PLOS ONE

RESEARCH ARTICLE

Effect of Spatial Dispersion on Evolutionary Stability: A Two-Phenotype and Two-Patch Model

Qing Li[1], **Jiahua Zhang**[2], **Boyu Zhang**[3]*, **Ross Cressman**[4], **Yi Tao**[2]

1 School of Mathematical Sciences, Capital Normal University, Beijing, China, **2** Key Lab of Animal Ecology and Conservational Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China, **3** Laboratory of Mathematics and Complex Systems, Ministry of Education, School of Mathematical Sciences, Beijing Normal University, Beijing, China, **4** Department of Mathematics, Wilfrid Laurier University, Waterloo, ON, Canada

* zhangby@bnu.edu.cn

OPEN ACCESS

Citation: Li Q, Zhang J, Zhang B, Cressman R, Tao Y (2015) Effect of Spatial Dispersion on Evolutionary Stability: A Two-Phenotype and Two-Patch Model. PLoS ONE 10(11): e0142929. doi:10.1371/journal.pone.0142929

Editor: Gui-Quan Sun, Shanxi University, CHINA

Received: July 2, 2015

Accepted: October 27, 2015

Published: November 13, 2015

Data Availability Statement: All relevant data are within the paper.

Funding: This work was supported by National Natural Science Foundation of China, No. 11471221, No. 11301032 and No. 31270439 (http://www.nsfc.gov.cn/); "the Fundamental Research Funds for the Central Universities" of China (http://www.gov.cn/); and Natural Science Foundation of Beijing Municipal. No. 1132003 (http://www.bjnsf.org/). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Abstract

In this paper, we investigate a simple two-phenotype and two-patch model that incorporates both spatial dispersion and density effects in the evolutionary game dynamics. The migration rates from one patch to another are considered to be patch-dependent but independent of individual's phenotype. Our main goal is to reveal the dynamical properties of the evolutionary game in a heterogeneous patchy environment. By analyzing the equilibria and their stabilities, we find that the dynamical behavior of the evolutionary game dynamics could be very complicated. Numerical analysis shows that the simple model can have twelve equilibria where four of them are stable. This implies that spatial dispersion can significantly complicate the evolutionary game, and the evolutionary outcome in a patchy environment should depend sensitively on the initial state of the patches.

Introduction

In order to explain the evolution of animal behavior, Maynard Smith and Price [1] developed the concept of evolutionarily stable strategy (ESS) (see also [2–5]). Prior et al. [6] investigated an evolutionary game model that incorporates both spatial dispersion and density effects in the evolutionary dynamics. In this model, the population is considered to be dispersed in a patchy environment, where the background fitness and payoff matrix in each patch can be different. Migration from region to region is considered as an incidental aspect of the population, i.e., the migration is a chance event unrelated to an individual's phenotype (strategy) or the fitness of the patch. As pointed out by Prior et al. [6], their assumptions differ from that of Ludwig and Levin [7] who treat the tendency to migrate as an individual characteristic subject to selection (see also [8–13]), and also differ from that of Hines and Maynard Smith [14] who interpret the effect of spatial dispersion as an increased tendency to interact with opponents sharing one's own characteristics (see also [15]). Recently, Cressman and Krivan [16] investigated the migration dynamics for the ideal free distribution (IFD) in a patchy environment. They showed that

IFD is evolutionarily stable under the assumptions that individuals never migrate from patches with a higher payoff to patches with a lower payoff and some individuals always migrate to the best patch. But migration does not necessarily lead to IFD if migration rates are independent of the payoffs of the patches.

For the evolutionary game dynamics in a patchy environment, Prior et al. [6] mainly focused their analysis on the stability of the homogeneous states, where they assumed that all patches have the same payoff matrix and density-dependent background fitness. Their main results showed that a stable equilibrium (e.g. an evolutionarily stable strategy) of the non-dispersed frequency dynamics becomes a stable equilibrium of the large system if population density stabilizes at these fixed frequencies.

In this paper, following Prior et al. [6], a simple two-patch and two-phenotype model is investigated. Three basic assumptions for this model are:

(i) The environment consists of two patches, called patch 1 and patch 2, respectively. Individuals can move from one patch to the other at any time t. The migration rates are patch-dependent but independent of individual's phenotype [6]. Let c_1 denote the probability that an individual moves from patch 1 to patch 2, and, similarly, c_2 the probability that an individual moves from patch 2 to patch 1.

(ii) In each of two patches, individuals display two possible phenotypes (strategies), denoted by R_1 and R_2, and individuals interact in random pairwise contests. The payoff matrix is $\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$ in patch 1 and $\mathbf{B} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}$ in patch 2, where a_{ij} (or b_{ij}) is the payoff of an individual displaying phenotype R_i when it plays against an individual displaying phenotype R_j in patch 1 (or in patch 2) for all $i, j = 1, 2$. Without loss of generality, we also assume that $a_{ij} \geq 0$ and $b_{ij} \geq 0$ for all $i, j = 1, 2$.

(iii) In each of the two patches, the background fitness is density-dependent [3–4], which is defined as $\alpha_1 - \beta_1 n_1$ in patch 1, and $\alpha_2 - \beta_2 n_2$ in patch 2, where n_1 is the total population size in patch 1 and n_2 the total population size in patch 2. We also assume that $\alpha_i > c_i$ for all $i = 1, 2$. That is, the migration rates are small enough to ensure that population size in a patch will increase when there are few individuals in the patch.

Let x_i denote the number of individuals with phenotype R_i in patch 1, and y_i the number of individuals with phenotype R_i in patch 2 ($i = 1, 2$). Clearly, $n_1 = x_1 + x_2$ and $n_2 = y_1 + y_2$. Similarly, let p denote the frequency of phenotype R_1 in patch 1, and q the frequency of phenotype R_1 in patch 2, i.e., $p = x_1/n_1$ and $q = y_1/n_2$. According to the basic assumption (ii), the expected payoff of an individual displaying phenotype R_i is $f_i = pa_{i1} + (1 - p)a_{i2}$ in patch 1, and $g_i = qb_{i1} + (1 - q)b_{i2}$ in patch 2 for $i = 1, 2$. Similarly, according to the basic assumption (iii), the (total) fitness of an individual displaying phenotype R_i is defined as $F_i = (\alpha_1 - \beta_1 n_1) + f_i$ in patch 1, and $G_i = (\alpha_2 - \beta_2 n_2) + g_i$ in patch 2 for $i = 1, 2$. Thus, the time evolution of x_i and y_i can be given by

$$\begin{aligned} \frac{dx_i}{dt} &= \left[f_i + (\alpha_1 - \beta_1 n_1)\right]x_i - c_1 x_i + c_2 y_i \ , \\ \frac{dy_i}{dt} &= \left[g_i + (\alpha_2 - \beta_2 n_2)\right]y_i - c_2 y_i + c_1 x_i \ , \end{aligned} \tag{1}$$

respectively, for $i = 1, 2$. Dynamics (1) also equivalent to the following system expressed in terms of phenotypic frequency and population size in each patch.

$$\begin{aligned}\frac{dp}{dt} &= p(1-p)(f_1 - f_2) + c_2(q-p)\frac{n_2}{n_1} \ , \\ \frac{dq}{dt} &= q(1-q)(g_1 - g_2) + c_1(p-q)\frac{n_1}{n_2} \ , \\ \frac{dn_1}{dt} &= \left[\bar{f} + (\alpha_1 - \beta_1 n_1)\right] n_1 - c_1 n_1 + c_2 n_2 \ , \\ \frac{dn_2}{dt} &= \left[\bar{g} + (\alpha_2 - \beta_2 n_2)\right] n_2 - c_2 n_2 + c_1 n_1 \ , \end{aligned} \tag{2}$$

where $\bar{f} = pf_1 + (1-p)f_2$ and $\bar{g} = qg_1 + (1-q)g_2$ are the average payoffs in patch 1 and patch 2, respectively.

In this paper, the equilibria of dynamics (2) and their stabilities are analyzed. Different from Prior et al. [6] who focused on the homogeneous states, we are primarily interested in analyzing the heterogeneous states, where two patches have different ESSs. Our main goal is to reveal the dynamical properties of the evolutionary game in a heterogeneous patchy environment.

Results

Symmetric equilibria of dynamics (2)

For given p and q with $0 \le p, q \le 1$, an equilibrium of dynamics

$$\begin{aligned}\frac{dn_1}{dt} &= n_1\left(\bar{f} + (\alpha_1 - \beta_1 n_1)\right) - c_1 n_1 + c_2 n_2 \ , \\ \frac{dn_2}{dt} &= n_2\left(\bar{g} + (\alpha_2 - \beta_2 n_2)\right) - c_2 n_2 + c_1 n_1 \ , \end{aligned} \tag{3}$$

denoted by $(n_1(p, q), n_2(p, q))$, satisfies

$$\begin{aligned} n_2 &= \frac{n_1}{c_2}\left(c_1 - \bar{f} - (\alpha_1 - \beta_1 n_1)\right) \ , \\ n_1 &= \frac{n_2}{c_1}\left(c_2 - \bar{g} - (\alpha_2 - \beta_2 n_2)\right) \ . \end{aligned} \tag{4}$$

It is clear that $(n_1, n_2) = (0, 0)$ is always a solution of Eq (4) for any given p and q. Furthermore, $(p, q, 0, 0)$ must be unstable under dynamics (2) since $\alpha_1 > c_1$ and $\alpha_2 > c_2$. Notice that n_2 is a parabolic function of n_1 and vice versa, Eq (4) also has a unique positive solution, denoted by $(\hat{n}_1, \hat{n}_2) = (n_1(p, q), n_2(p, q))$ with $\hat{n}_1 > 0$ and $\hat{n}_2 > 0$ (see Fig 1). When this solution corresponds to an equilibrium $(p, q, \hat{n}_1, \hat{n}_2)$ of dynamics (2), we call it a *positive* equilibrium. In the rest of this paper, we only focus on the number and stabilities of these positive equilibria.

A positive equilibrium, $(p, q, \hat{n}_1, \hat{n}_2)$, is called a *symmetric* equilibrium of dynamics (2) if $p = q$. That is, at a symmetric equilibrium, population compositions in the two patches are the same.

It is easy to see that dynamics (2) always have two symmetric boundary equilibria, $(1, 1, \hat{n}_1, \hat{n}_2)$ and $(0, 0, \hat{n}_1, \hat{n}_2)$, where at these equilibria, all individuals in the two patches display the same phenotype. Stabilities of the boundary equilibria can be characterized by analyzing the Jacobian matrix of dynamics (2) (see Method section). The main result is that if R_1 (or R_2) is an ESS for both payoff matrices **A** and **B**, then the boundary equilibrium $(1, 1, \hat{n}_1, \hat{n}_2)$ (or $(0, 0, \hat{n}_1, \hat{n}_2)$) must be asymptotically stable. This result is consistent with that of Prior et al. [6],

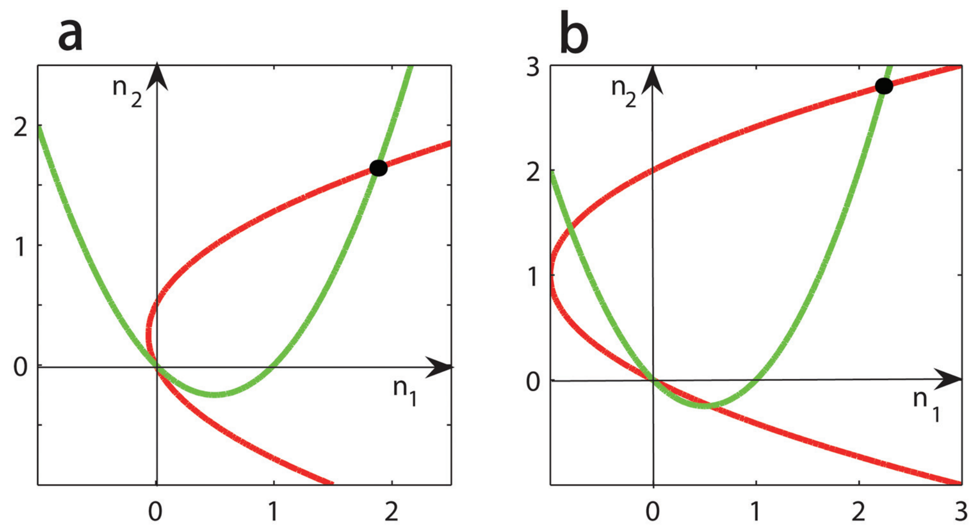

Fig 1. The unique positive equilibrium of dynamics (3). The red curves correspond to the second equation of Eq (4) and the green curves to the first equation of Eq (4). For any given p and q, the two curves have a unique positive intersection (see the black spots). Parameters are taken as $\beta_1 = \beta_2 = 0.01$, $\alpha_1 = 0.75$, $\bar{f} = 0.25$, $c_1 = 0.5$ and $c_2 = 0.5$ in all two panels. Furthermore, $\alpha_2 = 0.55$ and $\bar{g} = 0.2$ in panel **a**, and $\alpha_2 = 1$ and $\bar{g} = 0.5$ in panel **b**.

doi:10.1371/journal.pone.0142929.g001

where the stable equilibrium of the non-dispersed system becomes a stable equilibrium of dynamics (2). However, under the influence of migration, a symmetric boundary equilibria could be stable even if the corresponding phenotype is not an ESS in either patch. For instance, the boundary equilibrium $(1, 1, \hat{n}_1, \hat{n}_2)$ is asymptotically stable if $a_{11} < a_{21}$ as long as $a_{21} - a_{11}$ is small enough.

On the other hand, the symmetric interior equilibrium exists only for a very special case $p^* = q^* \in (0, 1)$, where $p^* = \frac{a_{12}-a_{22}}{a_{12}-a_{22}+a_{21}-a_{11}}$ and $q^* = \frac{b_{12}-b_{22}}{b_{12}-b_{22}+b_{21}-b_{11}}$. In this case, $(p^*, q^*, \hat{n}_1, \hat{n}_2)$ is an symmetric interior equilibrium of dynamics (2), where $(\hat{n}_1, \hat{n}_2)$ is the solution of Eq (4) for $p = p^*$ and $q = q^*$. Furthermore, it is asymptotically stable if p^* ($= q^*$) is an ESS for both **A** and **B** (see Method section).

General cases

For more general situations (i.e., $p^* \neq q^*$), it is very tedious to determine the equilibria of dynamics (2). In fact, numerical simulations show that dynamics (2) may have twelve equilibria. To investigate the properties of the equilibria of dynamics (2), two cases are considered below. The first case is special in that there is no migration in one direction (i.e., one of c_1 and c_2 is 0) and we analyze the number of stable equilibria for all possible payoff structures. The second case is more general (i.e., $c_1 > 0$ and $c_2 > 0$) and we show the equilibria of dynamics (2) and their stabilities for $0 < p^*, q^* < 1$.

Case 1. $c_1 > 0$ **and** $c_2 = 0$. Without loss of generality, we here assume that $c_1 > 0$ but $c_2 = 0$, i.e. individuals can only move from patch 1 to patch 2 but not from patch 2 to patch 1 (the case of $c_1 = 0$ and $c_2 > 0$ can be analyzed analogously). Then, dynamics (2) can be rewritten as

$$\begin{aligned} \frac{dp}{dt} &= p(1-p)(f_1 - f_2) \ , \\ \frac{dn_1}{dt} &= (\alpha_1 + \bar{f} - c_1 - \beta_1 n_1) n_1 \ , \end{aligned} \tag{5}$$

and

$$\begin{aligned} \frac{dq}{dt} &= q(1-q)(g_1 - g_2) + c_1(p-q)\frac{n_1}{n_2}, \\ \frac{dn_2}{dt} &= (\alpha_2 + \bar{g} - \beta_2 n_2)n_2 + c_1 n_1 \ . \end{aligned} \tag{6}$$

Notice that dynamics (5) is independent of dynamics (6). Thus, as an equilibrium of dynamics (2), $(\hat{p}, \hat{q}, \hat{n}_1, \hat{n}_2)$, is locally asymptotically stable if and only if $(\hat{p}, \hat{n}_1)$ is locally asymptotically stable under dynamics (5) and $(\hat{q}, \hat{n}_2)$ is locally asymptotically stable under dynamics (6), where p and n_1 in dynamics (6) correspond to the stable equilibrium, $(\hat{p}, \hat{n}_1)$, of dynamics (5).

We first look at the stability of dynamics (5). It is easy to see that: (i) the boundary equilibrium $(1, \hat{n}_1)$ (or $(0, \hat{n}_1)$) is locally asymptotically stable if and only if $p = 1$ (or $p = 0$) is an ESS for the payoff matrix **A**, i.e. $a_{11} > a_{12}$ (or $a_{22} > a_{12}$), where $\hat{n}_1 = \frac{\alpha_1 + a_{11} - c_1}{\beta_1}$ for $p = 1$ and $\hat{n}_1 = \frac{\alpha_1 + a_{22} - c_1}{\beta_1}$ for $p = 0$; and (ii) if the unique interior equilibrium $(p^*, \hat{n}_1)$ exists, then it is globally asymptotically stable if and only if p^* is an ESS for the payoff matrix **A**, where $p^* = \frac{a_{12} - a_{22}}{a_{12} - a_{22} + a_{21} - a_{11}} \in (0, 1)$ and $\hat{n}_1 = \frac{\alpha_1 + \bar{f}(p^*) - c_1}{\beta_1}$.

From dynamics (6), the frequency $\hat{q}$ in a stable equilibrium of dynamics (2), $(\hat{p}, \hat{q}, \hat{n}_1, \hat{n}_2)$, should obey the equation

$$q(1-q)(g_1 - g_2) + \frac{\hat{p} - q}{2}\left[\sqrt{(\alpha_2 + \bar{g})^2 + 4\beta_2 c_1 \hat{n}_1} - (\alpha_2 + \bar{g})\right] \quad = \quad 0 \ , \tag{7}$$

where $\hat{p} \in \{0, 1, p^*\}$ corresponds to the stable equilibrium, $(\hat{p}, \hat{n}_1)$, of dynamics (5). In the Method section, we analyze the solutions of Eq (7) and the stabilities of the corresponding equilibria under dynamics (6). According to the stability conditions of dynamics (5) and (6), the equilibria of dynamics (2) and their properties can be summarized as follows:

1. If R_1 (or R_2) is the only ESS for **A** and **B**, then the symmetric boundary equilibrium $(0, 0, \hat{n}_1, \hat{n}_2)$ (or $(1, 1, \hat{n}_1, \hat{n}_2)$) is unstable and the other $(1, 1, \hat{n}_1, \hat{n}_2)$ (or $(0, 0, \hat{n}_1, \hat{n}_2)$) is stable. Furthermore, Eq (7) has no interior solution. This implies that $(1, 1, \hat{n}_1, \hat{n}_2)$ (or $(0, 0, \hat{n}_1, \hat{n}_2)$) is also globally asymptotically stable, i.e., all individuals in the two patches will eventually display R_1 (or R_2) under evolutionary dynamics (2) (see Fig 2A and 2B).

2. If both R_1 and R_2 are ESSs for **A** but R_1 (or R_2) is the only ESS for **B**, then the symmetric boundary equilibrium $(0, 0, \hat{n}_1, \hat{n}_2)$ (or $(1, 1, \hat{n}_1, \hat{n}_2)$) is unstable and the other $(1, 1, \hat{n}_1, \hat{n}_2)$ (or $(0, 0, \hat{n}_1, \hat{n}_2)$) is stable. Furthermore, Eq (7) has a unique (interior) solution $\hat{q}$, which corresponds to an asymptotically stable equilibrium $(0, \hat{q}, \hat{n}_1, \hat{n}_2)$ (or $(1, \hat{q}, \hat{n}_1, \hat{n}_2)$) of dynamics (2). In this situation, either all individuals in the system display R_1 (or R_2), or individuals in patch 1 display R_2 (or R_1) and two phenotypes coexist in patch 2 (see Fig 2C and 2D).

3. If p^* is the only ESS for **A** ($0 < p^* < 1$) and R_1 (or R_2) is the only ESS for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has a unique (interior) solution $\hat{q}$, which corresponds to an asymptotically stable equilibrium $(p^*, \hat{q}, \hat{n}_1, \hat{n}_2)$ of dynamics (2). Numerical simulation shows that this equilibrium is also globally stable. This implies that the two phenotypes will stably coexist in the system (see Fig 2E and 2F).

4. If R_2 (or R_1) is the only ESS for **A** but R_1 (or R_2) is the only ESS for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has

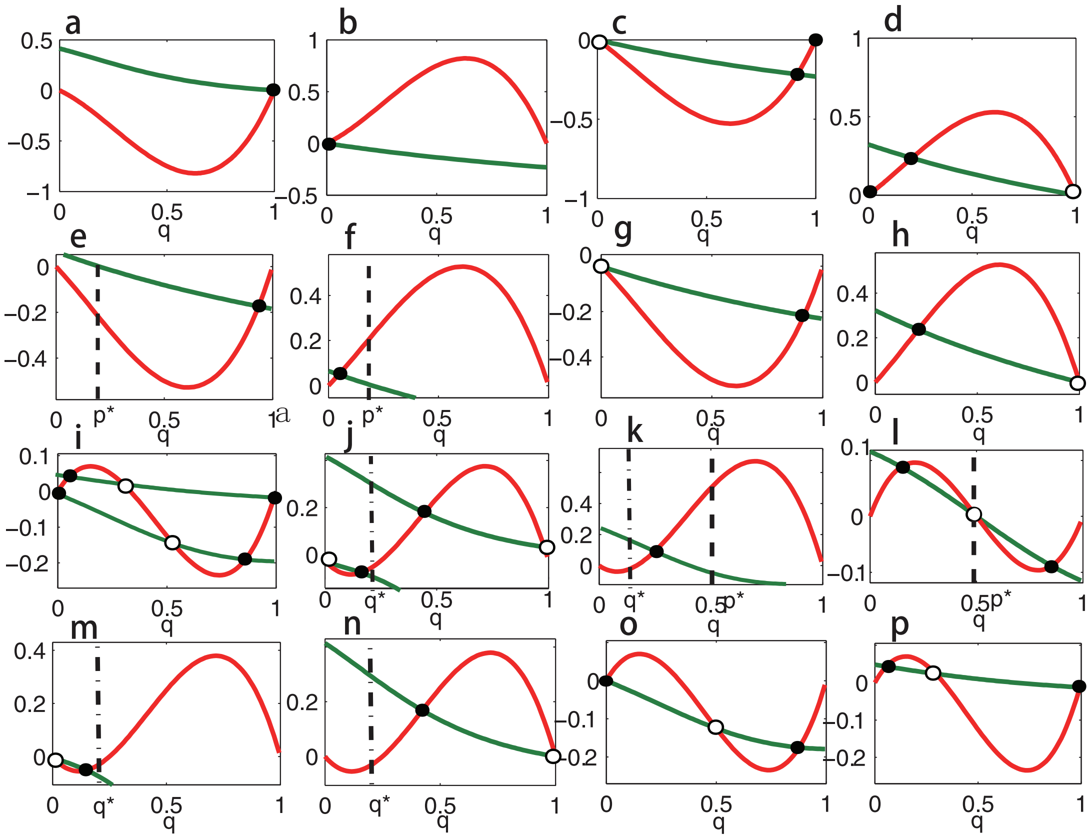

Fig 2. Solutions of Eq (7) and their stabilities under dynamics (2) when $c_1 > 0$ and $c_2 = 0$. Intersections of $h_1(q)$ and $h_2(q)$ (i.e., the solutions of Eq (7)) are shown for all sixteen possible situations. The red curves denote $h_1(q)$ and the green curves $h_2(q)$. The intersections denoted by black spots correspond to stable equilibria of dynamics (2), and the intersections denoted by black circles correspond to unstable equilibria. Parameters are taken as $\beta_1 = \beta_2 = 0.01$, $\alpha_1 = 1$, $\alpha_2 = 2$ and $c_1 = 0.5$ in all sixteen panels. Payoff matrixes in the panels are: In panel **a**, **A** = [1.5, 1.5; 0, 0], **B** = [5, 1; 0, 0]. In panel **b**, **A** = [0, 0; 1, 1], **B** = [0, 0; 5, 1]. In panel **c**, **A** = [1, 0; 0, 1], **B** = [3, 1; 0, 0]. In panel **d**, **A** = [1, 0; 0, 1], **B** = [0, 0; 3, 1]. In panel **e**, **A** = [0, 1.25; 5, 0], **B** = [3, 1; 0, 0]. In panel **f**, **A** = [0, 1.25; 5, 0], **B** = [0, 0; 3, 1]. In panel **g**, **A** = [0, 0; 1, 1], **B** = [3, 1; 0, 0]. In panel **h**, **A** = [1, 1; 0, 0], **B** = [0, 0; 3, 1]. In panel **i**, **A** = [1, 0; 0, 1], **B** = [2, 0; 0, 1]. In panel **j**, **A** = [1, 0; 0, 1], **B** = [0, 1; 4, 0]. In panel **k**, **A** = [0, 2; 2, 0], **B** = [0, 1; 5, 0]. In panel **l**, **A** = [0, 2; 2, 0], **B** = [1, 0; 0, 1]. In panel **m**, **A** = [0, 0; 1, 1], **B** = [0, 1; 4, 0]. In panel **n**, **A** = [1.5, 1.5; 0, 0], **B** = [0, 1; 4, 0]. In panel **o**, **A** = [0, 0; 1, 1], **B** = [2, 0; 0, 1]. In panel **p**, **A** = [1, 1; 0, 0], **B** = [2, 0; 0, 1]. The positions of the interior ESSs p^* and q^* ($0 < p^*, q^* < 1$) are marked by dashed lines.

doi:10.1371/journal.pone.0142929.g002

a unique (interior) solution $\hat{q}$, which corresponds to an asymptotically stable equilibrium $(0, \hat{q}, \hat{n}_1, \hat{n}_2)$ (or $(1, \hat{q}, \hat{n}_1, \hat{n}_2)$) of dynamics (2). Similarly as (**3**), this equilibrium is also globally stable, i.e., R_2 (or R_1) can invade patchy 2 under the influence of migration (see Fig 2G and 2H).

5. If both R_1 and R_2 are ESSs for **A** and **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are asymptotically stable. Furthermore, Eq (7) has at most four (interior) solutions, where two are stable equilibria of dynamics (2) and the other two are unstable. This implies that the evolutionary outcome in this situation is very difficult to predict since the system can have four stable states (see Fig 2I).

6. If both R_1 and R_2 are ESSs for **A** and q^* is an ESS for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has at most two (interior) solutions, where both of them are stable equilibria of dynamics (2) (see Fig 2J).

7. If p^* is an ESS for **A** and q^* is an ESS for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has a unique (interior) solution $\hat{q}$, which corresponds to an asymptotically stable equilibrium $(p^*, \hat{q}, \hat{n}_1, \hat{n}_2)$ of dynamics (2). Similarly as (**3**), this equilibrium is also globally stable and two phenotypes will stably coexist in the system (see Fig 2K).
8. If p^* is an ESS for **A** and both R_1 and R_2 are ESSs for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has at most three (interior) solutions, which are denoted by $\hat{q}_1$, $\hat{q}_2$ and $\hat{q}_3$ with $\hat{q}_1 < \hat{q}_2 < \hat{q}_3$. The two interior equilibria corresponding to $\hat{q}_1$ and $\hat{q}_3$ are stable under dynamics (2) and the interior equilibrium corresponding to $\hat{q}_2$ is unstable (see Fig 2L).
9. If R_2 (or R_1) is the only ESS for **A** and q^* is an ESS for **B**, then both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are unstable. Furthermore, Eq (7) has a unique (interior) solution $\hat{q}$, which corresponds to an asymptotically stable equilibrium $(0, \hat{q}, \hat{n}_1, \hat{n}_2)$ (or $(1, \hat{q}, \hat{n}_1, \hat{n}_2)$) of dynamics (2). Similarly as (**4**), this equilibrium is also globally stable and two phenotypes will stably coexist in patch 2 (see Fig 2M and 2N).
10. If R_2 (or R_1) is the only ESS for **A** and both R_1 and R_2 are ESSs for **B**, then the symmetric boundary equilibrium $(0, 0, \hat{n}_1, \hat{n}_2)$ (or $(1, 1, \hat{n}_1, \hat{n}_2)$) is stable and the other $(1, 1, \hat{n}_1, \hat{n}_2)$ (or $(0, 0, \hat{n}_1, \hat{n}_2)$) is unstable. Furthermore, Eq (7) has at most two (interior) solutions, where one corresponds to a stable equilibria of dynamics (2) and the other is unstable. Similarly as (**2**), either all individuals in the system display R_2 (or R_1), or individuals in patch 1 display R_2 (or R_1) and two phenotypes coexist in patch 2 (see Fig 2O and 2P).

Case 2. $c_1 > 0$ **and** $c_2 > 0$. We now consider the case with $c_1 > 0$ and $c_2 > 0$. It is easy to check that dynamics (2) only have two boundary equilibria, $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$, and the existence of asymmetric boundary equilibrium is impossible, for instance, if $p = 0$ and $q \neq 0$, then $\frac{dp}{dt} > 0$. We then focus on the number and stability of interior equilibria. Notice that an equilibrium of dynamics (2) should be the solution of equation

$$\begin{aligned}
\Delta_1 p(1-p)(p-p^*) + c_2(q-p)\frac{n_2}{n_1} &= 0 \ , \\
\Delta_2 q(1-q)(q-q^*) + c_1(p-q)\frac{n_1}{n_2} &= 0 \ , \\
\left[\bar{f} + (\alpha_1 - \beta_1 n_1)\right] n_1 - c_1 n_1 + c_2 n_2 &= 0 \ , \\
\left[\bar{g} + (\alpha_2 - \beta_2 n_2)\right] n_2 - c_2 n_2 + c_1 n_1 &= 0 \ .
\end{aligned} \tag{8}$$

So if both n_1 and n_2 are positive, then from the first two equations of Eq (8), an interior equilibrium of dynamics (2) should obey the equations

$$\Delta_1 \Delta_2 p(1-p)q(1-q)(p-p^*)(q-q^*) = -c_1 c_2 (p-q)^2. \tag{9}$$

Furthermore, from the third and the forth equations of Eq (8)

$$\frac{\Delta_1 p(1-p)(p-p^*)}{c_2(p-q)} = \frac{\beta_1}{\beta_2} \cdot \frac{\bar{g} + \alpha_2 - c_2 + \frac{\Delta_2 q(1-q)(q-q^*)}{q-p}}{\bar{f} + \alpha_1 - c_1 + \frac{\Delta_1 p(1-p)(p-p^*)}{p-q}}, \tag{10}$$

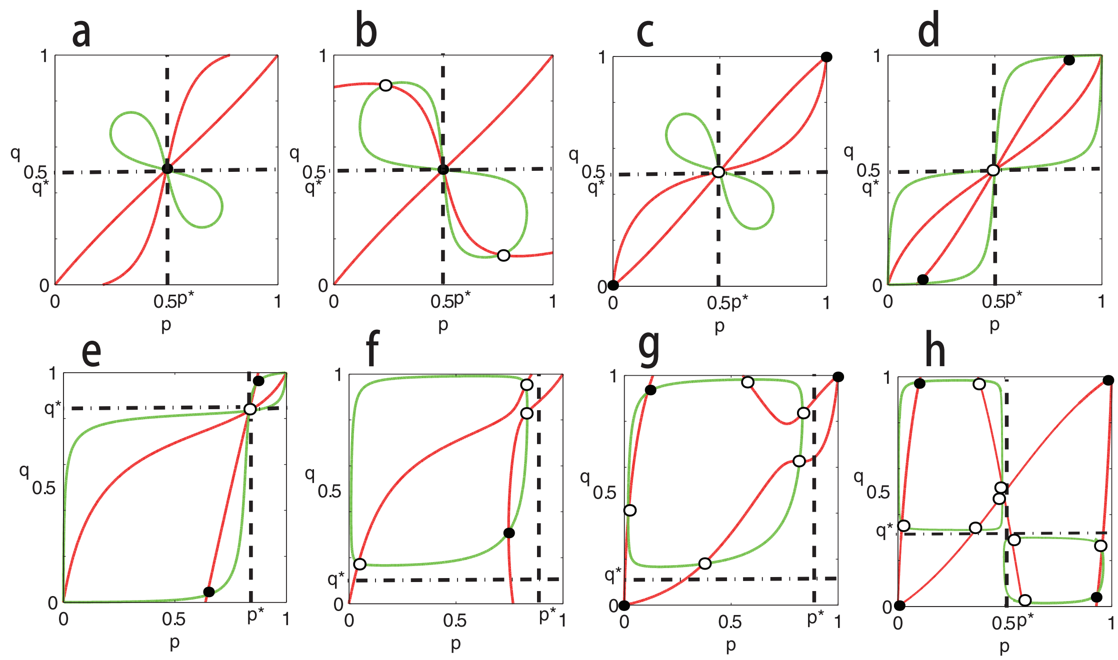

Fig 3. Equilibria of Eq (2) on the $p - q$ plane and their stabilities when $c_1 > 0$ and $c_2 > 0$. The red curves correspond to Eq (10) and the green curves Eq (9). The intersections denoted by black spot correspond to stable equilibria of dynamics (2), and the intersections denoted by black circle correspond to unstable equilibria. Parameters are taken as: In panel **a**, **A** = [0, 1; 1, 0], **B** = [0, 5; 5, 0], $\beta_1 = \beta_2 = 0.01$, $\alpha_1 = 1.25$, $\alpha_2 = 1.8$, $c_1 = 0.25$ and $c_2 = 0.8$. In panel **b**, **A** = [0, 1; 1, 0], **B** = [0, 5; 5, 0], $\beta_1 = \beta_2 = 0.01$, $\alpha_1 = 1.125$, $\alpha_2 = 0.1$, $c_1 = 0.125$ and $c_2 = 0.8$. In panel **c**, **A** = [1, 0; 0, 1], **B** = [5, 0; 0, 5], $\beta_1 = \beta_2 = 0.001$, $\alpha_1 = 1.4$, $\alpha_2 = 1.5$, $c_1 = 0.4$ and $c_2 = 0.5$. In panel **d**, **A** = [0, 1; 1, 0], **B** = [5, 0; 0, 5] $\beta_1 = \beta_2 = 0.001$, $\alpha_1 = 1.5$, $\alpha_2 = 1.2$, $c_1 = 0.5$ and $c_2 = 0.2$. In panel **e**, **A** = [0, 5; 1, 0], **B** = [1, 0; 0, 5], $\beta_1 = \beta_2 = 0.001$, $\alpha_1 = 1.5$, $\alpha_2 = 1.2$, $c_1 = 0.5$ and $c_2 = 0.2$. In panel **f**, **A** = [0, 5; 1, 0], **B** = [0, 1; 5, 0], $\beta_1 = \beta_2 = 0.001$, $\alpha_1 = 1.5$, $\alpha_2 = 1.2$, $c_1 = 0.5$ and $c_2 = 0.2$. In panel **g**, **A** = [1, 0; 0, 5], **B** = [5, 0; 0, 1], $\beta_1 = \beta_2 = 0.001$, $\alpha_1 = 1.4$, $\alpha_2 = 1.5$, $c_1 = 0.4$ and $c_2 = 0.5$. In panel **h**, **A** = [1, 0; 0, 1], **B** = [2, 0; 0, 1], $\beta_1 = 0.05$, $\beta_2 = 0.01$, $\alpha_1 = 1.75$, $\alpha_2 = 2$, $c_1 = 0.25$ and $c_2 = 0.01$. The positions of p^* and q^* are marked by dashed lines ($0 < p^*, q^* < 1$, and note that p^* and q^* may not be ESS).

doi:10.1371/journal.pone.0142929.g003

where we assume that both p^* and q^* are in the interval $0 < p^*, q^* < 1$ (i.e., we consider the most complicated payoff structures).

From Eq (9), it is easy to see that for the situation with $p^* \neq q^*$, if the interior equilibrium exists, then it should be in the region $(0, p^*) \times (q^*, 1)$, or $(p^*, 1) \times (0, q^*)$ if $\Delta_1\Delta_2 > 0$, and in the region $(0, p^*) \times (0, q^*)$, or $(p^*, 1) \times (q^*, 1)$ if $\Delta_1\Delta_2 < 0$. Of course, it is very difficult to get the exactly analytic solutions of Eqs (9) and (10) in general. The numerical analysis suggests that ten interior equilibria can exist (see Fig 3H). To show this, some examples are plotted in Fig 3. All of these examples show clearly that the equilibrium structure of dynamics (2) could be very complicated.

We further look at the bifurcation behaviors of system (2) for the case that both R_1 and R_2 are ESSs for **A** and **B** (i.e., the most complicated case), and assume equal migration rates between regions, i.e., $c_1 = c_2 = c$. In this case, both the symmetric boundary equilibria $(0, 0, \hat{n}_1, \hat{n}_2)$ and $(1, 1, \hat{n}_1, \hat{n}_2)$ are asymptotically stable, and the system can have ten interior equilibria. When $c = 0$, it is easy to see that the system has nine equilibria in total, including four stable (boundary) equilibria and five unstable equilibria. The number of equilibria jumps from nine to twelve as soon as the migration rates becomes positive although the number of stable equilibria keeps unchanged (see Fig 4A and 4B). Furthermore, numerical simulation shows that both the numbers of stable equilibria and unstable equilibria decrease as c increases. In particular, when $c > 0.019$, the system has only two stable equilibria (i.e., the two symmetric

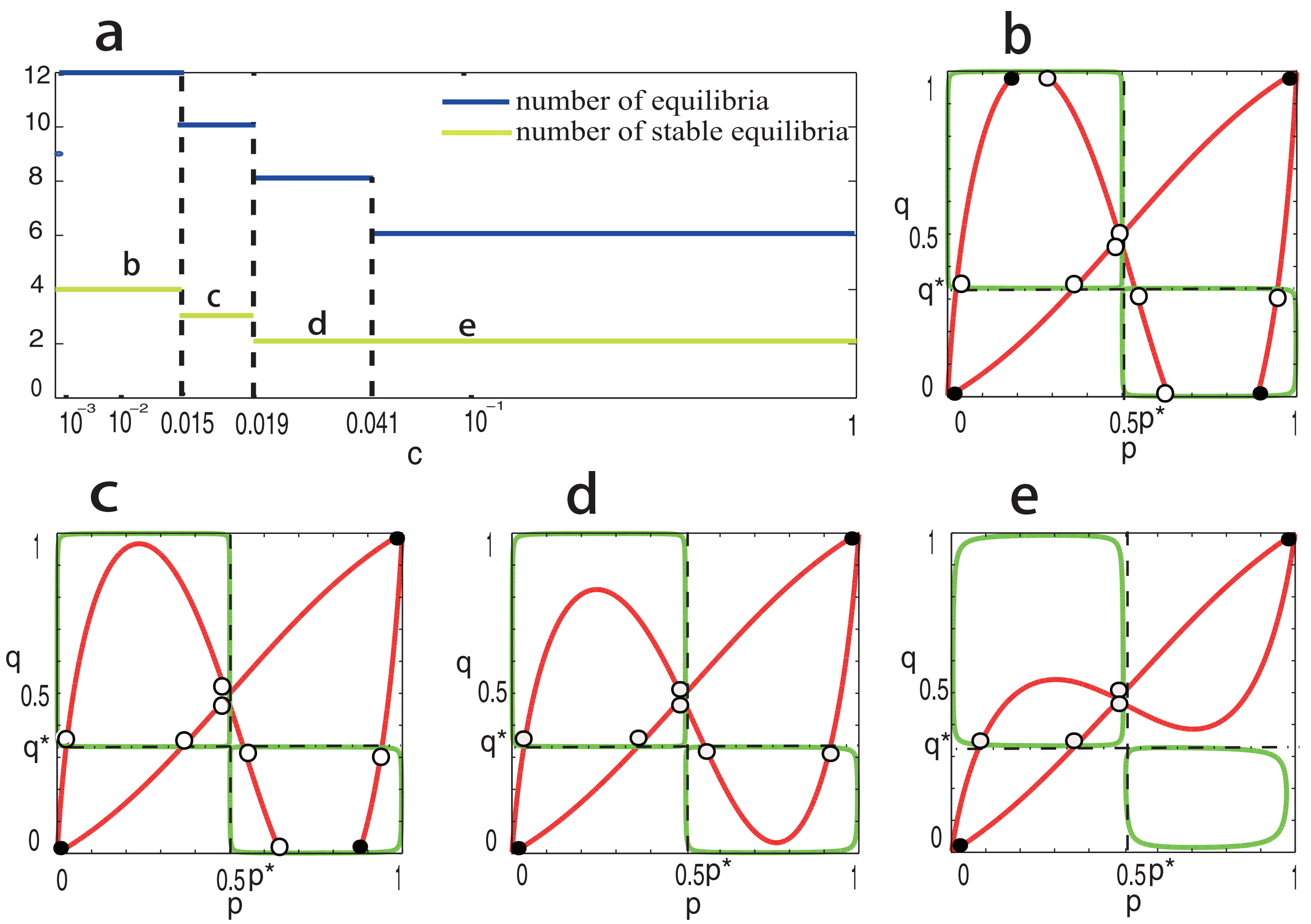

Fig 4. Bifurcation behaviors of Eq (2) when $c_1 > 0$ and $c_2 > 0$. In panel **a**, the number of equilibria and the number of stable equilibria are denoted by blue line and yellow line, respectively. In panels **b-e**, the red curves correspond to Eq (10) and the green curves Eq (9). The intersections denoted by black spot correspond to stable equilibria of dynamics (2), and the intersections denoted by black circle correspond to unstable equilibria. The positions of p^* and q^* are marked by dashed lines. Parameters are taken as: **A** = [1, 0; 0, 1], **B** = [2, 0; 0, 1], $\beta_1 = 0.05$, $\beta_2 = 0.01$, $\alpha_1 = 1.75$, $\alpha_2 = 2$. In panel **b**, $c_1 = c_2 = c = 0.014$; in panel **c**, $c_1 = c_2 = c = 0.015$; in panel **d**, $c_1 = c_2 = c = 0.02$; and in panel **e**, $c_1 = c_2 = c = 0.05$.

doi:10.1371/journal.pone.0142929.g004

boundary equilibria), and all interior equilibria are unstable (see Fig 4). These results suggest that small migration rates make the dynamical behavior of the system more complex.

Discussion

A vast amount of research has been devoted to analyze the influence of spatial diffusion on the evolutionary stability of ecology systems. One well known mathematical approach is the reaction-diffusion equation, where in this framework, individuals are dispersed in a continues space [10–11, 17–21]. For instance, Hofbauer et al. [11, 21] considered a population of two types of individuals distributed in an one-dimensional space, and assumed that the migration (or diffusion) rate is both individual-independent and location-independent. They showed that in two-strategy coordination games, if the reaction term of the reaction-diffusion equation is taken as replicator dynamics, then one strategy will drive out the other strategy in form of a traveling wave front, although there is no simple rule to decide which strategy can survive.

In this paper, we assume that individuals are distributed in a (discrete) patchy environment. Following Prior et al. [6], we investigate a simple two-phenotype and two-patch model, where individuals compete only with their immediate neighbors and the migration rates between patches are individual-independent but patch-dependent. Different from Prior et al. [6] who focused on the homogeneous patchy environment, we here are more interested in the dynamical stability in heterogeneous environment. Our main results show that: (i) if the pure strategy R_1 (or R_2) is an ESS for both two patches, then the boundary equilibrium corresponding to $p = 1$ and $q = 1$ (or $p = 0$ and $q = 0$) must be asymptotically stable; (ii) if the payoff matrices **A** and **B** satisfy $p^* = \frac{a_{12}-a_{22}}{a_{12}-a_{22}+a_{21}-a_{11}} = q^* = \frac{b_{12}-b_{22}}{b_{12}-b_{22}+b_{21}-b_{11}} \in (0,1)$, then the interior equilibrium corresponding to (p^*, q^*) is asymptotically stable if p^* is an ESS for **A** and q^* an ESS for **B**; (iii) as a special case with $c_1 > 0$ and $c_2 = 0$ (or $c_1 = 0$ and $c_2 > 0$), i.e. individuals can only move from patch 1 to patch 2 (or from patch 2 to patch 1), all possible situations for the existence and stability of boundary and interior equilibria are considered, and we find that dynamics (2) can have six equilibria where four of them are stable; (iv) for $c_1 > 0$ and $c_2 > 0$, the numerical analysis shows that the equilibrium structure and dynamical behavior of the system could be very complicated in general. In particular, dynamics (2) can have twelve equilibria where four of them are stable.

Our analysis provides an insight for understanding the effect of spatial dispersion on the evolutionary stability of patchy environment. Both the analytical analysis and the numerical simulation indicate that the original ESS formulations which ignore the dispersion process cannot be applied to predict the evolutionary outcome of the dispersion system even for small migration rates. For instance, in the case that both patches have multiple ESS's and no dispersal between patches, the system has four (boundary) stable equilibria and five unstable equilibria. However, if one of c_1 and c_2 becomes positive, the system can have two to four stable equilibria and four to eight unstable equilibria. Furthermore, we found that both the numbers of stable equilibria and unstable equilibria decrease in the migration rates. This observation has an intuitive biological interpretation [6]. In a heterogenous patchy environment, the effect of selection is to make the overall population more heterogeneous in the sense of different patches have different population compositions, while the effect of migration is to move the population composition in each patch towards the mean of the overall population, i.e., migration promotes homogeneity. Thus, when the migration rates are small (i.e., the effect of selection is strong), similarly as the case of no dispersal, the system has two stable symmetric boundary equilibria and two stable asymmetric equilibria; and when the migration rates are large (i.e., the effect of migration is strong), the existence of stable asymmetric equilibrium is impossible, and the system has only two stable symmetric boundary equilibria, where at these equilibria all individuals display the same phenotype.

In this paper, we focus on the effect of spatial dispersion on two-patch system only. A natural extension would be to consider the three-patch system. However, analyzing the dynamical behavior of the three-patch system may be an even more difficult issue because the equilibrium structure of the two-patch system is already very complex. Another possible development would be to compare the evolutionary stability of the patchy environment under different migration rules. One commonly used migration rule is that individuals know perfectly the payoff in all patches and they always move to the patch with the highest payoff (i.e., ideal animals) [15]. In contrast, a more realistic model is that individuals do not migrate to patches with lower payoff [22]. Recent studies have shown that these two migration rules can lead to the IFD [16, 23]. Since that the IFD corresponds to a stable equilibrium of the non-dispersed evolutionary dynamics, we can then expect that these migration rules may also lead to the ESS of the non-dispersed evolutionary dynamics [23].

Methods

Stability of the symmetric equilibria

The Jacobian matrix of the dynamics (2) about the symmetric boundary equilibrium $(1, 1, \hat{n}_1, \hat{n}_2)$, denoted by $\mathbf{J}_{(1,1)}$, is

$$\begin{pmatrix} -(a_{11}-a_{21})-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2\frac{\hat{n}_2}{\hat{n}_1} & 0 & 0 \\ c_1\frac{\hat{n}_1}{\hat{n}_2} & -(b_{11}-b_{21})-c_1\frac{\hat{n}_1}{\hat{n}_2} & 0 & 0 \\ (2a_{11}-a_{12}-a_{21})\hat{n}_1 & 0 & -\beta_1\hat{n}_1-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2 \\ 0 & (2b_{11}-b_{12}-b_{21})\hat{n}_2 & c_1 & -\beta_2\hat{n}_2-c_1\frac{\hat{n}_1}{\hat{n}_2} \end{pmatrix},$$

and similarly, the Jacobian matrix about $(0, 0, \hat{n}_1, \hat{n}_2)$, denoted by $\mathbf{J}_{(0,0)}$, is

$$\begin{pmatrix} (a_{12}-a_{22})-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2\frac{\hat{n}_2}{\hat{n}_1} & 0 & 0 \\ c_1\frac{\hat{n}_1}{\hat{n}_2} & (b_{12}-b_{22})-c_1\frac{\hat{n}_1}{\hat{n}_2} & 0 & 0 \\ (a_{12}+a_{21}-2a_{22})\hat{n}_1 & 0 & -\beta_1\hat{n}_1-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2 \\ 0 & (b_{12}+b_{21}-2b_{22})\hat{n}_2 & c_1 & -\beta_2\hat{n}_2-c_1\frac{\hat{n}_1}{\hat{n}_2} \end{pmatrix}.$$

For the matrix $\mathbf{J}_{(1,1)}$, notice that the eigenvalues of the matrix

$$\begin{pmatrix} -(a_{11}-a_{21})-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2\frac{\hat{n}_2}{\hat{n}_1} \\ c_1\frac{\hat{n}_1}{\hat{n}_2} & -(b_{11}-b_{21})-c_1\frac{\hat{n}_1}{\hat{n}_2} \end{pmatrix}$$

have negative real parts if $a_{11} - a_{21} > 0$ and $b_{11} - b_{21} > 0$, and that the real parts of the eigenvalues of the matrix

$$\begin{pmatrix} -\beta_1\hat{n}_1-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2 \\ c_1 & -\beta_2\hat{n}_2-c_1\frac{\hat{n}_1}{\hat{n}_2} \end{pmatrix}$$

must be negative. So, if the pure strategy R_1 is an ESS for both payoff matrices **A** and **B**, then the eigenvalues of $\mathbf{J}_{(1,1)}$ must have negative real parts [6]. Similar to the matrix $\mathbf{J}_{(0,0)}$, if the pure strategy R_2 is an ESS for both payoff matrices **A** and **B**, then the eigenvalues of $\mathbf{J}_{(0,0)}$ have negative real parts.

The Jacobian matrix about the symmetric interior equilibrium $(p^*, q^*, \hat{n}_1, \hat{n}_2)$, denoted by $\mathbf{J}_{(p^*,q^*)}$, is

$$\begin{pmatrix} p^*(1-p^*)\Delta_1-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2\frac{\hat{n}_2}{\hat{n}_1} & 0 & 0 \\ c_1\frac{\hat{n}_1}{\hat{n}_2} & q^*(1-q^*)\Delta_2-c_1\frac{\hat{n}_1}{\hat{n}_2} & 0 & 0 \\ (-a_{12}+a_{21})\hat{n}_1 & 0 & -\beta_1\hat{n}_1-c_2\frac{\hat{n}_2}{\hat{n}_1} & c_2 \\ 0 & (-b_{12}+b_{21})\hat{n}_2 & c_1 & -\beta_2\hat{n}_2-c_1\frac{\hat{n}_1}{\hat{n}_2} \end{pmatrix},$$

where $\Delta_1 = a_{11} - a_{12} - a_{21} + a_{22}$ and $\Delta_2 = b_{11} - b_{12} - b_{21} + b_{22}$. Also similar to the matrix $\mathbf{J}_{(1,1)}$

(or the matrix $\mathbf{J}_{(0,0)}$), the eigenvalues of $\mathbf{J}_{(p^*,\, q^*)}$ have the negative real parts if p^* (= q^*) is an ESS for both payoff matrices **A** and **B**, i.e., the equilibrium $(p^*, q^*, \hat{n}_1, \hat{n}_2)$ is asymptotically stable if p^* (= q^*) is an ESS for both **A** and **B**.

Stability analysis of dynamics (6) when $c_1 > 0$ and $c_2 = 0$

We first analyze the solutions of Eq (7). For convenience, let

$$\begin{aligned} h_1(q) &= -\Delta_2 q(1-q)(q-q^*) \ , \\ h_2(q) &= \frac{\hat{p}-q}{2}\left[\sqrt{(\alpha_2+\bar{g})^2+4\beta_2 c_1 \hat{n}_1}-(\alpha_2+\bar{g})\right] . \end{aligned}$$

It is easy to see that Eq (7) has a boundary solution $\hat{q} = 0$ (or $q = 1$) if and only if $\hat{p} = 0$ (or $\hat{p} = 1$). Furthermore, the interior solutions of Eq (7) should correspond to the intersections of the functions $h_1(q)$ and $h_2(q)$ in the interval $0 < q < 1$. Notice that $h_1(0) = h_1(1) = h_1(q^*) = 0$, $\Delta_2\, h_1(q) > 0$ for $0 < q < q^*$ and $\Delta_2\, h_1(q) < 0$ for $q^* < q < 1$ (if $0 < q^* < 1$), and that $h_2(0) \geq 0$, $h_2(1) \leq 0$, $h_2(\hat{p}) = 0$, $h_2(q) > 0$ for $0 < q < \hat{p}$ and $h_2(q) < 0$ for $\hat{p} < q < 1$ (if $0 < \hat{p} < 1$). Then, for the existence of intersections in the interval $0 < q < 1$, we have that:

1. If R_1 is the only ESS for both payoff matrices **A** and **B**, then, no intersection can exist (see Fig 2A); and, similarly, if R_2 is the only ESS for both **A** and **B**, then no intersection can exist (see Fig 2B).
2. If both R_1 and R_2 are ESSs for **A** but R_1 is the only ESS for **B**, then only one intersection exists (see Fig 2C); and, similarly, if both R_1 and R_2 are ESSs for **A** but R_2 is the only ESS for **B**, then only one intersection exists (see Fig 2D).
3. If $p^* \in (0, 1)$ is an ESS for **A** and R_1 is the only ESS for **B**, only one intersection exists (see Fig 2E); and, similarly, if p^* is an ESS for **A** and R_2 is the only ESS for **B**, then only one intersection exists (Fig 2F).
4. If R_2 is the only ESS for **A** and R_1 is the only ESS for **B**, then only one intersection exists (see Fig 2G); and, similarly, if R_1 is the only ESS for **A** and R_2 is the only ESS for **B**, then only one intersection exists (see Fig 2H).
5. If both R_1 and R_2 are ESSs for **A** and **B**, then at most four intersections can exist (see Fig 2I).
6. If both R_1 and R_2 are ESSs for **A** and $q^* \in (0, 1)$ is an ESS for **B**, only two intersections exist (see Fig 2J).
7. If p^* is an ESS for **A** and q^* is an ESS for **B**, the only one intersection exists (see Fig 2K).
8. If p^* is an ESS for **A** and both R_1 and R_2 are ESSs for **B**, then there are at most three intersections (see Fig 2L).
9. If R_2 is the only ESS for **A** and q^* is an ESS for **B**, then only one intersection exists (see Fig 2M); and, similarly, If R_1 is the only ESS for **A** and q^* is an ESS for **B**, then only one intersection exists (see Fig 2N).
10. If R_2 is the only ESS for **A** and both R_1 and R_2 are ESSs for **B**, then there are at most two intersections (see Fig 2O); and, similarly, if R_1 is the only ESS for **A** and both R_1 and R_2 are ESSs, then there are at most two intersections (see Fig 2P).

For the stability of the solutions of Eq (7) under dynamics (6), it is easy to see that for given $\hat{p}$ (i.e. $\hat{p} \in \{0, 1, p^*\}$ corresponds to the stable equilibrium of dynamics (5)), if $\tilde{q} = \hat{p}$ and $\tilde{q}$ is an ESS for the payoff matrix **B**, then the corresponding equilibrium $(\tilde{q}, \hat{n}_2)$ must be asymptotically stable under dynamics (6). On the hand, let $(\hat{q}, \hat{n}_2)$ be an interior equilibrium of dynamics (6), and the Jacobian matrix about $(\hat{q}, \hat{n}_2)$, denoted by $\mathbf{J}_{(\hat{q},\hat{n}_2)}$, is given by

$$\mathbf{J}_{(\hat{q},\hat{n}_2)} = \begin{pmatrix} -\frac{h_1(q)}{dq}|_{q=\hat{q}} - c_1\frac{\hat{n}_1}{\hat{n}_2} & -(\hat{p}-\hat{q})c_1\frac{\hat{n}_1}{\hat{n}_2^2} \\ \frac{d\bar{g}(q)}{dq}|_{q=\hat{q}}\hat{n}_2 & -c_1\frac{\hat{n}_1}{\hat{n}_2} - \beta_2\hat{n}_2 \end{pmatrix}.$$

Clearly, the interior equilibrium $(\hat{q}, \hat{n}_2)$ is asymptotically stable (i.e. the eigenvalues of $\mathbf{J}_{(\hat{q},\hat{n}_2)}$ have the negative real parts) if

$$-\frac{h_1(q)}{dq}|_{q=\hat{q}} - 2c_1\frac{\hat{n}_1}{\hat{n}_2} - \beta_2\hat{n}_2 < 0 ,$$
$$\left(\frac{h_1(q)}{dq}|_{q=\hat{q}} + c_1\frac{\hat{n}_1}{\hat{n}_2}\right)\left(c_1\frac{\hat{n}_1}{\hat{n}_2} + \beta_2\hat{n}_2\right) + (\hat{p}-\hat{q})c_1\frac{\hat{n}_1}{\hat{n}_2}\cdot\frac{d\bar{g}(q)}{dq}|_{q=\hat{q}} > 0 .$$

Thus, for given parameter values, stabilities of the interior equilibria of dynamics (6) (i.e., interior solutions of Eq (7)) can be analyzed numerically according to the above conditions (see the figure caption of Fig 2 for detailed parameters, note that the following results may not be true for all parameter values).

1. If R_1 (or R_2) is the only ESS for **A** and **B**, then the boundary equilibrium $(1, \hat{n}_2)$ with $\hat{p} = 1$ (or $(0, \hat{n}_2)$ with $\hat{p} = 0$) is asymptotically stable (see also Fig 2A and 2B).
2. If both R_1 and R_2 are ESSs for **A** but R_1 (or R_2) is the only ESS for **B**, then one boundary equilibrium $(0, \hat{n}_2)$ with $\hat{p} = 0$ (or $(1, \hat{n}_2)$ with $\hat{p} = 1$) is unstable and the other boundary equilibrium $(1, \hat{n}_2)$ with $\hat{p} = 1$ (or $(0, \hat{n}_2)$ with $\hat{p} = 0$) is asymptotically stable. Furthermore, the unique interior equilibrium $(\hat{q}, \hat{n}_2)$ is also asymptotically stable (see also Fig 2C and 2D).
3. If p^* is an ESS for **A** and R_1 (or R_2) is the only ESS for **B**, then the unique interior equilibrium is asymptotically stable (see also Fig 2E and 2F).
4. If R_2 (or R_1) is the only ESS for **A** but R_1 (or R_2) is the only ESS for **B**, then the boundary equilibrium $(0, \hat{n}_2)$ with $\hat{p} = 0$ (or $(1, \hat{n}_2)$ with $\hat{p} = 1$) is unstable and the unique interior equilibrium is asymptotically stable (see also Fig 2G and 2H).
5. If both R_1 and R_2 are ESSs for **A** and **B**, then the boundary equilibrium $(1, \hat{n}_2)$ with $\hat{p} = 1$, or the boundary equilibrium $(0, \hat{n}_2)$ with $\hat{p} = 0$, is stable, and for four interior equilibria, two are stable and the other two are unstable (see also Fig 2I).
6. If both R_1 and R_2 are ESSs for **A** and q^* is an ESS for **B**, then the boundary equilibrium $(1, \hat{n}_2)$ with $\hat{p} = 1$, or the boundary equilibrium $(0, \hat{n}_2)$ with $\hat{p} = 0$, is unstable, and the two interior equilibria are asymptotically stable (see also Fig 2J).
7. If p^* is an ESS for **A** and q^* is an ESS for **B**, then the unique interior equilibrium is asymptotically stable (see also Fig 2K).
8. If p^* is an ESS for **A** and both R_1 and R_2 are ESSs for **B**, then there are at most three interior equilibria corresponding to three intersections of h_1 and h_2, which are denoted by $\hat{q}_1$, $\hat{q}_2$ and $\hat{q}_3$ with $\hat{q}_1 < \hat{q}_2 < \hat{q}_3$, the two interior equilibria corresponding to $\hat{q}_1$ and $\hat{q}_3$, respectively, are stable and the interior equilibrium corresponding to $\hat{q}_2$ is unstable (see also Fig 2L).

9. If R_2 (or R_1) is the only ESS for **A** and q^* is an ESS for **B**, then the boundary equilibrium $(0, \hat{n}_2)$ with $\hat{p} = 0$ (or $(1, \hat{n}_2)$ with $\hat{p} = 1$) is unstable and the unique interior equilibrium is asymptotically stable (see also Fig 2M and 2N).

10. If R_2 (or R_1) is the only ESS for **A** and both R_1 and R_2 are ESSs for **B**, then there are at most two interior equilibria, the boundary equilibrium $(0, \hat{n}_2)$ for $\hat{p} = 0$ (or $(1, \hat{n}_2)$ for $\hat{p} = 1$) is stable, and one interior equilibrium is stable and the other unstable (see also Fig 2O and 2P).

Author Contributions

Conceived and designed the experiments: QL JZ BZ RC YT. Performed the experiments: QL JZ BZ RC YT. Analyzed the data: QL JZ BZ RC YT. Contributed reagents/materials/analysis tools: QL JZ BZ RC YT. Wrote the paper: QL JZ BZ RC YT.

References

1. Maynard Smith J, Price GR. The logical animal conflict. Nature. 1973; 246: 15–18. doi: 10.1038/246015a0
2. Taylor PD, Jonker LB. Evolutionarily stable strategies and game dynamics. Math. Biosci. 1978; 40: 145–156. doi: 10.1016/0025-5564(78)90077-9
3. Maynard Smith J. Evolution and the Theory of Games. Cambridge University Press; 1982.
4. Cressman R. The stability concept of evolutionary game theory: a dynamic approach. Lect Notes Bio-math. vol. 94, Berlin, Heildelberg New York: Springer; 1992.
5. Hofbauer J, Sigmund K. Evolutionary Games and Population Dynamics. Cambridege University Press; 1998.
6. Prior TG, Hines WGS, Cressman R. Evolutionary games for spatially dispersed populations. J. Math. Biol. 1993; 32: 55–65.
7. Ludwig D, Levin SA. Evolutionary stability of plant communities and the maintenance of multiple dispersal types. Theor. Popul. Biol. 1991; 40: 285–307. doi: 10.1016/0040-5809(91)90057-M
8. Comins HN, Hamilton WD, May RM. Evolutionary stable dispersal strategies. J. Theor. Biol. 1980; 82: 205–230.
9. Levin SA, Cohen D, Hastings A. Dispersal strategies in patchy environments. Theor. Popul. Biol. 1984; 26: 165–191. doi: 10.1016/0040-5809(84)90028-5
10. Hutson VCL, Vickers GT. Traveling waves and dominance of ESS's. J. Math. Biol, 1993; 30: 457–471. doi: 10.1007/BF00160531
11. Hofbauer J, Hutson VCL, Vickers GT. Travelling waves for games in economics and biology. Nonlinear. Anal. Theor. 1997; 30:1235–1244. doi: 10.1016/S0362-546X(96)00336-7
12. Dieckmann U, O'Hara B, Weisser W. The evolutionary ecology of dispersal. Trends Ecol. Evol. 1999; 14: 88–90. doi: 10.1016/S0169-5347(98)01571-7
13. Travis JMJ, Murrell DJ, Dytham C. The evolution of density dependent dispersal. Proc. R. Soc. Lond. B. 1999; 266: 1837–1842. doi: 10.1098/rspb.1999.0854
14. Hines WGS, Maynard Smith J. Games between relatives. J. Theor. Biol. 1979; 79: 19–30. doi: 10.1016/0022-5193(79)90254-6 PMID: 513800
15. Fretwell SD, Lucas HL. On Terriotorial behavior and other factors influcing habitat distribution in birds. Acta Bio-theoretica. 1970; 19: 16–32. doi: 10.1007/BF01601953
16. Cressman R, Krivan V. Migration dynamics for the ideal free distribution. Am. Nat. 2006; 168: 384–397. doi: 10.1086/506970 PMID: 16947113
17. Sun GQ, Jin Z, Li L, Haque M, Li BL. Spatial patterns of a predator-prey model with cross diffusion. Nonlinear. Dynam. 2012; 69: 1631–1638.
18. Sun GQ, Zhang J, Song LP, Jin Z, Li BL. Pattern formation of a spatial predator-prey system. Appl. Math. Comput. 2012; 218: 11151–11162. doi: 10.1016/j.amc.2012.04.071
19. Sun GQ, Chakraborty A, Liu QX, Jin Z, Anderson KE, Li BL. Influence of time delay and nonlinear diffusion on herbivore outbreak. Commun. Nonlinear. Sci. 2014; 19: 1507–1518. doi: 10.1016/j.cnsns.2013.09.016

20. Sun GQ, Wang SL, Ren Q, Jin Z, Wu YP. Effects of time delay and space on herbivore dynamics: linking inducible defenses of plants to herbivore outbreak. Sci. Rep. 2015; 5: 11246. doi: 10.1038/srep11246 PMID: 26084812

21. Hofbauer J. The spatially dominant equilibrium of a game. Ann. Oper. Res. 1999; 89: 233–251. doi: 10.1023/A:1018979708014

22. Hugie DM, Grand TC. Movement between patches, unequal competitors and the ideal free distribution. Evol. Ecol. 1998; 12: 1–19.

23. Cressman R, Krivan V, Garay J. Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. Am. Nat. 2004; 164: 473–489. doi: 10.1086/423827 PMID: 15459879