

Adaptation of prey and predators between patches

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Abstract

1

2 Mathematical models are proposed to simulate migrations of prey and predators
3 between patches. In the absence of predators, it is shown that the adaptation of
4 prey leads to an ideal spatial distribution in the sense that the maximal capacity
5 of each patch is achieved. With the introduction of co-adaptation of predators,
6 it is proved that both prey and predators achieve ideal spatial distributions when
7 the adaptations are weak. Further, it is shown that the adaptation of prey and
8 predators increases the survival probability of predators from the extinction in both
9 patches to the persistence in one patch. It is also demonstrated that there exists
10 a pattern that prey and predators cooperate well through adaptations such that
11 predators are permanent in every patch in the case that predators become extinct
12 in each patch in the absence of adaptations. For strong adaptations, it is proved
13 that the model admits periodic cycles and multiple stability transitions.

14

Key Words: Migration; distribution; stability; persistence; cycle.

15 **1 Introduction**

16 Population dispersal is one of the most important subjects in ecology. It is well
17 recognized that the spatial distribution of populations and population dynamics
18 are much affected by spatial heterogeneity and population mobility (Shigesada and
19 Kawasaki, 1997; Namba, Umemoto, and Minami, 1999; Diekmann, Law, and Meta,
20 2000; Murray, 2003; Arino and van den Driessche, 2006; Takeuchi, Iwasa, and Sato,
21 2007; Lou, 2008). For fragmented landscapes, which are common because popula-
22 tions of most species occupy mosaic habitats and because of rapid destruction of
23 natural habitats (Watkinson and Sutherland, 1995; Hanski, 1998), patch models
24 are ideal tools to mimic population dynamics. Within each patch, individuals in
25 each population are assumed to be identical and can migrate to other patches.
26 Levin (1974) proposed the two-species competition and prey-predator models with
27 population dispersal among patches. Lu and Takeuchi (1993) found that popula-
28 tion dispersals of single species among patches enhance the stability of populations.
29 For interactions of predators and prey, Takeuchi (1986) and Kuang and Takeuchi
30 (1994) found that stabilizing and destabilizing effects could be induced by prey
31 dispersal. More recently, Briggs and Hoopes (2004) identify three mechanisms
32 whereby limited dispersal of hosts and parasitoids combined with other features,
33 such as spatial and temporal heterogeneity, can promote persistence and stability
34 of populations.

35 The common points for most of papers in the studies of interactions of prey and
36 predators with patchy structures are the assumptions of density independent dis-
37 persal (constant traits of species) or random mobility (spatial flows of populations
38 move towards the patch with lower density and are proportional to their density
39 differences between patches). This means that population migration rates are not
40 influenced by biotic conditions. However, many observations indicate that popula-

41 tion dispersal rates may be regulated by population densities and habitat qualities.
42 Indeed, the density-dependent dispersal rates of populations were experimentally
43 observed in mites (Bernstein, 1984), insects (Fonseca and Hart, 1996) and verte-
44 brates (French and Travis, 2001; Matthysen, 2005). More recently, by using aquatic
45 experimental microcosms under controlled conditions, Hauzy et al. (2007) observed
46 that the dispersal rate of prey is influenced by its own density and predator's den-
47 sity, and the dispersal rate of predators is affected by prey's density. As a matter
48 of fact, prey migrations may be accelerated by poor reproduction conditions, high
49 predation risks in local habitat, or because of attraction from better reproductions
50 or less predation pressure at other patches, and predators may change behaviors on
51 the basis of prey abundance and demographic advantages (Abrams, 2007; Abrams
52 et al., 2007; Cressman and Krivan, 2006; DeAngelis et al., 2006; Hastings, 1983;
53 Hofbauer and Sigmund, 1998; Kisdi and Liu, 2006; Persson and de Roos, 2003).

54 To understand the effects of density-dependent dispersal of populations, Chior-
55 ino et al. (1999); Mchich et al. (2007) and Abdllaoui et al. (2007) considered
56 predator-prey models in a two-patch environment, where prey leave a patch at
57 a migration rate proportional to the local predator density and predators leave a
58 patch at a migration rate inversely proportional to local prey population density.
59 This means that prey's emigration is determined by predation pressure and preda-
60 tor's migration is mainly affected by prey's abundance. Based upon the assumption
61 that the time scale of population migrations between patches is much faster than
62 that of prey growth, predator mortality and predator-prey interactions, they find
63 that for a large class of density-dependent migration rules for predators and prey
64 there exists a unique and stable equilibrium for migration. Moreover, under some
65 particular conditions, the density dependence of migrations can generate a limit
66 cycle. de Roos et al. (2002) and Persson and de Roos (2003) examine flexible
67 behaviors in size-structured populations by assuming that the movement rate out

68 of a patch is purely a function of fitness of individuals within that patch. Note
69 that individuals may assess benefits and costs of migrations by learning to decide
70 whether to leave current patch or not. For prey individuals, they may compare the
71 difference of predation pressure between the home patch and a destination patch.
72 For predator individuals, they could compute the difference of food richness of the
73 two patches. Furthermore, the risk of higher mortality of the destination habitat
74 should also be considered. To explore the role of such habitat choice behaviors, let
75 us consider two patches, labeled by 1 and 2, and W_i be the instantaneous per capita
76 growth rate for an individual in patch i . Then the per individual dispersal rate
77 from patch i to patch j is assumed (Abrams, 2000, 2003; Abrams and Matsuda,
78 2004; Abrams, 2007; Abrams et al., 2007) to be given by $m \exp(\lambda(W_j - W_i))$, where
79 m is the basal per capita movement rate from patch i to patch j when fitness is
80 equal and λ is a positive constant that represents the sensitivity of movement to a
81 fitness difference. In contrast with the models that separate behavioral dynamics
82 and population dynamics, the combined behavioral-population systems indicate
83 that spatial cycling can stabilize population densities and qualitatively change the
84 responses of population densities to environmental perturbations (Abrams, 2007).
85 Note that the movement rule in previous studies is among possible choices and dif-
86 ferent movement rules can cause significant quantitative differences in population
87 dynamics (Abrams, 2007).

88 In this paper, we hope to extend the research by introducing two dynamical
89 variables to represent the adaptations of dispersal rates of prey and predators. This
90 alternative approach gives an advantage that more mathematical analysis can be
91 carried out. Especially, we can show that optimal states can be achieved by prey
92 and predators through adaptations and the adaptations can enhance the survival
93 probability of populations. Therefore, biological insights can be provided in a
94 different way.

95 The organization of this paper is as follows. In the next section, we present the
 96 formulation of mathematical model. Section 3 shows that ideal spatial distributions
 97 of populations can be established through weak adaptations. In section 4, we show
 98 that the adaptations can increase the permanence of populations. Finally, we show
 99 that large adaptations induce complicated dynamical behaviors.

100 2 Model formulations

101 We consider two patches. Let x_i be the density of prey in patch i and y_i be the
 102 density of predators in patch i . Without population dispersal, we assume that the
 103 interaction of prey and predators is described by

$$\begin{cases} \frac{dx_i}{dt} = x_i g_i(x_i) - f_i(x_i) y_i, \\ \frac{dy_i}{dt} = y_i (k_i f_i(x_i) - d_i), \end{cases} \quad (2.1)$$

104 where g_i is the per capita growth rate of the prey in patch i , d_i is the per capita
 105 death rate of predators in patch i , f_i is the functional response of predators in
 106 patch i and k_i is the conversion coefficient.

107 In order to incorporate population movements between the two patches, we
 108 consider those individuals of prey or predators that have ability and desire to
 109 disperse in unit time, which are called movable individuals. Movable individuals
 110 decide their habitats after comparing costs and benefits of migrations. Let u denote
 111 the ratio of movable individuals in prey to current individuals in prey in unit time,
 112 and v denote the ratio of movable individuals in predators to current individuals
 113 in predators in unit time. If $m_1, 0 \leq m_1 \leq 1$, is the migration probability of a
 114 movable individual of prey from the first patch to the second patch, we assume
 115 that the migration probability for a movable individual of prey to migrate from the
 116 second patch to the first patch is complementary to the probability of a movable

117 individual of prey from the first patch to the second patch, i.e., $1 - m_1$. Indeed, the
 118 migration probability m_1 just means that a prey individual in the first patch has
 119 the desirability m_1 to stay in the second patch and the desirability $1 - m_1$ to stay in
 120 the first patch, after evaluating the qualities of two patches. Since we assume that
 121 each individual knows clearly the conditions of two patches, all members of prey
 122 have the same desire to stay in a fixed patch wherever they stay. Hence, a prey
 123 individual in the second patch has also the desirability m_1 to stay in the second
 124 patch and the desirability $1 - m_1$ to stay in the first patch. As a consequence,
 125 $1 - m_1$ is the migration probability of a movable individual of prey from the second
 126 patch to the first patch. For example, if the quality of patch 2 is 2 times better
 127 than that of patch 1, then the probability that a prey individual has the desire
 128 to stay in the first patch is $1/3$ and the probability to stay in the second patch is
 129 $2/3$. Hence, the migration probability from the first patch to the second patch is
 130 $m_1 = 2/3$ and the migration probability from the second patch to the first patch is
 131 $1 - m_1 = 1/3$. Similarly, we let n_1 denote the migration probability of a movable
 132 predator to migrate from the first patch to the second patch and $1 - n_1$ denote the
 133 probability of a movable predator to disperse from the second patch to the first
 134 patch. With the inclusion of population dispersal (2.1) is modified into:

$$\left\{ \begin{array}{l} \frac{dx_1}{dt} = x_1(g_1(x_1) - um_1) - f_1(x_1)y_1 + u(1 - m_1)x_2, \\ \frac{dy_1}{dt} = y_1(k_1f_1(x_1) - d_1 - vn_1) + v(1 - n_1)y_2, \\ \frac{dx_2}{dt} = x_2(g_2(x_2) - u(1 - m_1)) - f_2(x_2)y_2 + um_1x_1, \\ \frac{dy_2}{dt} = y_2(k_2f_2(x_2) - d_2 - v(1 - n_1)) + vn_1y_1. \end{array} \right. \quad (2.2)$$

To include the adaptations of migration probabilities m_1 and n_1 in the process
 of population fluctuations, we assume that the migration process of prey and preda-
 tors is so quick that their fitness is determined by the within-habitat population

dynamics. Note that the fitness of prey in the first patch is

$$g_1(x_1) - f_1(x_1)y_1/x_1$$

and the fitness of prey in the second patch is

$$g_2(x_2) - f_2(x_2)y_2/x_2.$$

135 If an individual of prey in the first patch takes migration probability m_1 , then its
136 expected fitness is

$$E = m_1(g_2(x_2) - f_2(x_2)y_2/x_2) + (1 - m_1)(g_1(x_1) - f_1(x_1)y_1/x_1), \quad (2.3)$$

137 because its probability to stay in the second patch is m_1 and the probability to
138 stay in the first patch is $1 - m_1$. Let D denote the difference between the fitness
139 to stay in the second patch and the expected fitness E :

$$\begin{aligned} D &= (g_2(x_2) - f_2(x_2)y_2/x_2) - E \\ &= (1 - m_1)(g_2(x_2) - f_2(x_2)y_2/x_2 - (g_1(x_1) - f_1(x_1)y_1/x_1)). \end{aligned} \quad (2.4)$$

140 Following the principle of replication dynamics (Hofbauer and Sigmund, 1998),
141 which is the cornerstone of evolutionary dynamics, we suppose that the rate of
142 increase of $\frac{dm_1}{dt}/m_1$ is proportional to the fitness difference D to obtain

$$\frac{dm_1}{dt} = gm_1(1 - m_1) \left\{ \left[g_2(x_2) - \frac{f_2(x_2)y_2}{x_2} \right] - \left[g_1(x_1) - \frac{f_1(x_1)y_1}{x_1} \right] \right\}, \quad (2.5)$$

143 where g is the proportional constant. It is easy to see that (2.5) implies that
144 $0 < m_1(t) < 1$ for $t > 0$ if $0 < m_1(0) < 1$. Note that the expression in the first
145 square brackets of (2.5) is the fitness of prey in the second patch and the expression

146 in the second square brackets of (2.5) is the fitness of prey in the first patch. It
 147 follows from (2.5) that the migration probability m_1 of prey from the first patch
 148 to the second patch increases if the second patch is better than the first patch for
 149 prey, decreases if the first patch is better than the second patch for prey, and keeps
 150 constant if the two patches have the same quality.

151 Similarly, we can present the dynamical equation for n_1 :

$$\frac{dn_1}{dt} = hn_1(1 - n_1)(k_2f_2(x_2) - d_2 - (k_1f_1(x_1) - d_1)), \quad (2.6)$$

152 where h is the proportional constant. Consequently, the full model with population
 153 dynamics and adaption dynamics is given by

$$\left\{ \begin{array}{l} \frac{dx_1}{dt} = x_1(g_1(x_1) - um_1) - f_1(x_1)y_1 + u(1 - m_1)x_2, \\ \frac{dy_1}{dt} = y_1(k_1f_1(x_1) - d_1 - vn_1) + v(1 - n_1)y_2, \\ \frac{dx_2}{dt} = x_2(g_2(x_2) - u(1 - m_1)) - f_2(x_2)y_2 + um_1x_1, \\ \frac{dy_2}{dt} = y_2(k_2f_2(x_2) - d_2 - v(1 - n_1)) + vn_1y_1, \\ \frac{dm_1}{dt} = gm_1(1 - m_1) \left(g_2(x_2) - \frac{f_2(x_2)y_2}{x_2} - \left(g_1(x_1) - \frac{f_1(x_1)y_1}{x_1} \right) \right), \\ \frac{dn_1}{dt} = hn_1(1 - n_1)(k_2f_2(x_2) - d_2 - (k_1f_1(x_1) - d_1)). \end{array} \right. \quad (2.7)$$

154 We assume that $\lim_{x_i \rightarrow 0} f_i(x_i)/x_i = \alpha_i \geq 0$. Then (2.7) is well defined for $x_i \geq$
 155 $0, y_i \geq 0$ with $i = 1, 2, 0 \leq m_1 \leq 1$ and $0 \leq n_1 \leq 1$.

156 **3 Ideal distribution through adaptations**

157 In this section, we show that populations can achieve ideal spatial distributions
 158 through weak adaptations. We begin from the special case that predators are

159 absent. Without predators (2.7) is reduced to

$$\begin{cases} \frac{dx_1}{dt} = x_1(g_1(x_1) - um_1) + u(1 - m_1)x_2, \\ \frac{dx_2}{dt} = x_2(g_2(x_2) - u(1 - m_1)) + um_1x_1, \\ \frac{dm_1}{dt} = gm_1(1 - m_1)(g_2(x_2) - g_1(x_1)). \end{cases} \quad (3.1)$$

160 To ensure the survival of prey in the absence of predators, we make an assump-
161 tion

162 (H1) There exists a C_i such that $g_i(C_i) = 0$, $g_i(x_i) > 0$ for $0 \leq x_i < C_i$ and
163 $g_i(x_i) < 0$ for $x_i > C_i$.

164 Then C_i is the carrying capacity of prey in patch i . We say that ideal states of
165 prey are achieved if its carrying capacity in every patch is established.

166 **Theorem 1** *Let (H1) hold. Then system (3.1) admits a unique positive equilibrium*
167 $E_{prey} = (C_1, C_2, C_2/(C_1 + C_2))$.

168 The next theorem states that the unique positive equilibrium is globally stable
169 if the adaptation is weak (proofs of theorem 1 and theorem 2 are postponed to
170 Appendix).

171 **Theorem 2** *Let (H1) hold and $g'_i(x_i) < 0$. Then E_{prey} is globally stable if $0 < g \ll$*
172 *1.*

173 Theorem 2 indicates that the carrying capacity of prey population in each patch
174 is achieved through weak adaptations. Hence, an ideal spatial distribution is es-
175 tablished. Notice that E_{prey} is asymptotically stable irrespective of magnitude of
176 adaptation coefficient g . For the growth rates of logistic type, extensive numerical
177 calculations indicate that the equilibrium E_{prey} is also globally stable for large g .
178 This suggests that the adaptation always facilitates the formation of ideal spatial
179 distribution of prey.

180 Now, a natural question is what will happen when predators are present. By
 181 using the same arguments as above, we obtain

182 **Theorem 3** *Let (H1) hold. Suppose that functional responses f_i are strictly in-*
 183 *creasing functions and*

$$f_i(C_i) > \frac{d_i}{k_i}, \quad i = 1, 2. \quad (3.2)$$

184 Then system (2.7) admits a unique positive equilibrium $E^* = (x_1^*, y_1^*, x_2^*, y_2^*, m_1^*, n_1^*)$,
 185 where

$$\begin{aligned} x_i^* &= f_i^{-1}\left(\frac{d_i}{k_i}\right), & y_i^* &= \frac{x_i^* g_i(x_i^*)}{\frac{d_i}{k_i}}, & i &= 1, 2, \\ m_1^* &= \frac{x_2^*}{x_1^* + x_2^*}, & n_1^* &= \frac{y_2^*}{y_1^* + y_2^*}, & i &= 1, 2. \end{aligned} \quad (3.3)$$

186 Note that (x_i^*, y_i^*) with components defined in (3.3) is the coexistence state of
 187 prey and predators in the isolated patch i . If this state is globally asymptotically
 188 stable in the isolated patch i , then the community of prey population and predator
 189 population evolves to it through natural selection. Similar to the case of single
 190 species, we call it as the carrying capacity of the ecological community of the prey
 191 population and the predator population in patch i .

192 Note that m_1^* (n_1^*) given in (3.3) implies that the migration rate of prey (preda-
 193 tors) to patch 1 $u(1 - m_1^*)x_2^*$ ($v(1 - n_1^*)y_2^*$) equals the emigration rate of prey
 194 (predators) from patch 1 $um_1^*x_1^*$ ($vn_1^*y_1^*$). We expect that positive solutions of (2.7)
 195 approach E^* as $t \rightarrow \infty$ for small g and h , which means that prey population and
 196 predator population in patch i evolve, under weak adaptations of both prey and
 197 predators, to carrying capacity of the ecological community. To be tractable in
 198 analysis, we suppose that prey grow according to the logistic law:

$$g_i(x_i) = r_i - \mu_i x_i, \quad i = 1, 2,$$

200 and the functional responses are linear $f_i(x_i) = b_i x_i$. Then (2.7) is reduced to:

$$\left\{ \begin{array}{l} \frac{dx_1}{dt} = x_1(r_1 - \mu_1 x_1 - b_1 y_1) - u m_1 x_1 + u(1 - m_1)x_2, \\ \frac{dy_1}{dt} = y_1(k_1 b_1 x_1 - d_1 - v n_1) + v(1 - n_1)y_2, \\ \frac{dx_2}{dt} = x_2(r_2 - \mu_2 x_2 - b_2 y_2) - u(1 - m_1)x_2 + u m_1 x_1, \\ \frac{dy_2}{dt} = y_2(k_2 b_2 x_2 - d_2 - v(1 - n_1)) + v n_1 y_1, \\ \frac{dm_1}{dt} = g m_1(1 - m_1)(r_2 - \mu_2 x_2 - b_2 y_2 - (r_1 - \mu_1 x_1 - b_1 y_1)), \\ \frac{dn_1}{dt} = h n_1(1 - n_1)(k_2 b_2 x_2 - d_2 - (k_1 b_1 x_1 - d_1)). \end{array} \right. \quad (3.4)$$

201 By Theorem 3, (3.4) has a unique positive equilibrium $E^* = (x_1^*, y_1^*, x_2^*, y_2^*, m_1^*, n_1^*)$
 202 if

$$r_i k_i b_i > d_i \mu_i, \quad i = 1, 2, \quad (3.5)$$

203 where

$$\begin{aligned} x_1^* &= \frac{d_1}{k_1 b_1}, & x_2^* &= \frac{d_2}{k_2 b_2}, & y_1^* &= \frac{r_1 k_1 b_1 - \mu_1 d_1}{k_1 b_1^2}, \\ y_2^* &= \frac{r_2 k_2 b_2 - \mu_2 d_2}{k_2 b_2^2}, & m_1^* &= \frac{d_2 k_1 b_1}{d_1 k_2 b_2 + d_2 k_1 b_1}, \end{aligned} \quad (3.6)$$

204

$$n_1^* = \frac{(r_2 k_2 b_2 - \mu_2 d_2) k_1 b_1^2}{k_2 b_2^2 r_1 k_1 b_1 - k_2 b_2^2 \mu_1 d_1 + k_1 b_1^2 r_2 k_2 b_2 - k_1 b_1^2 \mu_2 d_2}. \quad (3.7)$$

205 By computing the Jacobian matrix of (3.4) at E^* and using the fact that u, v, g
 206 and h are small, we can verify, from the Hurwitz criteria, that all eigenvalues of
 207 the Jacobian matrix have negative real parts. Hence, E^* is asymptotically stable.
 208 Extensive numerical calculations indicate that E^* is also globally stable in this case.
 209 Thus, the community of prey and predators evolves to the ideal spatial distributions
 210 through weak adaptations.

211 For illustration purpose, we consider the following example.

212 **Example 4** We fix $r_1 = 3, r_2 = 2, \mu_1 = 1, \mu_2 = 1, b_1 = 1, b_2 = 0.5, k_1 =$
 213 $1, k_2 = 2.5, d_1 = 1, d_2 = 2, u = 0.1, v = 0.2, g = 0.1, h = 0.1$. Then $E^* =$

214 $(1, 2, 1.6, 0.8, 0.6154, 0.2857)$. Thus, the capacity for the community of prey and
 215 predators in the first patch is $(1, 2)$, and for the community in the second patch
 216 is $(1.6, 0.8)$. Computer simulation shows that population densities in each patch
 217 approach the ideal state (see Figure 1). In contrast, if we remove the adaptations,
 218 and fix m_1 and n_1 as constants, for example, $m_1 = n_1 = 0.5$, then densities of prey
 219 and predators in the first patch approach $(1.0521, 1.9698)$, and densities of prey and
 220 predators in the second patch approach $(1.513, 0.9436)$. Note that the fitness of
 221 prey is -0.0219 in the first patch and 0.0152 in the second patch, whereas the fitness
 222 of a predator is 0.052 in the first patch and -0.1087 in the second patch. Hence, the
 223 first patch is better for predators, but worse for prey, and the second patch is better
 224 for prey, but worse for predators. By contrast, the weak co-adaptations lead to the
 225 spatial distribution that there is no difference in patch fitness for both prey and
 226 predators by choosing $m_1^* = 0.6154 > 0.5$ and $n_1^* = 0.2857 < 0.5$. This means that
 227 an ideal free distribution for the prey population and the predator population has
 228 been achieved. In fact, the ideal free distribution for a single species, introduced
 229 by Fretwell and Lucas (1970), requires that all occupied patches have equal fitness.
 230 Further, the ideal free distribution for two species was defined by Cressman et al.
 231 (2004) as the distribution yielding equal fitness across occupied habitats for each
 232 species.

233 4 Influences on persistence

234 In this section, we study the influences of adaptations on persistence of populations
 235 in (3.4). We begin from the effect of adaptations on survival of predators. Let
 236 $m_1 = m_{10}$ be the baseline transfer probability of prey from the first patch to the
 237 second patch when there is no fitness difference between the two patches for prey
 238 and $n_1 = n_{10}$ be the baseline transfer probability of a predator from the first patch

239 to the second patch when there is no fitness difference between the two patches for
 240 predators. If there is no adaptation of prey and predators for patch selection, we
 241 have $m_1 = m_{10}$ and $n_1 = n_{10}$ for all t . Then (3.4) is reduced to

$$\begin{cases} \frac{dx_1}{dt} = x_1(r_1 - \mu_1 x_1 - um_{10} - b_1 y_1) + u(1 - m_{10})x_2, \\ \frac{dy_1}{dt} = y_1(k_1 b_1 x_1 - d_1 - vn_{10}) + v(1 - n_{10})y_2, \\ \frac{dx_2}{dt} = x_2(r_2 - \mu_2 x_2 - u(1 - m_{10}) - b_2 y_2) + um_{10}x_1, \\ \frac{dy_2}{dt} = y_2(k_2 b_2 x_2 - d_2 - v(1 - n_{10})) + vn_{10}y_1. \end{cases} \quad (4.1)$$

242 We will compare the dynamical behaviors of (3.4) with (4.1) to see the influences
 243 of adaptations of the prey and predators.

244 Set

$$245 \quad A = \begin{bmatrix} k_1 b_1 \bar{x}_1 - d_1 - vn_{10} & v(1 - n_{10}) \\ vn_{10} & k_2 b_2 \bar{x}_2 - d_2 - v(1 - n_{10}) \end{bmatrix},$$

246 where (\bar{x}_1, \bar{x}_2) is the unique positive equilibrium of the following system:

$$247 \quad \begin{cases} \frac{dx_1}{dt} = x_1(r_1 - \mu_1 x_1 - um_{10}) + u(1 - m_{10})x_2, \\ \frac{dx_2}{dt} = x_2(r_2 - \mu_2 x_2 - u(1 - m_{10})) + um_{10}x_1. \end{cases}$$

248 We assume $0 < m_{10} < 1$ and $0 < n_{10} < 1$. By similar discussions to those in
 249 Wang and Zhao (2004, 2005a,b), we see that predators in (4.1) become extinct if

$$\lambda_{dom} := \text{tr}(A) + \sqrt{(\text{tr}(A))^2 - 4\det(A)} < 0, \quad (4.2)$$

250 and is persistent if

$$\lambda_{dom} = \text{tr}(A) + \sqrt{(\text{tr}(A))^2 - 4\det(A)} > 0. \quad (4.3)$$

251 A key point that we should emphasize is that predators in (4.1) are either
 252 persistent in both patches, or become extinct in both patches. This means that it
 253 is impossible that predators survive in one patch and die out in the other patch,
 254 which seems a contradiction to many ecological observations. Now, we show that
 255 the phenomenon that predators survive only in one patch could occur through
 256 adaptations. Indeed, (3.4) admits equilibria

$$257 \quad E_{00y}^0 = \left(\frac{r_1}{\mu_1}, 0, \frac{r_2}{\mu_2}, 0, \frac{r_2\mu_1}{r_1\mu_2 + r_2\mu_1}, 0 \right),$$

$$E_{00y}^1 = \left(\frac{r_1}{\mu_1}, 0, \frac{r_2}{\mu_2}, 0, \frac{r_2\mu_1}{r_1\mu_2 + r_2\mu_1}, 1 \right).$$

258 By direct calculations, we obtain

259 **Theorem 5** E_{00y}^0 is stable if

$$\begin{aligned} k_1 b_1 r_1 &< \mu_1 d_1, \\ k_2 b_2 r_2 &< \mu_2 (d_2 + v), \\ k_1 b_1 \frac{r_1}{\mu_1} - d_1 &> k_2 b_2 \frac{r_2}{\mu_2} - d_2, \end{aligned} \tag{4.4}$$

260 and is unstable if one of the inequalities in (4.4) is reversed.

261 **Theorem 6** E_{00y}^1 is stable if

$$\begin{aligned} k_1 b_1 r_1 &< \mu_1 (d_1 + v), \\ k_2 b_2 r_2 &< \mu_2 d_2, \\ k_1 b_1 \frac{r_1}{\mu_1} - d_1 &< k_2 b_2 \frac{r_2}{\mu_2} - d_2, \end{aligned} \tag{4.5}$$

262 and is unstable if one of the inequalities in (4.5) is reversed.

263 The stability of E_{00y}^0 and E_{00y}^1 presents opportunity that predators live well in
 264 a better habitat, but desert the worse one. Indeed, we first choose parameters such

265 that $k_1 b_1 r_1 / \mu_1 - d_1 < 0$, $k_2 b_2 r_2 / \mu_2 - d_2 - v < 0$ and $k_2 b_2 r_2 / \mu_2 - d_2 - (k_1 b_1 r_1 / \mu_1 - d_1) <$
 266 0 . Then we vary k_1 such that $k_1 b_1 r_1 / \mu_1 - d_1 > 0$, which leads to a stability
 267 transition of E_{00y}^0 from a stable state to an unstable state. As a consequence,
 268 E_{00y}^0 repels predators in the first patch away from extinction, at least locally, and
 269 another equilibrium

$$270 \quad E_{0y}^0 = (x_1^*, y_1^*, \frac{r_2}{\mu_2}, 0, \bar{m}_1, 0)$$

271 emerges, where x_1^* and y_1^* are defined in (3.6) and

$$272 \quad \bar{m}_1 = \frac{r_2 / \mu_2}{x_1^* + r_2 / \mu_2}.$$

273 Numerical calculations show that E_{0y}^0 is globally stable for a certain range of pa-
 274 rameters, which confirms that predators can survive in the first patch and become
 275 extinct in the second patch in this case (see Figure 2).

276 Next, we show that the co-adaptation of prey and predators can enhance the
 277 survival probability of predators. To see this, we first select parameters such that

$$\begin{aligned} k_1 b_1 \frac{r_1}{\mu_1} - d_1 &> 0, \\ k_2 b_2 \frac{r_2}{\mu_2} - d_2 &< 0. \end{aligned} \tag{4.6}$$

278 Note that (4.6) implies that n_1 decreases and converges to 0 as t increases in a
 279 small neighborhood of E_{0y}^0 . By using the Routh-Hurwitz criteria, we can obtain
 280 the following theorem for the stability of E_{0y}^0 , the proof of which is postponed to
 281 Appendix.

282 **Theorem 7** E_{0y}^0 is asymptotically stable if (4.6) holds and g is small.

283 Theorem 7 supports the persistence of predators in the first patch and the
 284 extinction of predators in the second patch. On the other hand, if there is no
 285 adaptation of prey and predators, the persistence and extinction of predators are

286 determined by the sign of λ_{dom} . Note that in a small neighborhood of $v = 0$, we
 287 have

$$\lambda_{dom} = \frac{1}{2}[k_1 b_1 \bar{x}_1 - d_1 + k_2 b_2 \bar{x}_2 - d_2 - n_{10} v + o(v)], \quad (4.7)$$

288 which suggests that λ_{dom} may be a decreasing function of v , and may be negative
 289 for large v . To confirm this, we fix $r_1 = 1, r_2 = 1, \mu_1 = 2, \mu_2 = 1, d_1 = 1, d_2 =$
 290 $2, b_1 = 1, b_2 = 1, k_1 = 2.1, k_2 = 1, u = 1, m_{10} = 0.5, n_{10} = 0.6$. Then $\bar{x}_1 = 0.6036$
 291 and $\bar{x}_2 = 0.8536$, and

$$\lambda_{dom} = -0.4395 - 0.5 v + 0.5 \sqrt{1.9991 - 0.5656 v + v^2}.$$

293 The graph of λ_{dom} with respect to v is given in Figure 3, which shows that the
 294 dominant eigenvalue λ_{dom} of A is a decreasing function of v and $\lambda_{dom} < 0$ for larger
 295 v . Thus, without any adaptation of prey and predators, the increase of the maxi-
 296 mal potential migration rate v of predators from the first patch to the second patch
 297 tends to reduce the survival probability of predators, and leads to the extinction
 298 of predators after a threshold value. However, by reviewing the proof of Theorem
 299 7, we see that the stability of E_{0y}^0 is not influenced by the magnitude of v . Thus,
 300 we can fix v such that $\lambda_{dom} < 0$ and then choose small g , the adaptation coefficient
 301 of prey, such that E_{0y}^0 is stable, which is possible as the second inequality in (4.6)
 302 holds. It follows that predators survive in the first patch. Therefore, the adap-
 303 tation of prey and predators increases the survival probability of predators from
 304 the extinction in both patches to the persistence in one patch. Biological mech-
 305 anism behind this phenomenon is that predators exploit better patches to escape
 306 extinction through adaptations. Nevertheless, Figure 3 also shows the possibility
 307 that predators can survive in both patches for small v under the assumptions that
 308 there is no adaptation, but can survive only in the first patch with adaptations.
 309 The reason for the latter is that the first patch is better than the second patch for

310 predators and adaptations make predators aggregate in the first patch.

311 We now present an example to show that there exists a pattern that prey and
312 predators cooperate well through adaptations such that predators are permanent in
313 every patch in the case that predators become extinct in each patch in the absence
314 of adaptations. We take $r_1 = 1.2, r_2 = 1, \mu_1 = 2, \mu_2 = 1, d_1 = 1, d_2 = 2, b_1 = 1, b_2 =$
315 $1, k_1 = 2, k_2 = 2.1, u = 1, n_{10} = 0.4, v = 4$. By numerical calculations we obtain the
316 graph of λ_{dom} versus m_{10} in Figure 4, which indicates $\lambda_{dom} < 0$ when m_{10} is close
317 to 0 or close to 1. Thus, if there is no adaptation of prey and predators, predators
318 become extinct in each patch when m_{10} is close to 0 or close to 1. If the adaptation
319 of predators emerges and the adaptation of prey is absent, numerical calculations
320 show that predators survive in the first patch for small m_{10} , and survive in the
321 second patch when m_{10} is close to 1. But predators become extinct in the second
322 patch for the former case, and become extinct in the first patch for the latter case
323 (see Figure 5). Hence, the benefit of adaptation of only predators is to facilitate the
324 survival in one patch. However, if both predators and prey adopt the adaptation
325 strategies, things are different because the parameter values ensure that the full
326 model with the adaptation of prey and predators admits a positive equilibrium.
327 Further numerical simulations indicate that the positive equilibrium is globally
328 stable (see Figure 6). Hence, prey and predators coordinate well so that predators
329 survive in every patch. We now explain why there exist such patterns through the
330 adaptations. First, in the absence of prey adaptation, predators test the better
331 patch to migrate to that patch to survive. For example, if we fix $m_{10} = 0.1$ and
332 keep other parameters as above, the first patch is better for predators through less
333 prey emigration from the first patch and more prey migration to the first patch. In
334 fact, with the adaptation of predators, the fitness of a predator tends to 0 in the
335 first patch and -1.41389 in the second patch. Although predators can survive in the
336 first patch in this case, the fitness of prey is -0.4024 in the first patch and 0.7209 in

337 the second patch. This means that the second patch is better for prey, the reason
338 of which is that the prey in the first patch faces more predation pressure. Thus, if
339 the adaptation of prey is allowed, more prey will migrate to the second patch. As
340 a result, the fitness of a predator increases in the second patch and decreases in
341 the first patch. This encourages a fraction of predators to migrate to the second
342 patch so that the coexistence patter of prey and predators occurs.

343 5 Behaviors from strong response

344 In this section, by considering (3.4) we show that strong adaptations of prey and
345 predators may induce complicated dynamical behaviors.

346 First, equilibrium E_{0y}^0 exhibits stability transitions as the adaptation coefficient
347 g increases, which suggests the possibility of a Hopf bifurcation. This is confirmed
348 by numerical simulations. For the parameters with larger r_1 and g in Figure 7,
349 prey's densities in the two patches approach periodic cycles, and predators always
350 stay in the first patch, but exhibit periodic fluctuations after a transient time.
351 Biological reason for this type of cycles could be given as follows. Rich prey in
352 the first patch attracts a large number of predators, which in turn give the higher
353 predation pressure on prey. Then a strong response leads to a quick migration
354 of prey to the second patch, which decreases the prey density in the first patch.
355 In the process, predators always stay in the first patch as the large r_1 leads to
356 rich prey in the first patch, which implies that the fitness of a predator in the
357 first patch is higher. Thus, the decrease of prey reduces predators in the first
358 patch. The cycles emerge from repetitions of the processes. In contrast, in the
359 absence of the adaptations, simulations with the parameters given in Figure 7
360 indicate that populations in each patch approach to globally stable states with
361 $x_1 = 1.7767, x_2 = 0.4893, y_1 = 5.8610, y_2 = 2.8262$ (see Figure 8). Hence, the

362 adjustment of prey to equality in patch fitness destroys the stable coexistence of
363 ecological community of prey and predators in each patch, and leads to periodic
364 cycles.

365 We now consider influences of strong adaptations on the stability of positive
366 equilibrium E^* . For larger g and h , E^* becomes unstable in several cases. First,
367 E^* becomes unstable for a larger intrinsic growth rate of prey (see the left panel in
368 Figure 9). Secondly, there exists a region of u and v , which is similar to a bottle,
369 such that E^* is unstable inside the region and is stable outside the region (see
370 the right panel in Figure 9). Variations of k_1 and k_2 , or b_1 and b_2 , exhibit similar
371 influences on the stability of E^* . Clearly, the figures show that there are multiple
372 stability switches if we fix one parameter and vary the other. For example, for the
373 case described by the left panel of Figure 9, if we fix $r_1 = 3$ and vary r_2 , then
374 there are Hopf bifurcations when $r_2 = 1.7357, r_2 = 6.0363$ and $r_2 = 11.7166$. E^* is
375 unstable when r_2 lies in $(1.7357, 6.0363)$ and $r_2 > 11.7166$. There are a family of
376 stable periodic solutions when r_2 varies in $(1.7357, 6.0363)$ and a family of stable
377 periodic solutions when r_2 varies in $r_2 > 11.7166$ (see Figure 10).

378 **6 Discussions**

379 In this paper, we have proposed a prey-predator model that incorporates density-
380 dependent migrations through the adaptations of prey and predators between the
381 two patches. We have assumed that a movable individual decides its migration
382 probability in terms of the law that the rate of migration probability is proportional
383 to the difference of the fitness of the destination patch and the average fitness. This
384 modeling method, based upon the assumption that an individual has the ability to
385 know the fitness in each patch, gives an alternative migration rule and allows more
386 mathematical analysis to find more interesting phenomena.

387 In Theorem 1 and Theorem 2, we have shown that prey evolves, through weak
388 adaptation, to the ideal spatial distribution where the carrying capacity of prey
389 population in each patch is achieved. By means of analytic method in Theorem 3
390 and simulations, we have verified that the full system of prey-predator interactions
391 with weak adaptations and small migration amplitudes implies that the ideal spatial
392 distribution is established in the sense that the carrying capacity of prey-predator
393 community in each patch is approached.

394 For classical patchy models of prey and predators without adaptations, either
395 predator population survives in every patch, or becomes extinct in every patch
396 unless there is no barrier to predators between two patches. With the introduction
397 of the adaptations, we have shown that the predator population can survive only in
398 the better patch, and desert the worse one. This means that there is no need to use
399 barriers to limit predators in a favorable patch if predators are able to adapt. We
400 have also analyzed that the adaptation of prey and predators increases the survival
401 probability of predators from the extinction in both patches to the persistence in
402 one patch. Furthermore, we have presented the example that prey and predators
403 cooperate well through adaptations to ensure the permanence of predators in every
404 patch in the case that predators become extinct in each patch in the absence of
405 adaptations.

406 For the strong responses of prey and predators, we have shown that the adjust-
407 ment of prey to establish equality in patch fitness destroys the stable coexistence
408 of ecological community of prey and predators in each patch, and leads to periodic
409 cycles. As a result, the objective of equal fitness in every patch cannot be realized.
410 Moreover, we have presented the stability regions for large adaptations that show
411 the possibility of multiple stability transitions if we vary one parameter.

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415 Appendix

416 Proof of Theorem 1

417 To find a positive equilibrium, we set the right-hand side of the third equation
418 of (3.1) to 0 to obtain

$$419 \quad g_2(x_2) = g_1(x_1).$$

420 It follows from the first equation and the second equation of (3.1) that

$$421 \quad u(1 - m_1) - um_1 \frac{x_1}{x_2} = um_1 - u(1 - m_1) \frac{x_2}{x_1},$$

422 which leads to

$$m_1 = \frac{x_2}{x_1 + x_2}. \quad (\text{A-1})$$

423 Thus, at a positive equilibrium (3.1) we have

$$424 \quad \text{migration rate of prey to patch 1} = u(1 - m_1)x_2 = u \frac{x_1 x_2}{x_1 + x_2},$$

$$\text{emigration rate of prey from patch 1} = um_1 x_1 = u \frac{x_1 x_2}{x_1 + x_2}.$$

425 It follows that the inflow rate of prey to patch 1 equals the outflow rate of prey
426 from patch 1. Then it is easy to see that E_{prey} is the unique positive equilibrium
427 of (3.1). The proof is complete. \square

428 Proof of Theorem 2

429 We begin by showing that E_{prey} is asymptotically stable. The Jacobian matrix

430 of (3.1) at E_{prey} is

$$431 \quad \begin{bmatrix} -um_1^* + C_1 g_1'(C_1) & u(1 - m_1^*) & -u(C_1 + C_2) \\ um_1^* & -u(1 - m_1^*) + C_2 g_2'(C_2) & u(C_1 + C_2) \\ -gm_1^*(1 - m_1^*)g_1'(C_1) & gm_1^*(1 - m_1^*)g_2'(C_2) & 0 \end{bmatrix}.$$

432 Its characteristic equation is

$$433 \quad \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0,$$

434 where

$$a_1 = -C_1 g_1'(C_1) - C_2 g_2'(C_2) + u > 0,$$

$$435 \quad a_2 = -gum_1^*(C_1 + C_2)(1 - m_1^*)(g_1'(C_1) + g_2'(C_2)) \\ + C_1 C_2 g_1'(C_1) g_2'(C_2) - u C_1 g_1'(C_1)(1 - m_1^*) - um_1^* C_2 g_2'(C_2) > 0,$$

$$a_3 = um_1^* g g_1'(C_1) g_2'(C_2) (C_1 + C_2)^2 (1 - m_1^*) > 0.$$

436 Set

$$Q_1 = um_1^*(C_1 + C_2)(1 - m_1^*)((g_1'(C_1))^2 C_1 + C_2 (g_2'(C_2))^2 - u(g_1'(C_1) + g_2'(C_2))), \\ 437 \quad Q_2 = (u - C_1 g_1'(C_1) - C_2 g_2'(C_2))(C_1 g_1'(C_1) C_2 g_2'(C_2) \\ - um_1^* C_2 g_2'(C_2) - u C_1 g_1'(C_1)(1 - m_1^*)).$$

438 Then direct calculations lead to

$$439 \quad a_1 a_2 - a_3 = g Q_1 + Q_2 > 0.$$

440 It follows from the Hurwitz criteria that E_{prey} is asymptotically stable.

441 Now, we use techniques of singular perturbation theory to show that each pos-

442 itive solution of (3.1) approaches E_{prey} as $t \rightarrow \infty$ when the adaptation coefficient
 443 g is small. If $\tau = gt$, we obtain

$$\begin{cases} gx'_1 = x_1(g_1(x_1) - um_1) + u(1 - m_1)x_2, \\ gx'_2 = x_2(g_2(x_2) - u(1 - m_1)) + um_1x_1, \\ m'_1 = m_1(1 - m_1)(g_2(x_2) - g_1(x_1)), \end{cases} \quad (\text{A-2})$$

444 where prime denotes the derivative with respect to τ . Since g is a small parameter,
 445 (A-2) is a slow system and (3.1) is a fast system. The slow manifold is determined
 446 by

$$\begin{aligned} F_1(x_1, x_2, m_1) &:= x_1(g_1(x_1) - um_1) + u(1 - m_1)x_2 = 0, \\ F_2(x_1, x_2, m_1) &:= x_2(g_2(x_2) - u(1 - m_1)) + um_1x_1 = 0. \end{aligned} \quad (\text{A-3})$$

447 The Jacobian matrix of (F_1, F_2) is

$$448 \quad J(x_1, x_2, m_1) = \begin{pmatrix} g_1(x_1) - um_1 + x_1g'_1(x_1) & u(1 - m_1) \\ um_1 & g_2(x_2) - u(1 - m_1) + x_2g'_2(x_2) \end{pmatrix}.$$

449 Note that

$$\begin{aligned} 450 \quad g_1(x_1) - um_1 &= -u(1 - m_1)\frac{x_2}{x_1}, \\ g_2(x_2) - u(1 - m_1) &= -um_1\frac{x_1}{x_2}. \end{aligned}$$

451 It follows from $g'_i(x_i) < 0$ that

$$452 \quad \det J(x_1, x_2, m_1) = -u(1 - m_1)g'_2(x_2)\frac{x_2^2}{x_1} - um_1g'_1(x_1)\frac{x_1^2}{x_2} + x_1x_2g'_1(x_1)g'_2(x_2) > 0.$$

453 Since $F_1 = 0$ and $F_2 = 0$ at E_{prey} , it follows from the implicit function theorem
 454 that (A-3) determines a manifold $x_1 = x_1(m_1), x_2 = x_2(m_1)$, denoted by S .

455 Set

$$456 \quad J_{x_1} = \begin{pmatrix} -u(C_1 + C_2) & u(1 - m_1^*) \\ u(C_1 + C_2) & -u(1 - m_1^*) + C_2 g_2'(C_2) \end{pmatrix}$$

457 and

$$458 \quad J_{x_2} = \begin{pmatrix} -um_1^* + C_1 g_1'(C_1) & -u(C_1 + C_2) \\ um_1^* & u(C_1 + C_2) \end{pmatrix}$$

459 with $m_1^* = C_2/(C_1 + C_2)$. Then $\det J_{x_1} > 0$ and $\det J_{x_2} < 0$. Hence, on S we have

$$460 \quad x_1'(m_1^*) = -\det J_{x_1} / \det J(C_1, C_2, m_1^*) < 0,$$

$$x_2'(m_1^*) = -\det J_{x_2} / \det J(C_1, C_2, m_1^*) > 0.$$

461 If we denote the right-hand side of the third equation of (A-2) by $F_3(x_1, x_2, m_1)$, it

462 follows that $F_3(x_1(m_1), x_2(m_1), m_1)$ satisfies

$$463 \quad F_3 \begin{cases} < 0 & \text{if } m_1^* < m_1 < m_1^* + \epsilon \\ > 0 & \text{if } m_1^* > m_1 > m_1^* - \epsilon \end{cases}$$

464 for some positive ϵ . From the argument in the proof of Theorem 1 we see that

465 $F_3(x_1(m_1), x_2(m_1), m_1)$ can not be zero for $m_1 > m_1^*$ or $m_1 < m_1^*$. Therefore,

466 equilibrium $m_1 = m_1^*$ is globally asymptotically stable on S .

467 We consider a subsystem of (3.1):

$$\begin{cases} x_1' = x_1(g_1(x_1) - um_1) + u(1 - m_1)x_2, \\ x_2' = x_2(g_2(x_2) - u(1 - m_1)) + um_1x_1. \end{cases} \quad (\text{A-4})$$

468 By the monotonic flow techniques (Lu and Takeuchi, 1993; Smith, 1995; Zhao,

469 2003) we see that the positive equilibrium $(x_1(m_1), x_2(m_1))$ is globally stable in

470 the interior of R_+^2 for (3.1). Thus, given $\epsilon > 0$, for any interval $M_0 := [m_{00}, m^{00}]$

471 with $0 < m_{00} < m_1^* < m^{00} < 1$, and a compact set X_0 in the interior of R_+^2 , there
 472 is a $T_0 > 0$ such that any positive solution $(x_1(t), x_2(t))$ of (A-4) starting in X_0 with
 473 $m_{00} \leq m_1 \leq m^{00}$ satisfies

$$|x_i(t) - x_i(m)| < \epsilon, \quad i = 1, 2, \quad t \geq T_0. \quad (\text{A-5})$$

474 Note that E_{prey} is the unique positive equilibrium of (3.1) and is asymptotically
 475 stable. It follows from the theory of geometric singular perturbation (Fenichel,
 476 1979; Jones, 1994) that E_{prey} is globally stable for small adaptation coefficient g .
 477 The proof is complete. \square

478 **Proof of Theorem 7:**

479 The characteristic equation of the Jacobian matrix of (3.4) at E_{0y}^0 has 2 roots:

$$\begin{aligned} \lambda_1 &= k_2 b_2 \frac{r_2}{\mu_2} - d_2 - v < 0, \\ \lambda_2 &= h(k_2 b_2 \frac{r_2}{\mu_2} - d_2) < 0. \end{aligned} \quad (\text{A-6})$$

480 The other roots satisfy the following equation

$$A_0 \lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4 = 0, \quad (\text{A-7})$$

where

$$A_0 = b_1 k_1 (d_1 \mu_2 + r_2 k_1 b_1),$$

$$A_1 = (d_1 \mu_2 + r_2 k_1 b_1)(r_2 k_1 b_1 + b_1 u k_1 + \mu_1 d_1),$$

$$A_2 = g b_1 r_2 k_1 d_1 u (\mu_2 + \mu_1) + \mu_1 d_1 (-d_1^2 \mu_2 + u d_1 \mu_2 - d_1 r_2 k_1 b_1 + r_2 d_1 \mu_2 + r_2^2 k_1 b_1) \\ + b_1 k_1 (k_1 b_1 r_2 d_1 r_1 + b_1 r_2^2 k_1 u + d_1^2 \mu_2 r_1),$$

$$A_3 = d_1 g u r_2 (b_1 k_1 \mu_1 r_2 - k_1 b_1 \mu_1 d_1 + \mu_1 \mu_2 d_1 + k_1^2 b_1^2 r_1) \\ + d_1 (r_2 d_1 \mu_2 + r_2^2 k_1 b_1 + u d_1 \mu_2)(r_1 k_1 b_1 - \mu_1 d_1),$$

$$A_4 = u r_2 d_1 g (d_1 \mu_2 + r_2 k_1 b_1)(r_1 k_1 b_1 - \mu_1 d_1).$$

Evidently, $A_0 > 0$, $A_1 > 0$ and $A_4 > 0$. By the Routh–Hurwitz criteria, we need to consider the signs:

$$D_2 = A_1 A_2 - A_0 A_3, \quad D_3 = \begin{vmatrix} A_1 & A_3 & 0 \\ A_0 & A_2 & A_4 \\ 0 & A_1 & A_3 \end{vmatrix}.$$

By direct calculations, we see that the sign of D_2 is determined by

$$D_{20} = g u r_2 k_1 d_1 b_1 (-r_1 k_1^2 b_1^2 + k_1 b_1 u \mu_2 + k_1 b_1 u \mu_1 + r_2 k_1 b_1 \mu_2 + \mu_1 k_1 b_1 d_1 + d_1 \mu_1^2) \\ + \varphi_0(\mu_1, \mu_2, r_1, r_2, k_1, b_1, b_2, u, d_1),$$

where

$$\varphi_0 = r_2^3 b_1^2 k_1^2 (b_1 k_1 u + \mu_1 d_1) + r_2^2 b_1 k_1 (u^2 b_1^2 k_1^2 + 2 b_1 d_1 u \mu_1 k_1 + \mu_1^2 d_1^2 + \mu_1 d_1^2 \mu_2) \\ + r_2 d_1 (-b_1 d_1^2 \mu_1^2 k_1 + \mu_1^2 d_1^2 \mu_2 + d_1 b_1^2 \mu_1 k_1^2 r_1 - b_1^2 d_1 u k_1^2 \mu_1 + 2 u k_1 b_1 d_1 \mu_2 \mu_1 + b_1^3 u k_1^3 r_1) \\ + \mu_1 d_1^2 \mu_2 (-d_1^2 \mu_1 + u d_1 \mu_1 + b_1 d_1 k_1 r_1 + b_1 k_1 u^2).$$

⁴⁸¹ Since $k_1 b_1 \frac{r_1}{\mu_1} > d_1$, it is easy to see $\varphi_0 > 0$. It follows that D_{20} is positive if g is

482 small, and therefore D_2 is positive if g is small.

The sign of D_3 is determined by

$$D_{30} = g^2(-r_1 k_1^2 b_1^2 + k_1 b_1 u \mu_2 + k_1 b_1 u \mu_1 + r_2 k_1 b_1 \mu_2 + \mu_1 k_1 b_1 d_1 + d_1 \mu_1^2) \varphi_2 \\ + g \varphi_1 + \varphi_0(\mu_1, \mu_2, r_1, r_2, k_1, b_1, b_2, u, d_1),$$

483 where φ_1 and φ_2 are polynomials of parameters of the model without g, k_2, c_2, v .

484 Hence, D_3 is positive when g is small. Consequently, the Routh–Hurwitz criteria

485 imply that all roots of (A-7) admit negative real parts. \square

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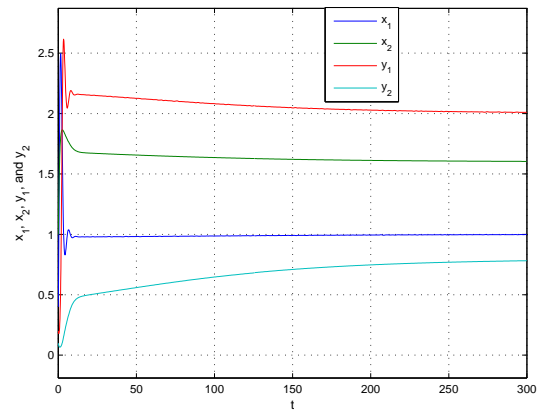


Figure 1: Prey and predators are adjusted to the carrying capacities of ecological community through weak adaptation.

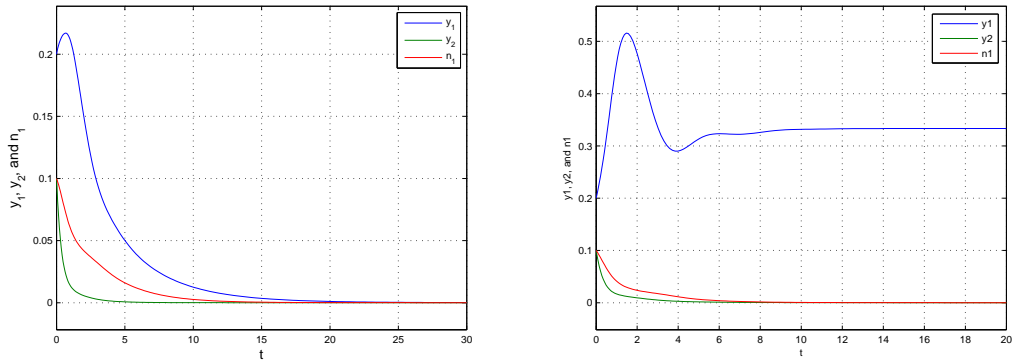


Figure 2: Left panel shows the extinction of predators in the two patches where the parameters are fixed as $r_1 = 1, r_2 = 1, \mu_1 = 2, \mu_2 = 1, u = 1, v = 2, k_1 = 1.5, k_2 = 1, b_1 = 1, b_2 = 1, d_1 = 1, d_2 = 2, g = 5, h = 0.5$. The right panel shows that predators survive in the first patch, but become extinct in the second patch where the parameters are fixed as $r_1 = 1, r_2 = 1, \mu_1 = 2, \mu_2 = 1, u = 1, v = 2, k_1 = 3, k_2 = 1, b_1 = 1, b_2 = 1, d_1 = 1, d_2 = 2, g = 5, h = 0.5$.

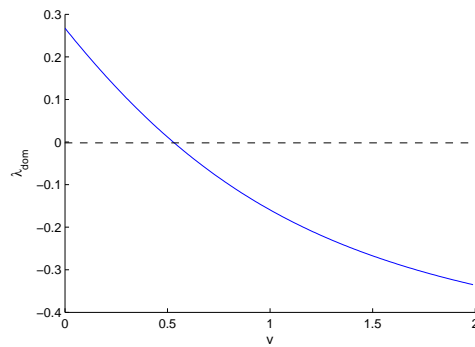


Figure 3: The graph of dominant eigenvalue λ_{dom} versus v .

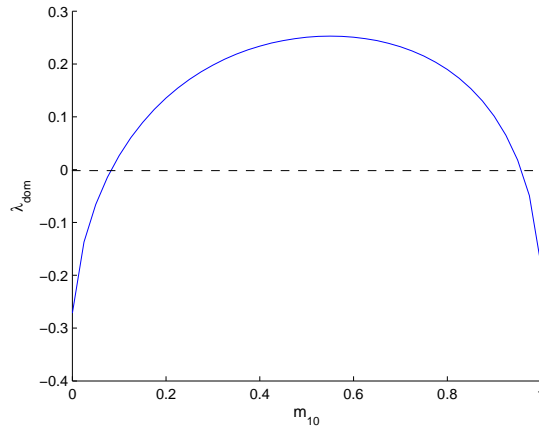


Figure 4: The graph of dominant eigenvalue λ_{dom} versus m_{10} .

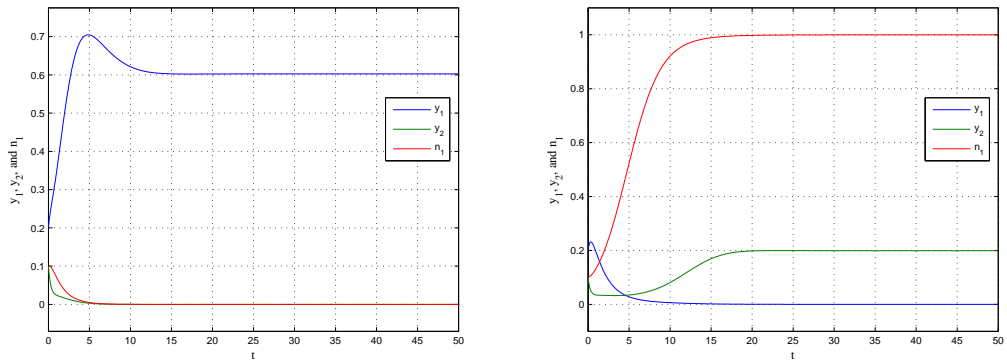


Figure 5: Left panel shows that the adaptation of only predators leads to the persistence of predators in the first patch for small m_{10} , where the parameters are fixed as $r_1 = 1.2, r_2 = 1, \mu_1 = 2, \mu_2 = 1, d_1 = 1, d_2 = 2, b_1 = 1, b_2 = 1, k_1 = 2, k_2 = 2.1, u = 1, v = 4, h = 0.5$ and $m_{10} = 0.1$. The right panel shows that the adaptation of only predators leads to the persistence of predators in the second patch for m_{10} close to 1, where the parameters are fixed as $r_1 = 1.2, r_2 = 1, \mu_1 = 2, \mu_2 = 1, d_1 = 1, d_2 = 2, b_1 = 1, b_2 = 1, k_1 = 2, k_2 = 2.1, u = 1, v = 4, h = 0.5$ and $m_{10} = 0.98$.

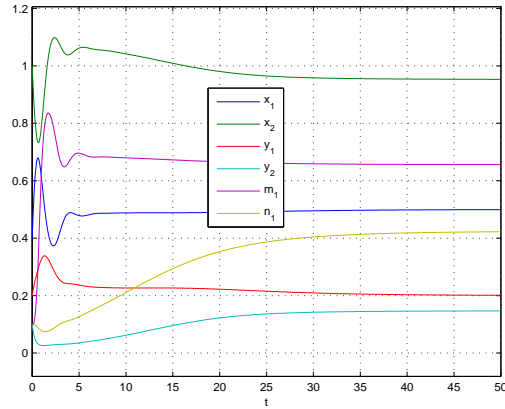


Figure 6: Predators survive in two patches where parameters are fixed as $r_1 = 1.2, r_2 = 1.1, \mu_1 = 2, \mu_2 = 1, d_1 = 1, d_2 = 2, b_1 = 1, b_2 = 1, k_1 = 2, k_2 = 2.1, u = 1, v = 4, g = 5, h = 0.5$.

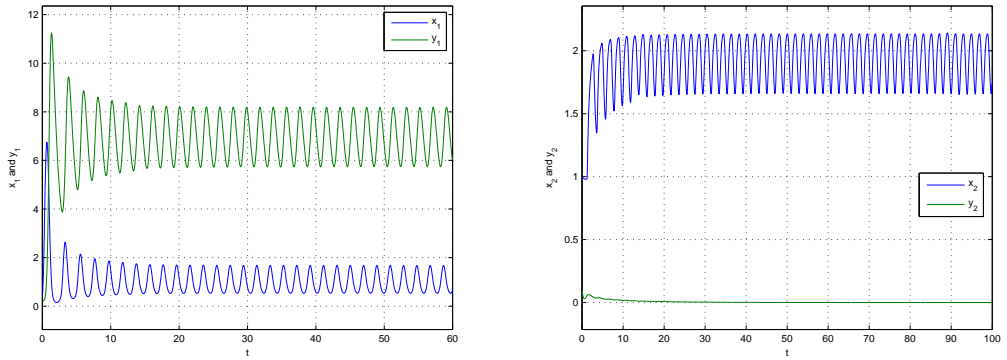


Figure 7: Left panel shows the periodic oscillations of prey and predators in the first patch and right panel indicates the periodic oscillation of prey and the extinction of predators in the second patch, where the parameters are fixed as $r_1 = 8, r_2 = 2, d_1 = 1, d_2 = 2.1, \mu_1 = 1, \mu_2 = 1, u = 1, v = 3, k_1 = 1, k_2 = 1, b_1 = 1, b_2 = 1, g = 5, h = 0.5$.

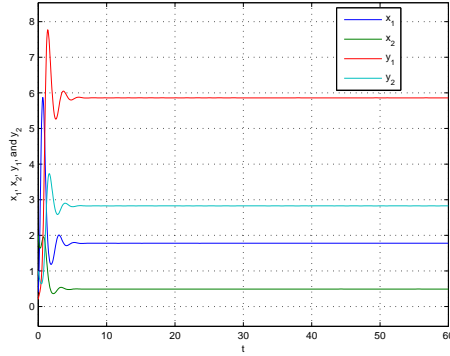


Figure 8: Prey and predators approach globally stable states when there is no adaptation for prey and predators, where parameters are fixed as $r_1 = 8, r_2 = 2, d_1 = 1, d_2 = 2.1, \mu_1 = 1, \mu_2 = 1, u = 1, v = 3, k_1 = 1, k_2 = 1, b_1 = 1, b_2 = 1, m_1 = 0.5, n_1 = 0.5$.

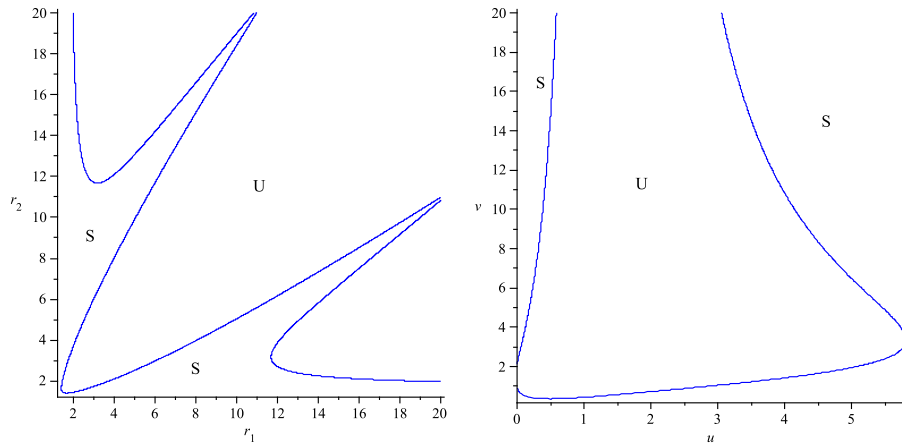


Figure 9: Left panel describes the curve below which E^* is stable and above which E^* is unstable, where $g = 3, h = 4, k_1 = 1, k_2 = 1, u = 0.5, v = 0.4, d_1 = 2, d_2 = 2, b_1 = 2, b_2 = 2, \mu_1 = 1, \mu_2 = 1$, and right panel shows boundaries between stable region and unstable region where $k_1 = 1, k_2 = 1, r_1 = 2, r_2 = 1.5, g = 3, h = 4, d_1 = 2, d_2 = 2, b_1 = 2, b_2 = 2, \mu_1 = 1, \mu_2 = 1$. U represents an unstable region and S represents a stable region.

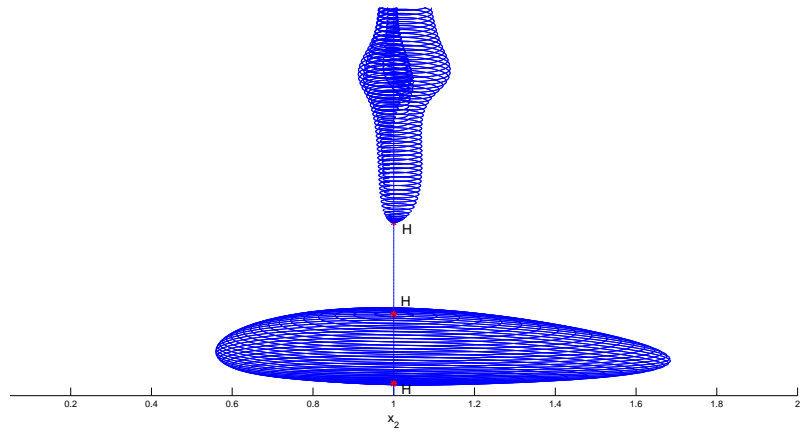


Figure 10: The graph shows a family of stable periodic solutions, where H represents a bifurcation point.