\mu_1(\mathcal{R}_0^1 - 1)}{\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2},$$

$$\mathcal{P}_2 \quad : \quad \frac{\mu_1(\mathcal{R}_0^1 - 1)}{\alpha_1^2 K_1 + \beta_1^2 K_2} < \frac{\mu_2(\mathcal{R}_0^2 - 1)}{\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2}.$$

Remark 3. We point out that each of the seven sets of conditions in Theorem 3.7 is feasible in the sense that it can hold for certain range of parameters. For example, in the case (vii) with $\mu_j = \mu$ and $K_j = K$ for $j = 1, 2$, $\hat{\mathcal{R}}_k^j < 1$ holds true for $j, k = 1, 2$ when

$$\max\left\{\alpha_j\left(1 - \frac{\alpha_j}{\beta_j}\right), \beta_j\left(1 - \frac{\beta_j}{\alpha_j}\right), \ j = 1, 2\right\} < \frac{\mu}{peK}, \tag{8}$$

and the inequalities $\mathcal{P}_1$ and $\mathcal{P}_2$ are equivalent to

$$\frac{peK}{\mu} > 1, \ \text{and} \ \alpha_1 < \frac{1}{2} < \alpha_2 \ \text{or} \ \alpha_2 < \frac{1}{2} < \alpha_1. \tag{9}$$

There is a wide range of parameters such that (8) and (9) hold true. Hence, the conditions in Theorem 3.7 (vii) can also hold true for some case with $\mu_1 \neq \mu_2$ and $K_1 \neq K_2$. A set of eligible parameters will be adopted in later numerical simulation.

Since each solution of system (1) is eventually bounded, the generated solution flow is point dissipative. From the uniform persistence theory in [35, Theorem 2.4], (1) permits at least one positive equilibrium E^* under the conditions in Theorem 3.7. However, when only one predator species persists, the system (1) will have the dynamics of global convergence to the corresponding equilibrium, as shown in following theorems. Although the proofs by using Lyapunov method is standard, we will see the choice the Lyapunov functions and the estimates of their derivatives are *subtle and dedicate* in relating to the required criteria which turn out to be exactly the same as those for the local asymptotical stability .

Theorem 3.8. *The following statements hold.*

  (i) *Assume $\mathcal{R}_1^1 > 1$ so that the equilibrium E_1^1 exists. If, in addition, $\hat{\mathcal{R}}_1^1 > 1$ and $\mathcal{R}_1^2 < \mathcal{R}_1^1$ also hold, then E_1^1 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_1 > 0\}$.*
  (ii) *Assume $\mathcal{R}_2^1 > 1$ so that the equilibrium E_2^1 exists. If, in addition, $\hat{\mathcal{R}}_2^1 > 1$ and $\mathcal{R}_2^2 < \mathcal{R}_2^1$ also hold, then E_2^1 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_1 > 0\}$.*

(iii) *Assume $\mathcal{R}_0^1 > 1$, $\hat{\mathcal{R}}_1^1 < 1$ and $\hat{\mathcal{R}}_2^1 < 1$ so that the equilibrium E_3^1 exists. If, in addition,*

$$\frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2 e_2(\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2)} < \frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1 e_1(\alpha_1^2 K_1 + \beta_1^2 K_2)}$$

also holds, then E_3^1 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_1 > 0\}$.

(iv) *Assume $\mathcal{R}_1^2 > 1$ so that the equilibrium E_1^2 exists. If, in addition, $\hat{\mathcal{R}}_1^2 > 1$ and $\mathcal{R}_1^1 < \mathcal{R}_1^2$ also hold, then E_1^2 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_2 > 0\}$.*

(v) *Assume $\mathcal{R}_2^2 > 1$ so that the equilibrium E_2^2 exists. If, in addition, $\hat{\mathcal{R}}_2^2 > 1$ and $\mathcal{R}_2^1 < \mathcal{R}_2^2$ also hold, then E_2^2 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_2 > 0\}$.*

(vi) *Assume $\mathcal{R}_0^2 > 1$, $\hat{\mathcal{R}}_1^2 < 1$ and $\hat{\mathcal{R}}_2^2 < 1$ so that the equilibrium E_3^2 exists. If, in addition,*

$$\frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1 e_1(\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2)} < \frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2 e_2(\alpha_2^2 K_1 + \beta_2^2 K_2)}$$

also hold, then E_3^2 is GAS in $\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_2 > 0\}$.

Proof. We present the poofs for (i) and (iii), and the others can be proved by the same method. For (i), firstly the existence and local stability of E_1^1 follows from previous discussions. It suffices to show that E_1^1 is globally attractive in $\tilde{X}$, where $\tilde{X} = \{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_1 > 0\}$. Denote $E_1^1 = (\tilde{u}_1, \tilde{u}_2, \tilde{v}_1, \tilde{v}_2)$ and define

$$V_1(t) = u_1 - \tilde{u}_1 - \tilde{u}_1 \ln \frac{u_1}{\tilde{u}_1} + u_2 + \frac{1}{e_1}\left(v_1 - \tilde{v}_1 - \tilde{v}_1 \ln \frac{v_1}{\tilde{v}_1}\right) + \frac{v_2}{e_2}.$$

Calculating the derivative of V_1 along the solution of (1) yields

$$
\begin{aligned}
\frac{dV_1(t)}{dt} &= \frac{u_1 - \tilde{u}_1}{u_1}u_1' + u_2' + \frac{1}{e_1}\frac{v_1 - \tilde{v}_1}{v_1}v_1' + \frac{v_2'}{e_2} \\
&= (u_1 - \tilde{u}_1)\left(r\left(1 - \frac{u_1}{K_1}\right) - p_1\alpha_1 v_1 - p_2\alpha_2 v_2\right) \\
&\quad + ru_2\left(1 - \frac{u_2}{K_2}\right) - p_1\beta_1 u_2 v_1 - p_2\beta_2 u_2 v_2 \\
&\quad + (v_1 - \tilde{v}_1)\left(-\frac{\mu_1}{e_1} + p_1\alpha_1 u_1 + p_1\beta_1 u_2\right) \\
&\quad + v_2\left(-\frac{\mu_2}{e_2} + p_2\alpha_2 u_1 + p_2\beta_2 u_2\right) \\
&= (u_1 - \tilde{u}_1)\left(r\left(1 - \frac{u_1}{K_1}\right) - p_1\alpha_1 v_1 - p_2\alpha_2 v_2 \right. \\
&\quad \left. -r\left(1 - \frac{\tilde{u}_1}{K_1}\right) + p_1\alpha_1\tilde{v}_1 + p_2\alpha_2\tilde{v}_2\right) \\
&\quad + ru_2 - \frac{r}{K_2}u_2^2 - p_1\beta_1(u_2 - \tilde{u}_2)(v_1 - \tilde{v}_1) - p_1\beta_1 u_2\tilde{v}_1 \\
&\quad - p_2\beta_2(u_2 - \tilde{u}_2)(v_2 - \tilde{v}_2) - p_2\beta_2 u_2\tilde{v}_2 \\
&\quad + (v_1 - \tilde{v}_1)\left(-\frac{\mu_1}{e_1} + p_1\alpha_1 u_1 + p_1\beta_1 u_2 + \frac{\mu_1}{e_1} - p_1\alpha_1\tilde{u}_1 - p_1\beta_1\tilde{u}_2\right) \\
&\quad - \frac{\mu_2}{e_2}v_2 + p_2\alpha_2 u_1 v_2 + p_2\beta_2 u_2 v_2
\end{aligned}
$$

$$= -\frac{r}{K_1}(u_1 - \tilde{u}_1)^2 - \frac{r}{K_2}u_2^2 + v_2\left(p_2\alpha_2\tilde{u}_1 - \frac{\mu_2}{e_2}\right) + u_2(r - p_1\beta_1\tilde{v}_1).$$

Note that

$$p_2\alpha_2\tilde{u}_1 - \frac{\mu_2}{e_2} = p_2\alpha_2\left(\frac{\mu_1}{p_1e_1\alpha_1} - \frac{\mu_2}{p_2e_2\alpha_2}\right) < 0$$

due to the assumption $\mathcal{R}_1^2 < \mathcal{R}_1^1$, and

$$r - p_1\beta_1\tilde{v}_1 = r\left(1 - \frac{\beta_1}{\alpha_1}\right)\left(1 - \frac{1}{\hat{\mathcal{R}}_1^1}\right) < 0$$

implied by $\hat{\mathcal{R}}_1^1 > 1$ (also implying $0 \le \alpha_1 < \frac{1}{2}$). Since the solution to (1) remains nonnegative, we derive that $\frac{dV_1(t)}{dt} \le 0$. Let $M_1 = \{(u_1, u_2, v_1, v_2) \in \tilde{X}|\frac{dV_1(t)}{dt} = 0\}$ and M_1' be the largest invariant subset in M_1. By the LaSalle invariance principle, all solutions with initial conditions in $\tilde{X}$ tend to M_1'. Obviously, $M_1' \subset M_1 = \{(\tilde{u}_1, 0, v_1, 0)|v_1 > 0\}$. Since the set M_1' is positively invariant under the solution flow of (1), it is easy to see that $M_1' = \{(\tilde{u}_1, 0, \tilde{v}_1, 0)\}$ and it completes the proof of the assertion (i).

Suppose that the conditions in (iii) hold. The existence and local stability of E_3^1 follows from previous discussions. It suffices to show that E_3^1 is globally attractive in $\tilde{X}$. Denote $E_3^1 = (\bar{u}_1, \bar{u}_2, \bar{v}_1, \bar{v}_2)$ and define

$$V_2(t) = u_1 - \bar{u}_1 - \bar{u}_1 \ln\frac{u_1}{\bar{u}_1} + u_2 - \bar{u}_2 - \bar{u}_2 \ln\frac{u_2}{\bar{u}_2} + \frac{1}{e_1}\left(v_1 - \bar{v}_1 - \bar{v}_1 \ln\frac{v_1}{\bar{v}_1}\right) + \frac{v_2}{e_2}.$$

Calculating the derivative of V_2 along the solution of (1), it yields that

$$\begin{aligned}
\frac{dV_2(t)}{dt} &= \frac{u_1 - \bar{u}_1}{u_1}u_1' + \frac{u_2 - \bar{u}_2}{u_2}u_2' + \frac{1}{e_1}\frac{v_1 - \bar{v}_1}{v_1}v_1' + \frac{v_2'}{e_2} \\
&= (u_1 - \bar{u}_1)\left(r\left(1 - \frac{u_1}{K_1}\right) - p_1\alpha_1v_1 - p_2\alpha_2v_2\right. \\
&\qquad\left. -r\left(1 - \frac{\bar{u}_1}{K_1}\right) + p_1\alpha_1\bar{v}_1 + p_2\alpha_2\bar{v}_2\right) \\
&\quad + (u_2 - \bar{u}_2)\left(r\left(1 - \frac{u_2}{K_2}\right) - p_1\beta_1v_1 - p_2\beta_2v_2 - r\left(1 - \frac{\bar{u}_2}{K_2}\right)\right. \\
&\qquad\left. + p_1\beta_1\bar{v}_1 + p_2\beta_2\bar{v}_2\right) \\
&\quad + (v_1 - \bar{v}_1)\left(-\frac{\mu_1}{e_1} + p_1\alpha_1u_1 + p_1\beta_1u_2 + \frac{\mu_1}{e_1} - p_1\alpha_1\bar{u}_1 - p_1\beta_1\bar{u}_2\right) \\
&\quad + v_2\left(-\frac{\mu}{e} + p\alpha_2u_1 + p\beta_2u_2\right) \\
&= -\frac{r}{K_1}(u_1 - \bar{u}_1)^2 - p_2\alpha_2(u_1 - \bar{u}_1)(v_2 - \bar{v}_2) - \frac{r}{K_2}(u_2 - \bar{u}_2)^2 \\
&\quad - p_2\beta_2(u_2 - \bar{u}_2)(v_2 - \bar{v}_2) + v_2\left(-\frac{\mu_2}{e_2} + p_2\alpha_2u_1 + p_2\beta_2u_2\right) \\
&= -\frac{r}{K_1}(u_1 - \bar{u}_1)^2 - \frac{r}{K_2}(u_2 - \bar{u}_2)^2 + v_2\left(p_2\alpha_2\bar{u}_1 + p_2\beta_2\bar{u}_2 - \frac{\mu_2}{e_2}\right).
\end{aligned}$$

By a direct calculation, it yields that

$$p_2\alpha_2\bar{u}_1 + p_2\beta_2\bar{u}_2 - \frac{\mu_2}{e_2}$$

$$
\begin{aligned}
&= & p_2\alpha_2\left(K_1 - \frac{K_1}{r}p_1\alpha_1\bar{v}_1\right) + p_2\beta_2\left(K_2 - \frac{K_2}{r}p_1\beta_1\bar{v}_1\right) - \frac{\mu_2}{e_2} \\
&= & p_2\alpha_2 K_1 + p_2\beta_2 K_2 - \frac{\mu_2}{e_2} - (\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2)\frac{p_1 p_2 \bar{v}_1}{r} \\
&= & p_2\left(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2\right) \times \\
& & \left(\frac{\mu_2(\mathcal{R}_0^2 - 1)}{p_2 e_2(\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2)} - \frac{\mu_1(\mathcal{R}_0^1 - 1)}{p_1 e_1(\alpha_1^2 K_1 + \beta_1^2 K_2)}\right) \\
&< & 0.
\end{aligned}
$$

Since the solution to (1) remains nonnegative, we derive that $\frac{dV_2(t)}{dt} \leq 0$. Let $M_2 = \{(u_1, u_2, v_1, v_2) \in \tilde{X} | \frac{dV_2(t)}{dt} = 0\}$ and M_2' be the largest invariant subset in M_2. By the LaSalle invariance principle, all solutions with initial conditions in $\tilde{X}$ tend to M_2'. Obviously, $M_2' \subset M_2 = \{(\bar{u}_1, \bar{u}_2, v_1, 0)|v_1 > 0\}$. Since the set M_2' is positively invariant under the solution flow of (1), it is easy to see that $M_2' = \{(\bar{u}_1, \bar{u}_2, \bar{v}_1, 0)\}$ and it completes the proof of the assertion (iii). □

When the system (1) is uniformly persistent as stated in Theorem 3.6, there exists a positive equilibrium E^*. We claim that it is unique and attracts all positive solutions.

Theorem 3.9. *Under the assumption of Theorem 3.6, all solutions with initial conditions in $X := \{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^4 | u_1, u_2, v_1, v_2 > 0\}$ converge to the unique positive equilibrium E^*.*

Proof. Denote $E^* = (u_1^*, u_2^*, v_1^*, v_2^*)$ and define

$$
\begin{aligned}
V_3(t) &= & u_1 - u_1^* - u_1^* \ln\frac{u_1}{u_1^*} + u_2 - u_2^* - u_2^* \ln\frac{u_2}{u_2^*} \\
& & + \frac{1}{e_1}\left(v_1 - v_1^* - v_1^* \ln\frac{v_1}{v_1^*}\right) + \frac{1}{e_2}\left(v_1 - v_1^* - v_1^* \ln\frac{v_1}{v_1^*}\right).
\end{aligned}
$$

Calculating the derivative of V_3 along the solution of (1), it yields that

$$
\begin{aligned}
\frac{dV_3(t)}{dt} &= & \frac{u_1 - u_1^*}{u_1}u_1' + \frac{u_2 - u_2^*}{u_2}u_2' + \frac{1}{e_1}\frac{v_1 - v_1^*}{v_1}v_1' + \frac{1}{e_2}\frac{v_2 - v_2^*}{v_2}v_2' \\
&= & (u_1 - u_1^*)\left(r\left(1 - \frac{u_1}{K_1}\right) - p_1\alpha_1 v_1 - p_2\alpha_2 v_2\right. \\
& & \left. -r\left(1 - \frac{u_1^*}{K_1}\right) + p_1\alpha_1 v_1^* + p_2\alpha_2 v_2^*\right) \\
& & +(u_2 - u_2^*)\left(r\left(1 - \frac{u_2}{K_2}\right) - p_1\beta_1 v_1 - p_2\beta_2 v_2 - r\left(1 - \frac{u_2^*}{K_2}\right)\right. \\
& & \left. +p_1\beta_1 v_1^* + p_2\beta_2 v_2^*\right) \\
& & +(v_1 - v_1^*)\left(-\frac{\mu_1}{e_1} + p_1\alpha_1 u_1 + p_1\beta_1 u_2 + \frac{\mu_1}{e_1} - p_1\alpha_1 u_1^* - p_1\beta_1 u_2^*\right) \\
& & +(v_2 - v_2^*)\left(-\frac{\mu_2}{e_2} + p_2\alpha_2 u_1 + p_2\beta_2 u_2 + \frac{\mu_2}{e_2} - p_2\alpha_2 u_1^* - p_2\beta_2 u_2^*\right) \\
&= & -\frac{r}{K_1}(u_1 - u_1^*)^2 - \frac{r}{K_2}(u_2 - u_2^*)^2 \\
&\leq & 0.
\end{aligned}
$$

Let $M_3 = \{(u_1, u_2, v_1, v_2) \in X | \frac{dV_3(t)}{dt} = 0\}$ and M_3' be the largest invariant subset in M_3. By the LaSalle invariance principle, all solutions with initial conditions in X tend to M_3'. Obviously, $M_3' \subset M_3 = \{(u_1^*, u_2^*, v_1, v_2) | v_1, v_2 > 0\}$. Suppose that $(u_1^*, u_2^*, v_1(t), v_2(t))$ is a solution remaining in M_3' for $t \geq 0$. Then, it follows from the u equations in (1) that

$$p_1 \alpha_1 v_1(t) + p_2 \alpha_2 v_2(t) = r \left(1 - \frac{u_1^*}{K_1} \right),$$
$$p_1 \beta_1 v_1(t) + p_2 \beta_2 v_2(t) = r \left(1 - \frac{u_2^*}{K_2} \right), \tag{10}$$

and the v equations in (1) become

$$\frac{dv_1(t)}{dt} = c_1 v_1, \ \frac{dv_2(t)}{dt} = c_2 v_2, \ \text{for } t \geq 0, \tag{11}$$

where $c_j = -\mu_j + p_j e_j \alpha_j u_1^* + p_j e_j \beta_j u_2^*$ are constants for $j = 1, 2$. Combining (10) and (11) implies that $c_1 = c_2 = 0$, and then $v_1(t)$, $v_2(t)$ are constants. Hence, the set M' contains only equilibria of the system (1).

We claim that M' contains a singleton. If $\alpha_1 \neq \alpha_2$ holds then $\frac{\alpha_1}{1-\alpha_1} \neq \frac{\alpha_2}{1-\alpha_2}$ and the solution $v_1(t) = v_1^*$ and $v_2(t) = v_2^*$ to (10) is unique. If $\alpha_1 = \alpha_2 = \alpha$, (10) admits a solution $v_1(t) = v_1^*$ and $v_2(t) = v_2^*$ only if

$$\frac{\alpha}{1-\alpha} = \frac{1 - \frac{u_1^*}{K_1}}{1 - \frac{u_2^*}{K_2}}. \tag{12}$$

On the other hand, from the v-equation in (1), u_1^* and u_2^* satisfy

$$p_1 e_1 \alpha u_1^* + p_1 e_1 (1 - \alpha) u_2^* = \mu_1,$$
$$p_2 e_2 \alpha u_1^* + p_2 e_2 (1 - \alpha) u_2^* = \mu_2, \tag{13}$$

which admits solutions only if

$$\frac{p_1 e_1}{\mu_1} = \frac{p_2 e_2}{\mu_2}, \tag{14}$$

and under which (13) becomes

$$p_1 e_1 \alpha u_1^* + p_1 e_1 (1 - \alpha) u_2^* = \mu_1. \tag{15}$$

It is easy to see that there exist positive u_1^* and u_2^* satisfying (12) and (15) only if $\hat{\mathcal{R}}_1^1 (= \hat{\mathcal{R}}_1^2) < 1$ or $\hat{\mathcal{R}}_2^1 (= \hat{\mathcal{R}}_2^2) < 1$. From this factor and Remark 2 (iv), none of the criteria in (7) holds true. Thus, it concludes that the set M' contains only a singleton and the proof is completed. □

4. **Evolutionary implications.** In this section, we discuss the implications of the results in the previous section from the perspective of evolution, under some simpler cases.

4.1. **A mutation scenario — impact of spatial heterogeneity.** We start by considering the special case $p_j = p$, $e_j = e$ and $\mu_j = \mu$, for $j = 1, 2$. This corresponds to the scenario of the two predator species being biologically identical in all aspects except for adopting different allocation strategies α_1 and α_2 respectively. To be more specific, we consider species 2 as the wild (original) species playing strategy α_2, species 1 as a mutant from species differing only in allocation strategy α_1.

Assume that in the absent of the mutant species 1, predator 2 can persistent. By Theorem 3.5-(i), this is implied by the condition $\mathcal{R}_0^2 > 1$. We would like

know whether or not the mutant species 1 can invade; and if it can, whether it will replace the wild species or it will co-persist with the wild species. For convenience of exploring the above questions, we let $\xi = K_2/K_1$; and without loss of generality we assume $\xi \geq 1$ (i.e., $K_2 \geq K_1$), meaning that patch 2 is no worse than patch 1. Uniform persistence of species-1 predator answers the first question, and the global convergence to one of the equilibria E_k^1, $k = 1, 2, 3$ corresponds to the second question above. We now explore below.

By Theorem 3.5-(ii), species 1 will persist (successfully invade) if one of the following holds:

(P_1) $\alpha_1 > \alpha_2$, if $\frac{pe\alpha_2 K_1}{\mu}\left(1 - \frac{\alpha_2}{1-\alpha_2}\right) > 1$ $(\Longleftrightarrow \hat{\mathcal{R}}_1^2 > 1)$;

(P_2) $\alpha_1 < \alpha_2$ (i.e., $\beta_1 > \beta_2$), if $\frac{pe(1-\alpha_2)\xi K_1}{\mu}\left(1 - \frac{1-\alpha_2}{\alpha_2}\right) > 1$ $(\Longleftrightarrow \hat{\mathcal{R}}_2^2 > 1)$;

(P_3) $\hat{\mathcal{R}}_1^2 < 1$ and $\hat{\mathcal{R}}_2^2 < 1$, and moreover,

$$\frac{\mathcal{R}_0^2 - 1}{\alpha_2^2 K_1 + \beta_2^2 K_2} < \frac{\mathcal{R}_0^1 - 1}{\alpha_1\alpha_2 K_1 + \beta_1\beta_2 K_2}$$

which is equivalent to

$$F(\alpha_1, \alpha_2) := (a\alpha_2 - b)(\alpha_1 - \alpha_2) > 0, \tag{16}$$

where

$$a = (\xi + 1)\frac{\mu}{peK_1} - 2\xi, \; b = \xi\left(\frac{\mu}{peK_1} - 1\right).$$

Note that from Lemma 3.3, cases (P_1) and (P_2) simply indicate that if species 2 playing allocation strategy α_2 can persist in a single patch, then species 1 can also invade that patch by allocating more to that patch (i.e., $\alpha_1 > \alpha_2$ for case (P_1) and $\beta_1 > \beta_2$ for case (P_2)). However, in the case that predator 2 cannot persist in any single patch alone in the absence of predator 1 but can persist in both patch by playing strategy α_2 (case (P_3)), in order for predator 1 to be able to invade, it needs to play a strategy α_1 more complicatedly determined by (16).

In order to further explore the condition (16), we first note that when $\xi = 1$, the presumption $\mathcal{R}_0^2 > 1$ is equivalent to $peK_1 > \mu$ which is independent in α_2; while when $\xi > 1$, the presumption $\mathcal{R}_0^2 > 1$ is equivalent to

$$\alpha_2 < \frac{\xi - \mu/peK_1}{\xi - 1} =: \alpha_{20}.$$

For convenience of discussion, we divide the interval $(0, \infty)$ for μ into four sub-intervals I-1, I-2, I-3 and I-4 in terms of the signs of parameters a and b, as depicted in Fig. 1. In the case of $\xi = 1$, I-2 and I-3 do not exist. Note that $\alpha_{20} > 1$ for $\mu \in$ I-1, $0 < \alpha_{20} < 1$ for $\mu \in$ I-2 or I-3, and $\alpha_{20} < 0$ for $\mu \in$ I-4. Based on such a division, the signs of the two terms in $F(\alpha_1, \alpha_2)$ are determined as Table 2, and the corresponding regions in the α_1-α_2 plane in which (16) are shown in Fig. 2, marked by red colour.

We may also use Theorem 3.8 to explore the conditions under which the mutant species-1 predator can *replace (outcompete)* the species 2, and this is implied by the global stability of the boundary equilibria with the v_2 component being zero, namely E_k^1, $k = 1, 2, 3$. More specifically, by Theorem 3.8-(i)~(iii), the following hold:

(S_1) if $\hat{\mathcal{R}}_1^1 > 1$ and $\alpha_1 > \alpha_2$, then E_1^1 is GAS;

(S_2) if $\hat{\mathcal{R}}_2^1 > 1$ and $\alpha_1 < \alpha_2$, then E_1^2 is GAS;

(S_3) if $\mathcal{R}_0^1 > 1$, $\hat{\mathcal{R}}_1^1 < 1$, $\hat{\mathcal{R}}_2^1 < 1$ and

$$\frac{\mathcal{R}_0^2 - 1}{\alpha_1 \alpha_2 K_1 + \beta_1 \beta_2 K_2} < \frac{\mathcal{R}_0^1 - 1}{\alpha_1^2 K_1 + \beta_1^2 K_2},$$

or equivalently

$$G(\alpha_1, \alpha_2) := (a\alpha_1 - b)(\alpha_1 - \alpha_2) > 0, \tag{17}$$

then E_3^1 is GAS.

Here a and b are same as in (16). Again using the same division of the interval $(0, \infty)$ for μ into sub-intervals as in Fig. 1 which are in terms of the signs of a, b and $(b/a) - 1$, we can determine the signs of the two terms in $G(\alpha_1, \alpha_2)$ as shown in Table 3, and accordingly, depict the regions in the α_1-α_2 plane for (17) in Fig. 3, marked by red colour.

Observe that when μ is in I-1, the red region in Fig. 2 (A) is larger than that in Fig. 3 (A), indicating that species-1 predator's invasion may not necessarily lead to replacing the native predator. For this case, Fig. 3 (A), shows that when the native species (species-2 predators) plays the critical strategy at $(\alpha_2, \beta_2) = (\alpha^*, \beta^*)$ where

$$\alpha^* = \alpha^*(\xi) := \frac{b}{a} = \frac{1 - \frac{\mu}{peK_1}}{2 - \frac{\xi+1}{\xi} \frac{\mu}{peK_1}}, \quad \beta^* = \beta^*(\xi) = 1 - \alpha^*(\xi), \tag{18}$$

it cannot be outcompeted by predator 1 regardless of the strategy predator 1 takes. This means that the strategy α^* is actually an evolutionarily stable strategy (ESS).

We remark that in evolutionary biology, an evolutionarily stable strategy (ESS) is a strategy that cannot be invaded by other strategies [10]. An ESS is often related to the notion of ideal free distribution (IFD) which was introduced in [2, 10] to illustrate the optimization of species distribution when individuals can completely detect their environment and are free to relocated themselves. Several studies have explored the relationship between distribution and ESS through different models, for example, single-species [7], a predator-prey [16], competitive [6] models and a model involving general interaction between species [1, 2, 7]. These studies have concluded that under certain conditions, the IFD is the evolutionarily stable state.

Now, since α^* is a strategy that cannot be invaded, it is worthwhile to see how the spatial heterogeneity parameter ξ affects it. Firstly, note that $\alpha^*(1) = 1/2$, indicating that, in the spatially homogeneous case, the even allocation $\alpha = 1/2$ is the optimal strategy and it is an ESS. Furthermore, direct calculation gives

$$\frac{d\alpha^*(\xi)}{d\xi} < 0, \text{ for } \xi \geq 1 \text{ with } \lim_{\xi \to \infty} \alpha^*(\xi) = \frac{1 - \frac{\mu}{peK_1}}{2 - \frac{\mu}{peK_1}} =: \alpha_\infty^*.$$

This shows how this ESS evolves with respective to the carrying capacity ξ that accounts for by how much Patch 2 is superior to Patch 1. With the superiority level ξ increases, the allocation portion β^* to Patch 2 in the ESS should also increase following (18).

On the other hand, when μ is in I-2 or I-3, the read regions in Fig. 2 (B) and Fig. 3 (B) are the same in the α_1-α_2 plane, implying that the invasion of species-1 predator means it outcompeting (replacing) the native predator. Note that $\mu \in$ I-2 or I-3 is equivalent to

$$\frac{peK_1}{\mu} < 1 < \frac{\xi peK_1}{\mu} = \frac{peK_2}{\mu}.$$

This means patch 2 is a "suitable habitat" and patch 1 is a "unsuitable habitat" for a predator with predation rate p, biomass transform efficiency e and death rate μ, and hence, in order to invade (persist), predator 1 should allocate more than species 2 to patch 2; that is, $\beta_1 > \beta_2$ which is equivalent to $\alpha_1 < \alpha_2$, hence the red colour region in Fig. 16-(B) and Fig. 17-(B).
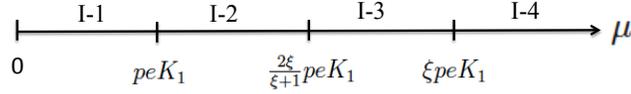
FIGURE 1. Different regions of μ to examine the criterion $F(\alpha_1, \alpha_2) > 0$ (when $\xi > 1$).

Value of μ	I-1		I-2	I-3	I-4	
Conditions	$\begin{cases} \alpha_1 > \alpha_2 \\ \alpha_2 < b/a \\ \alpha_1 < \alpha_2 \\ \alpha_2 > b/a \end{cases}$	or	$\alpha_1 < \alpha_2$	$\alpha_1 < \alpha_2$	$\begin{cases} \alpha_1 > \alpha_2 \\ \alpha_2 > b/a \\ \alpha_1 < \alpha_2 \\ \alpha_2 < b/a \end{cases}$	or

TABLE 2. Conditions for $F(\alpha_1, \alpha_2) > 0$ in variant values of μ.

FIGURE 2. Strategies α_1 vs α_2 for $F(\alpha_1, \alpha_2) > 0$ (with $\xi > 1$): (A) for μ in I-1, (B) for μ in I-2 and I-3, (C) for μ in I-4.

Value of μ	I-1		I-2	I-3	I-4	
Conditions	$\begin{cases} \alpha_1 > \alpha_2 \\ \alpha_1 < b/a \\ \alpha_1 < \alpha_2 \\ \alpha_1 > b/a \end{cases}$	or	$\alpha_1 < \alpha_2$	$\alpha_1 < \alpha_2$	$\begin{cases} \alpha_1 > \alpha_2 \\ \alpha_1 > b/a \\ \alpha_1 < \alpha_2 \\ \alpha_1 < b/a \end{cases}$	or

TABLE 3. Conditions for $G(\alpha_1, \alpha_2) > 0$ in variant values of μ.
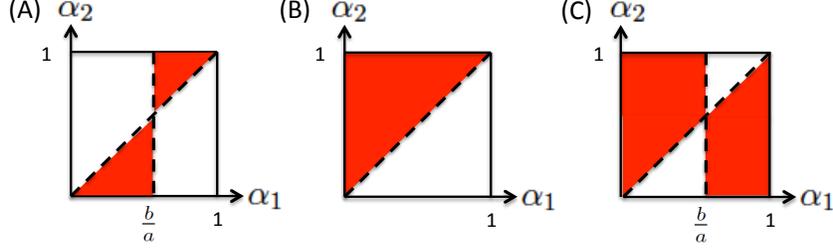
FIGURE 3. Strategies α_1 vs α_2 for $G(\alpha_1, \alpha_2) > 0$ (with $\xi > 1$). (A) for μ in the region I-1, (B) for μ in the regions I-2 and I-3, (C) for μ in the region I-4.

4.2. **Two species differing in mortality rate.** In this section, we consider a case which is slight more difficulty than in Subsection 4.2, namely, $p_1 = p_2 = p$ and $e_1 = e_2 = e$ but $\mu_1 \neq \mu_2$. From theorem 3.8, we see that the strategy for outcompeting a rival in a single patch can be simply explored by focusing on conditions for that patch, as is done in Subsection 4.1. However strategy for outcompeting in both patches is relatively more complicated. We briefly discuss below. For the scenario for the two predator species differing only in death rate, the criterion of global convergence to E_3^1 (predator 1 outcompeting predator 2 in both patches) given in Theorem 3.8-(iii) becomes

$$\tilde{G}(\alpha_1, \alpha_2) = \left[\left(2\xi - \frac{\mu_1(\xi + 1)}{peK_1} \right) \alpha_2 + \xi \left(\frac{\mu_1 - 2\mu_2}{peK_1} + 1 \right) \right] \alpha_1 \tag{19}$$
$$+ \left(\frac{\mu_2(\xi + 1)}{peK_1} - 2\xi \right) \alpha_1^2 + \xi \left[\left(\frac{\mu_1}{peK_1} - 1 \right) \alpha_2 + \frac{\mu_2 - \mu_1}{peK_1} \right] > 0.$$

Here, we suppose that both predator species can respectively survive in the environment when the rival is absent, i.e.

$$\mathcal{R}_0^1 > 1, \ \mathcal{R}_0^2 > 1. \tag{20}$$

In general, condition (19) is not easy to verify at all. We first study the spatial homogeneous case, that is , $K_1 = K_2 =: K$ and hence $\xi = 1$. With this spatial homogeneity, the criterion (19) has a compact form

$$\left(\frac{\mu_2}{peK} - 1 \right) \left[(2\alpha_1 - 1) \left(\alpha_1 - \frac{peK - \mu_1}{peK - \mu_2} \alpha_2 + \frac{\mu_2 - \mu_1}{2(peK - \mu_2)} \right) + \frac{\mu_1 - \mu_2}{2(peK - \mu_2)} \right]$$
$$=: \left(\frac{\mu_2}{peK} - 1 \right) \Gamma_1(\alpha_1, \alpha_2) > 0. \tag{21}$$

Note that the presumption condition in (20) implies that

$$\mu_j < peK, \ j = 1, 2. \tag{22}$$

We explore the regions for (α_1, α_2) in the α_1-α_2 plane under (22) for which (21) holds. To this end, we define two lines in the α_1-α_2 plane by

$$L_0 : \alpha_1 = \alpha_2, \ L_1 : \alpha_1 - \frac{peK - \mu_1}{peK - \mu_2} \alpha_2 + \frac{\mu_2 - \mu_1}{2(peK - \mu_2)} = 0.$$

It is easy to see that the line L_1 passes through the point $(\frac{1}{2}, \frac{1}{2})$ with the positive slope $\frac{peK-\mu_1}{peK-\mu_2}$. Define

$$\Gamma_2(\alpha_1, \alpha_2) := (2\alpha_1 - 1)\left(\alpha_1 - \frac{peK - \mu_1}{peK - \mu_2}\alpha_2 + \frac{\mu_2 - \mu_1}{2(peK - \mu_2)}\right).$$

Obviously, the region $\Gamma_2(\alpha_1, \alpha_2) < 0$ is bounded by two lines $\alpha_1 = \frac{1}{2}$ and L_1 which intersect at the point $(\frac{1}{2}, \frac{1}{2})$. In addition, the graph of the saddle surface $\Gamma_1(\alpha_1, \alpha_2) = 0$ is a upward (downward) shift of that of $\Gamma_2(\alpha_1, \alpha_2) = 0$ when $\mu_1 > \mu_2$ ($\mu_1 < \mu_2$). These geometric observations conclude that

$$L_0, L_1 \cap \{(\alpha_1, \alpha_2) | \Gamma_1(\alpha_1, \alpha_2) < 0\} = \emptyset, \text{ if } \mu_1 > \mu_2; \text{ and}$$
$$L_0, L_1 \subset \{(\alpha_1, \alpha_2) | \Gamma_1(\alpha_1, \alpha_2) < 0\}, \text{ if } \mu_1 < \mu_2.$$

Thus, smaller mortality rate of species-1 predator is beneficial for its invading the environment (corresponding to a wider range for (α_1, α_2) in the case with $\mu_1 < \mu_2$).

For the spatial heterogeneous case $\xi \neq 1$, analysis become much more difficult. Thus we just numerically explore the effect of different mortality rates in terms of the criterion (19). Here, to be specific, we choose parameters satisfying $\mu_i < peK_1$ for $i = 1, 2$ to focus the discussion on the interval I-1 for μ_i, $i = 1, 2$. Choosing $p = 0.5$, $e = 0.2$, $K_1 = 1$, $\xi = 2$ ($K_2 = 2$), $\mu_1 = 0.022$ and $\mu_2 = 0.02$, the region of (α_1, α_2) for $\tilde{G}(\alpha_1, \alpha_2) > 0$ is depicted in Fig. 4 by the shaded area. We see that due to the advantage of smaller mortality rate ($\mu_2 < \mu_1$), if the species-2 predator plays an allocation strategy α_2 within a range of medium values, it will outcompete the species-1 predator. If reduce μ_1 from $\mu_1 = 0.022$ to $\mu_1 = 0.018$ but all other parameters remain the same, the region of (α_1, α_2) for $\tilde{G}(\alpha_1, \alpha_2) > 0$ is depicted in Fig. 5 by the shaded area. In this case species-1 predator has a better biological fitness than species-2 predator ($\mu_1 < \mu_2$), and hence, no matter what strategy species-2 predator plays, it can always be invaded by species-1 predator by playing an appropriate strategy.
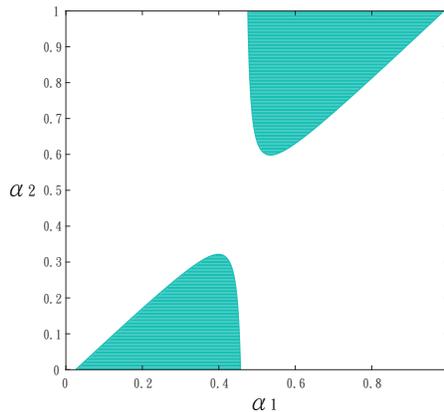
FIGURE 4. $\tilde{G}(\alpha_1, \alpha_2) > 0$ for $p = 0.5$, $e = 0.2$, $K_1 = 1$, $\xi = 2$ ($K_2 = 2$), $\mu_1 = 0.022$ and $\mu_2 = 0.02$.
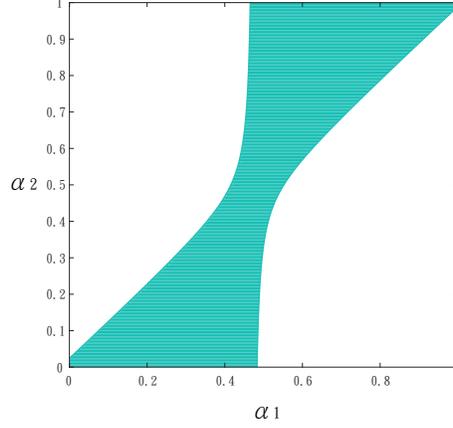
FIGURE 5. $\tilde{G}(\alpha_1, \alpha_2) > 0$ for $p = 0.5$, $e = 0.2$, $K_1 = 1$, $\xi = 2$
$(K_2 = 2)$, $\mu_1 = 0.018$ and $\mu_2 = 0.02$.

5. **Discussions.** In this paper, we have formulated a population model for the interactions of two predators investing their foraging time for the same non-dispersing preys in two different patches. We have analyzed the dynamics of the model in Section 3, and discussed some biological implications of the theoretical results on dynamics in two special but biologically meaning cases, including the the impact of spatial heterogeneity and the fitness of the two predator species in Section 4. In this section, we would like to add more discussion, mainly on possible extension of the model, as well as possible future research along this line.

Note that in model (1), we have assumed that the prey species distributed in the two patches are the same, and accordingly, the predating rate for predator j species predator in both patches as well as the biomass transfer efficiency can be considered the same, represented by p_j and e_j respectively for $j = 1, 2$. However, the fact that a prey will evolve and the evolution of the prey in different patches may result in significant variance in some biological features for the prey in different patches. This requires us to treat the preys in the two patches as different species, leading to different predation rates and biomass transfer efficiencies for the same predator. Therefore, we are motivated to modify the mode (1) to the following

$$
\begin{cases}
\dfrac{du_1(t)}{dt} = ru_1\left(1 - \dfrac{u_1}{K_1}\right) - p_{11}u_1[\alpha_1 v_1] - p_{21}u_1[\alpha_2 v_2], \\[2mm]
\dfrac{du_2(t)}{dt} = ru_2\left(1 - \dfrac{u_2}{K_2}\right) - p_{12}u_2[\beta_1 v_1] - p_{22}u_2[\beta_2 v_2], \\[2mm]
\dfrac{dv_1(t)}{dt} = -\mu_1 v_1 + p_{11}e_{11}u_1[\alpha_1 v_1] + p_{12}e_{12}u_2[\beta_1 v_1], \\[2mm]
\dfrac{dv_2(t)}{dt} = -\mu_2 v_2 + p_{21}e_{21}u_1[\alpha_2 v_2] + p_{22}e_{22}u_2[\beta_2 v_2],
\end{cases}
\tag{23}
$$

where p_{ji} is the rate of specise-j predator predating on the prey in patch-i and e_{ji} is the biomass transfer efficiency to specise-j predator from the prey in patch-i.

Observe that in system (1), the equilibria E_1^1 and E_2^2 can not be locally asymptotically stable *simultaneously*. This can be seen from Table 1: such a bi-stability

can occur only if $\hat{\mathcal{R}}_1^1 > 1$, $\hat{\mathcal{R}}_2^2 > 1$ and $\alpha_1 > \alpha_2$, which is impossible since the first two conditions respectively imply $0 \leq \alpha_1 < \frac{1}{2}$ and $\frac{1}{2} < \alpha_2 \leq 1$, contradicting to the third one. Now let us look at system (23). Firstly, we point out that the bi-stability of either the pair (E_1^1, E_1^2) or the pair (E_2^1, E_2^2) cannot happen. This is because the criteria for local stability of each of the equilibrium pairs requires the following contradicting conditions:

$$\mu_1 < \frac{p_{11}e_{11}\alpha_1}{p_{21}e_{21}\alpha_2}\mu_2 \text{ and } \mu_2 < \frac{p_{21}e_{21}\alpha_2}{p_{11}e_{11}\alpha_1}\mu_1. \tag{24}$$

However, (23) may allow bi-stability of some other pairs of equilibria, including the following pairs:

$$\begin{aligned}
\mathcal{B}_1 &: (E_1^1, E_2^2), (E_2^1, E_1^2), \\
\mathcal{B}_2 &: (E_1^1, E_3^2), (E_2^1, E_3^2), (E_3^1, E_1^2), (E_3^1, E_2^2), \\
\mathcal{B}_3 &: (E_3^1, E_3^2).
\end{aligned}$$

We briefly explore the bi-stability of type $\mathcal{B}_3$ and see how the heterogeneous biomass transfer efficiencies contribute to the bi-stability. The other cases can be shown by a similar manner. As in the proof of Theorem 3.4, the criteria for local stability (besides that for existence) of E_3^1 and E_3^2 for (23) now becomes

$$\begin{aligned}
\frac{p_{21}e_{21}\alpha_2 K_1 + p_{22}e_{22}\beta_2 K_2 - \mu_2}{p_{11}p_{21}e_{21}\alpha_1\alpha_2 K_1 + p_{12}p_{22}e_{22}\beta_1\beta_2 K_2} &< \frac{p_{11}e_{11}\alpha_1 K_1 + p_{12}e_{12}\beta_1 K_2 - \mu_1}{p_{11}^2 e_{11}\alpha_1^2 K_1 + p_{12}^2 e_{12}\beta_1^2 K_2}, \\
\frac{p_{11}e_{11}\alpha_1 K_1 + p_{12}e_{12}\beta_1 K_2 - \mu_1}{p_{11}p_{21}e_{11}\alpha_1\alpha_2 K_1 + p_{12}p_{22}e_{12}\beta_1\beta_2 K_2} &< \frac{p_{21}e_{21}\alpha_2 K_1 + p_{22}e_{22}\beta_2 K_2 - \mu_2}{p_{21}^2 e_{21}\alpha_2^2 K_1 + p_{22}^2 e_{22}\beta_2^2 K_2},
\end{aligned} \tag{25}$$

respectively. It is easy to see a contradiction from two inequalities in (25) under the assumption in (1) that

$$p_{j1} = p_{j2} = p_j \text{ and } e_{j1} = e_{j2} = e_j \text{ for } j = 1, 2. \tag{26}$$

However, the two inequalities in (25) may hold true in the general case without the restriction (26), and then bi-stability may emerge for the pair in $\mathcal{B}_3$. We present some numerical simulation results to demonstrate different types of bi-stability in the following examples.

Example 1. By choosing $r = 1$, $K_1 = K_2 = 1$, $p = 0.5$, $\mu = 0.0133$, $e_{11} = 0.2$, $e_{12} = 0.05$, $e_{21} = 0.05$ and $e_{22} = 0.2$, $\alpha_1 = \frac{1}{3}$ and $\alpha_2 = \frac{2}{3}$, a solution can either converges to E_1^1 or E_2^2 depending on the initial condition, see Fig. 6.

Example 2. By choosing $r = 1$, $K_1 = K_2 = 1$, $p = 0.5$, $\mu = 0.025$, $e_{11} = 0.5$, $e_{12} = 0.1$, $e_{21} = 0.3$ and $e_{22} = 0.3$, $\alpha_1 = 0.4$ and $\alpha_2 = 0.6$, a solution can either converges to E_1^1 or E_3^2 depending on the initial condition, see Fig. 7.

Example 3. By choosing $r = 1$, $K_1 = K_2 = 1$, $p = 0.5$, $\mu = 0.05$, $e_{11} = 0.2$, $e_{12} = 0.1$, $e_{21} = 0.1$ and $e_{22} = 0.2$, $\alpha_1 = 0.4$ and $\alpha_2 = 0.6$, a solution can either converges to E_3^1 or E_3^2 depending on the initial condition, see Fig. 8.

In addition to modifying (1) by incorporating heterogeneous predation rates and biomass transfer rates, one may also consider replace the Holling Type I functional responses in (1) by more reasonable Holling Type II or other type functional responses. In the single prey and single predator case, it is well-known that if logistic growth for the prey and the Holling Type II functional response is adopted, Hopf bifurcation about a positive equilibrium will occur when the carrying capacity of the prey is increased, leading to a stable periodic solution. Assuming a local periodic scenario in one patch or two for a single predator, what would happen if another

predator species is brought into the two patches? Will it be able invade? If yes, in what manner — also periodic or converging to a positive equilibrium? These are all very interesting questions, but we will have to leave them as future research projects.
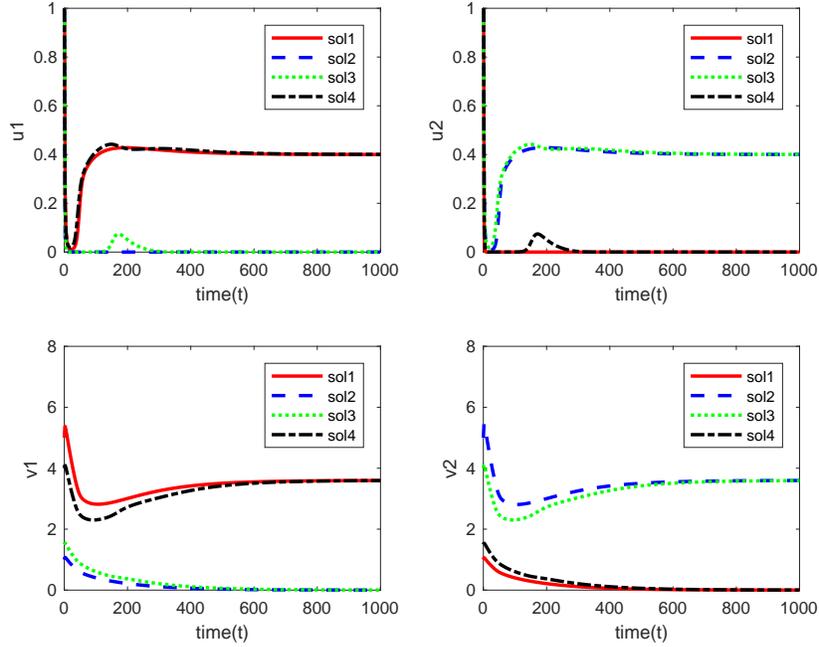
FIGURE 6. Bi-stability in the system (1) with $r = 1$, $K_1 = K_2 = 1$, $p_1 = p_2 = 0.5$, $\mu_1 = \mu_2 = 0.1333$, $e_{11} = 0.2$, $e_{12} = 0.05$, $e_{21} = 0.05$ and $e_{22} = 0.2$, $\alpha_1 = \frac{1}{3}$ and $\alpha_2 = \frac{2}{3}$. A solution either converges to E_1^1 or E_2^2 depending on the initial condition.

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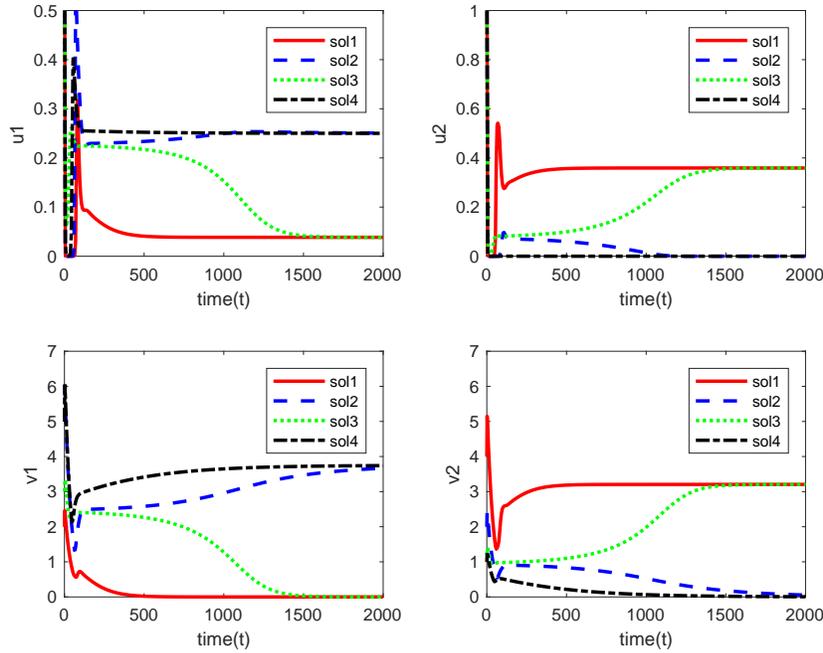
FIGURE 7. Bi-stability in the system (1) with $r = 1$, $K_1 = K_2 = 1$, $p = 0.5$, $\mu = 0.025$, $e_{11} = 0.5$, $e_{12} = 0.1$, $e_{21} = 0.3$ and $e_{22} = 0.3$, $\alpha_1 = 0.4$ and $\alpha_2 = 0.6$. A solution either converges to E_1^1 or E_3^2 depending on the initial condition.

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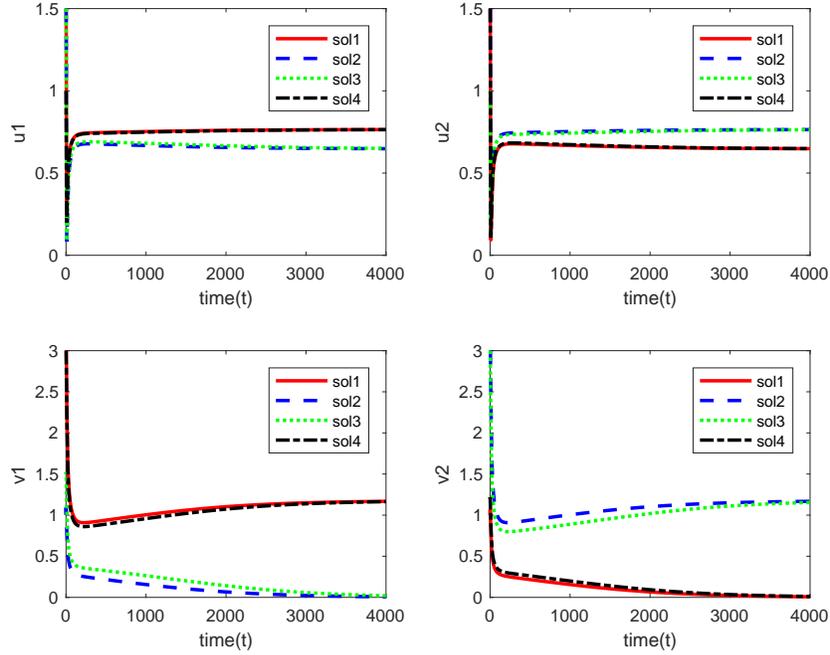
FIGURE 8. Bi-stability in the system (1) with $r = 1$, $K_1 = K_2 = 1$, $p = 0.5$, $\mu = 0.05$, $e_{11} = 0.2$, $e_{12} = 0.1$, $e_{21} = 0.1$ and $e_{22} = 0.2$, $\alpha_1 = 0.4$ and $\alpha_2 = 0.6$. A solution either converges to E_3^1 or E_3^2 depending on the initial condition.

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