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ON THE ASYMPTOTIC BEHAVIOR OF SPATIALLY IMPLICIT MODELS OF COMPETITION OF TWO SPECIES WITH OVERCOLONIZATION

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Dedicated to Professor John R. Graef on the occasion of his 70th birthday.

ABSTRACT. We consider patch-based population dynamics, called metapopulations, and investigate the spread of two species and their competition for habitat areas. Let $0 \leq p_1, p_2$ denote the proportion (density) of the areas occupied by the species 1 and 2, respectively. Obviously, $0 \leq p_1 + p_2 \leq 1$. Both species can locally extinct and colonize empty patches or patches occupied by the other with different rates. Hence the model is

$$p_1' = k_1 p_1 (1 - p_1 - p_2) - e_1 p_1 + c_1 p_1 p_2 - c_2 p_1 p_2$$
$$p_2' = k_2 p_2 (1 - p_1 - p_2) - e_2 p_2 - c_1 p_1 p_2 + c_2 p_1 p_2,$$

where e_i are the extinction rates, k_i are the rates of colonization of empty patches, and species "i" overcolonize "j" with the rate c_i $(i, j = 1, 2; i \neq j)$.

We investigate the asymptotic stability properties of the equilibria of such systems and we give a complete characterization of the parameter space. We prove that there can appear a globally asymptotically stable coexisting equilibrium. On the other hand, this equilibrium can become unstable and then the exclusive equilibria are only locally asymptotically stable. We have also developed dynamic applications in Wolfram *Mathematica* to illustrate our results.

AMS (MOS) Subject Classification. 92D40, 34D20.

1. INTRODUCTION

A generalized model of competition of two species that are living in a patchy environment is investigated. Classical metapopulation concept provides spatially implicit approach of population dynamics. A metapopulation consists of several local populations in a patchy environment. The size of local populations on the patches (habitat areas) is ignored, but the temporal change of the proportion of the occupied

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patches is examined. Empty patches can be colonized by a species, consequently a local population is established and considered to be in equilibrium. Local populations can die out as a result of some local event or some other species may overcolonize them in cases of multispecies models. Metapopulation models have several applications in conservation biology, since human activity transforms naturally continuous landscapes into some collection of (still) habitable patches. The concept of metapopulation was developed by Levins [6, 7]. His simple, single species model provided a base of many other more complex models [3, 11, 13, 17]. Levins' model build upon the main assumptions, that patches are uniform, equally distributed and equally connected, hence the probability of the local extinction and the colonization of patches are independent of spatial location. Levins' model describes the dynamics of the fraction of occupied patches ($0 \leq p \leq 1$)

$$p' = kp(1-p) - ep, \tag{1.1}$$

where k is the global rate of colonization ($k > 0$) and e is the global rate of extinction ($e \geq 0$). As the patches occupied by a species are uniformly distributed, the colonization of available patches, which denotes the speed of the spreading is proportional to $p(1-p)$. Local extinction is proportional to fraction of occupied patches. The long-term survivor of the single species metapopulation depends on the balance between local extinction and colonization. It is trivial that the equilibrium 0 is globally asymptotically stable if $k < e$. On the other hand, there appears a positive, globally asymptotically stable equilibrium $1 - \frac{e}{k}$ if $e < k$. Many publications discuss extensions of the Levins model but it is still considered as a basic model up to now, see [3, 11, 12, 14, 17, 18, 19] and references therein.

Dealing with one species, the conditions of the survival are analyzed, while in the cases when more species fight for habitats, the basic question is if they can coexist or their competition is exclusive. This problem has been widely investigated in ecology and different kinds of models have been developed for competing systems. [3, 4, 10, 11, 12, 13, 14, 17, 18, 19]. There can be several strategies of competition for areas depending on the type of interaction. Certain species can colonize only empty patches, others can colonize even those which have been already occupied by others. The latter is called overcolonization. From this point, generalizing the Levins model, we consider two-species models, where $p_1 = p_1(t)$ and $p_2 = p_2(t)$ denote the proportions of the occupied patches by species 1 and 2, respectively, where $0 \leq p_1, 0 \leq p_2$ and $p_1 + p_2 \leq 1$. A patch can be occupied by at most one of the species.

Since the systems investigated in our paper are restricted to the region $D = \{(p_1, p_2) :\ p_1 \geq 0, p_2 \geq 0, p_1 + p_2 \leq 1\}$ and it turns out to be invariant for these systems, global asymptotic stability (G.A.S.) of an equilibrium $P \in D$ is understood in

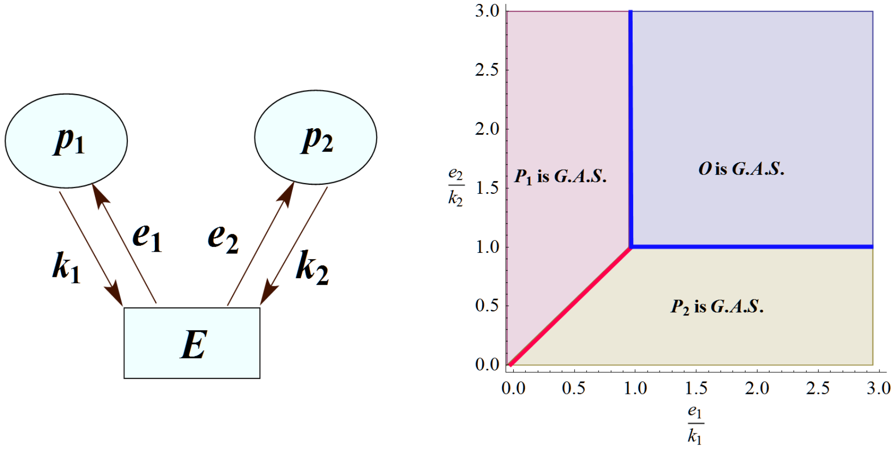


FIGURE 1. Two-species Levins model without overcolonization: interactions and attractivity domains on the parameter space $\left\{\frac{e_1}{k_1}, \frac{e_2}{k_2}\right\}$

the sense that P is stable with respect to D, and every solution $(p_1(t), p_2(t))$ tends to P as $t \to \infty$, provided $(p_1(0), p_2(0)) \in D$.

The simplest case is a two-species model without overcolonization (part 1 of Fig. 1), i.e., species can occupy only empty patches.

$$\begin{aligned} p_1' &= k_1 p_1 \left(1 - p_1 - p_2\right) - e_1 p_1, \\ p_2' &= k_2 p_2 \left(1 - p_1 - p_2\right) - e_2 p_2, \end{aligned} \tag{1.2}$$

where k_1 and k_2 are the global rates of colonization $(k_1, k_2 > 0)$, e_1 and e_2 are the global rates of extinction $(e_1, e_2 \geq 0)$. If $\frac{e_1}{k_1} \neq \frac{e_2}{k_2}$, three boundary equilibria exist: the trivial (0, 0) equilibrium and two other equilibria $\left(1 - \frac{e_1}{k_1}, 0\right)$ and $\left(0, 1 - \frac{e_2}{k_2}\right)$, and at most one of the species can survive. There is no interior equilibrium when both species would coexist. The stability properties of equilibria are summarized in Table 1. The global dynamics of the system can be easily seen on the right in Fig. 1.

Equilibrium	*Exists*	*G.A.S.*	*Unstable*
$O = (0,0)$	always	$1 \leq \frac{e_1}{k_1}$ and $1 \leq \frac{e_2}{k_2}$	$\frac{e_1}{k_1} < 1$ or $\frac{e_2}{k_2} < 1$
$P_1 = \left(1 - \frac{e_1}{k_1}, 0\right)$	$\frac{e_1}{k_1} < 1$	$\frac{e_1}{k_1} < \frac{e_2}{k_2}$	$\frac{e_1}{k_1} > \frac{e_2}{k_2}$
$P_2 = \left(0, 1 - \frac{e_2}{k_2}\right)$	$\frac{e_2}{k_2} < 1$	$\frac{e_1}{k_1} > \frac{e_2}{k_2}$	$\frac{e_1}{k_1} < \frac{e_2}{k_2}$

TABLE 1. Summary of attractivity properties of system (1.2)

Note that in the singular case $\frac{e_1}{k_1} = \frac{e_2}{k_2} =: d$, every point of the line $p_1 + p_2 = 1 - d$ is a stable equilibrium.

Competitive hierarchy is quite common among plant species. In the simplest overcolonization model species 1 is dominant (called superior), and it can colonize any other patches at the same rate even they are occupied by species 2. Meanwhile,

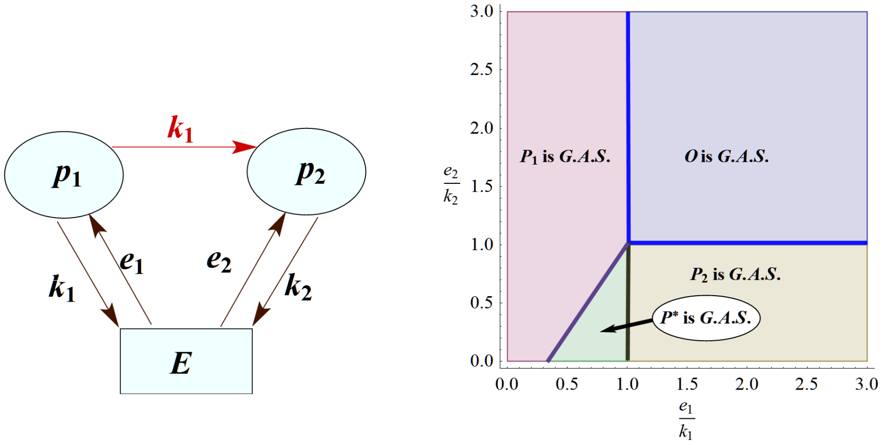


FIGURE 2. Hierarchic overcolonization: interactions and attractivity domains on the parameter space $\left\{\frac{e_1}{k_1}, \frac{e_2}{k_2}\right\}$ at $\frac{k_1}{k_2} = 0.5$

species 2 (called inferior) can colonize only empty patches (Fig. 2). We can formulate the hierarchical overcolonization model as

$$\begin{aligned} p_1' &= k_1 p_1 (1 - p_1) - e_1 p_1, \\ p_2' &= k_2 p_2 (1 - p_1 - p_2) - k_1 p_1 p_2 - e_2 p_2, \end{aligned} \tag{1.3}$$

where all the notations are the same as before. Three boundary equilibria can exist: the trivial (0, 0) and two other $\left(1 - \frac{e_1}{k_1}, 0\right)$ and $\left(0, 1 - \frac{e_2}{k_2}\right)$ when one species survives and the other dies out. There can appear a G.A.S. interior equilibrium $\left(\frac{-k_1(e_2+k_1)+e_1(k_1+k_2)}{k_1 k_2}, 1 - \frac{e_1}{k_1}\right)$. For more hierarchically competing species the existence of such coexisting equilibrium is also proved [5, 15]. The properties are summarized in Table 2. The global dynamics of the system can be easily seen on the second part of Fig. 2 (the domains depend on the parameters). Note that the concerned equilibria coincide at the common borders of the domains.

Equilibrium	*Exists*	*G.A.S.*	*Unstable*
$O = (0, 0)$	always	$1 \leq \frac{e_1}{k_1}$ and $1 \leq \frac{e_2}{k_2}$	otherwise
$P_1 = \left(1 - \frac{e_1}{k_1}, 0\right)$	$\frac{e_1}{k_1} < 1$	$\frac{e_1}{k_1} \leq \frac{k_1+e_2}{k_1+k_2}$	otherwise
$P_2 = \left(0, 1 - \frac{e_2}{k_2}\right)$	$\frac{e_2}{k_2} < 1$	$1 \leq \frac{e_1}{k_1}$	otherwise
$P^* = \left(\frac{e_1(k_1+k_2)-k_1(e_2+k_1)}{k_1 k_2}, 1 - \frac{e_1}{k_1}\right)$	$\frac{k_1+e_2}{k_1+k_2} < \frac{e_1}{k_1} < 1$	always	–

TABLE 2. Summary of attractivity properties of system (1.3)

In our paper we release strict hierarchy between the competing species and allow reciprocal overcolonization. We define a general overcolonization model of two species. Then, we consider the local asymptotic stability properties of the the equilibria and

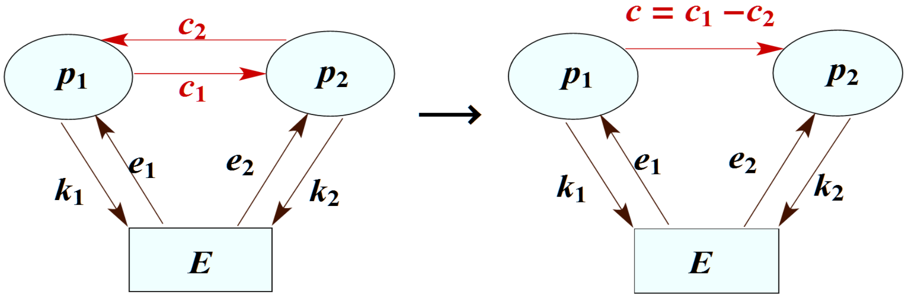


FIGURE 3. The general overcolonization model

investigate the globality of them. Finally, we give examples by some interactive applications developed in Wolfram *Mathematica*.

2. GENERAL OVERCOLONIZATION

Let us modify the model (1.3) by introducing reciprocal overcolonization as Fig. 3 shows. The model equations are

$$\begin{aligned} p_1' &= k_1 p_1 (1 - p_1 - p_2) - e_1 p_1 + c_1 p_1 p_2 - c_2 p_1 p_2, \\ p_2' &= k_2 p_2 (1 - p_1 - p_2) - e_2 p_2 - c_1 p_1 p_2 + c_2 p_1 p_2, \end{aligned}$$

where the meaning of $p_1, p_2, k_1, k_2, e_1, e_2$ is as before. In addition, c_1 and c_2 are the global rates of overcolonization of species 1 and 2, respectively. Without loss of generality, we can introduce $c = c_1 - c_2$, the relative overcolonization rate, and since the role of p_1, p_2 is symmetrical, we can assume $c \geq 0$, i.e., species 1 is better at overcolonization than species 2. Thus, the model becomes

$$\begin{aligned} p_1' &= k_1 p_1 (1 - p_1 - p_2) - e_1 p_1 + c p_1 p_2, \\ p_2' &= k_2 p_2 (1 - p_1 - p_2) - e_2 p_2 - c p_1 p_2. \end{aligned} \tag{2.1}$$

Although the model itself looks quite simple, its dynamics is not trivial. Note that similar simple compartmental networks are also widely used in epidemiology. An analogous system is studied by Röst and Dénes in [16].

Obviously, the region D is invariant for system (2.1). Apart from some singular cases, the system can have four equilibria: the trivial boundary equilibrium $O = (0, 0)$ when both species die out; two non-trivial boundary equilibria $P_1 = \left(1 - \frac{e_1}{k_1}, 0\right)$ and $P_2 = \left(0, 1 - \frac{e_2}{k_2}\right)$ when one of the species survives the other one dies out. If $c\,(c - k_1 + k_2) \neq 0$, an interior equilibrium $P^* = \left(\frac{e_2 k_1 - e_1 k_2 + c(-e_2 + k_2)}{c(c - k_1 + k_2)}, \frac{c(e_1 - k_1) - e_2 k_1 + e_1 k_2}{c(c - k_1 + k_2)}\right)$ can also appear, when the two species coexist.

If $c = 0$, the interior equilibrium does not exist and we obtain system (1.2) without any interaction between the competitors.

The hierarchic model (1.3) is also a special case of system (2.1) with $c = k_1$. Note that in (2.1) $c > k_1$ can happen, i.e., overcolonization can be more intensive than colonizing empty patches.

If $c = k_1 - k_2$, system (2.1) would take the form

$$\begin{aligned} p_1' &= k_1 p_1 \left(1 - p_1 - \tfrac{k_2}{k_1} p_2\right) - e_1 p_1, \\ p_2' &= k_2 p_2 \left(1 - \tfrac{k_1}{k_2} p_1 - p_2\right) - e_2 p_2. \end{aligned} \tag{2.2}$$

The behavior is the same as of system (1.2). Either no interior equilibrium exists or, if in addition $c = e_1 - e_2$, every point of the line $p_2 = -p_1 \left(\frac{c}{k_2} + 1\right) + 1 - \frac{e_2}{k_2}$ is a stable equilibrium.

In this paper we are mainly interested in the properties of P^*, hence we can assume that $c > 0$ and $c \neq k_1 - k_2$.

Concerning the asymptotic properties of equilibria, the absence of periodic solutions is a useful information. Using the Poincaré-Bendixson theory [2] the following lemma holds.

Lemma 2.1. *System* (2.1) *does not have any periodic solution in the domain* $D = \{(p_1, p_2) : p_1 \geq 0, p_2 \geq 0, p_1 + p_2 \leq 1\}$.

Proof. Let f_1 and f_2 denote the right hand sides of the equations of (2.1) and let $B(p_1, p_2) = \frac{1}{p_1 p_2}$ be the so called Dulac function. Then, for $p_1, p_2 > 0$:

$$\frac{\partial}{\partial p_1}(B f_1) + \frac{\partial}{\partial p_2}(B f_2) =$$

$$\frac{\partial}{\partial p_1}\left(\frac{k_1}{p_2} - \frac{k_1 p_1}{p_2} - k_1 - \frac{e_1}{p_2} + c\right) + \frac{\partial}{\partial p_2}\left(\frac{k_2}{p_1} - \frac{k_2 p_2}{p_1} - k_2 - \frac{e_2}{p_1} - c\right) = -\frac{k_1}{p_2} - \frac{k_2}{p_1} < 0$$

Thus, the Bendixson-Dulac theorem [2] guarantees that system (2.1) has no periodic solutions in the region $p_1 > 0$, $p_2 > 0$. Finally, it is obvious that solutions are monotonic on the axes. Thus, the lemma is proved. □

3. ASYMPTOTIC STABILITY OF BOUNDARY EQUILIBRIA

Now, let us consider the local dynamics of the system around the boundary equilibria. In most of the proofs of asymptotic stability, we use the method linear approximation [10].

Theorem 3.1. *The trivial boundary equilibrium* $O = (0, 0)$ *always exists. It is globally asymptotically stable if* $1 \leq \frac{e_1}{k_1}$ *and* $1 \leq \frac{e_2}{k_2}$. *It is unstable if either* $\frac{e_1}{k_1} < 1$ *or* $\frac{e_2}{k_2} < 1$.

Proof. Since $0 \leq p_1$, $0 \leq p_2$ and $p_1 + p_2 \leq 1$ are always true, the trivial boundary equilibrium $O = (0, 0)$ always exists. The Jacobian of system (2.1) at O is $\begin{pmatrix} k_1 - e_1 & 0 \\ 0 & k_2 - e_2 \end{pmatrix}$ with eigenvalues $k_1 - e_1$ and $k_2 - e_2$. If they are negative, that is if $1 < \frac{e_1}{k_1}$ and $1 < \frac{e_2}{k_2}$ then O is asymptotically stable. If either $\frac{e_1}{k_1} < 1$ or $\frac{e_2}{k_2} < 1$ then the O is unstable.

Using the function $V(p_1, p_2) = p_1 + p_2$ as Lyapunov function, the asymptotic stability of O can be easily proved under the weaker conditions $\frac{e_1}{k_1} \geq 1, \frac{e_2}{k_2} \geq 1$. The derivative of V with respect to (2.1) is

$$\begin{aligned}\dot{V}(p_1, p_2) &= -(e_1 - k_1)p_1 - (e_2 - k_2)p_2 - (p_1 + p_2)(k_1 p_1 + k_2 p_2)\\ &\leq -\min(k_1, k_2)\, V(p_1, p_2)^2,\end{aligned}$$

and it holds globally. Hence the theorem is proved. □

Theorem 3.2. I. *The equilibrium* $P_1 = \left(1 - \frac{e_1}{k_1}, 0\right)$ *exists and nontrivial if* $\frac{e_1}{k_1} < 1$.

II. *In addition,* P_1 *is locally asymptotically stable if* $\frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$.

III. *In the special case* $\max(0, k_1 - k_2) < c$, P_1 *is locally asymptotically stable if* $\frac{e_1}{k_1} \leq \frac{c+e_2}{c+k_2}$.

IV. *Otherwise,* P_1 *is unstable.*

Proof. As $0 \leq p_1$, $0 \leq p_2$, $p_1 + p_2 \leq 1$, and all the parameters are positive, P_1 exists and nontrivial if $\frac{e_1}{k_1} < 1$. The Jacobian of (2.1) at P_1 is $\begin{pmatrix} e_1 - k_1 & c + e_1 - \frac{ce_1}{k_1} - k_1 \\ 0 & \frac{ce_1 - ck_1 - e_2k_1 + e_1k_2}{k_1} \end{pmatrix}$ with negative eigenvalues $e_1 - k_1$ and $\frac{ce_1 - ck_1 - e_2k_1 + e_1k_2}{k_1}$. By doing some arithmetics, the negativity of the second one follows from the condition $\frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$, and hence P_1 is asymptotically stable. On the other hand, if any of the eigenvalues is positive, i.e. either $\frac{e_1}{k_1} > 1$ or $\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1}$, then P_1 is unstable. In the critical case $\frac{e_1}{k_1}$=1, this equilibrium coexists with O.

Characterizing the special case $\frac{c+e_2}{c+k_2} = \frac{e_1}{k_1}$ needs further study. Expressing e_2 from this equality and substituting into system (2.1), we obtain that the system has only the equilibria O, P_1, P_2. The Jacobian at P_1 is obviously singular, but the eigenvalues of it at O are $-e_1+k_1$ and $\left(1 - \frac{e_1}{k_1}\right)(c + k_2)$ which are positive. Hence O is unstable. What concerns P_2, the eigenvalues of the Jacobian are $\left(\frac{e_1}{k_1} - 1\right)(c + k_2)$ and $\left(1 - \frac{e_1}{k_1}\right)\frac{c\,(c-k_1+k_2)}{k_2}$. The first one is negative, but the second one is positive provided $c > 0$ and $c > k_1 - k_2$. As the region D is invariant, Poincaré-Bendixson theorem and Lemma 2.1 implies that at least one of the equilibria must be asymptotically stable. Consequently, if $c > \max(0, k_1 - k_2)$, $\frac{e_1}{k_1} < 1$ and $\frac{c+e_2}{c+k_2} = \frac{e_1}{k_1}$, P_1 is asymptotically stable. □

Note that the condition $\frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$ is more restrictive than $\frac{e_1}{k_1} < 1$ only if $\frac{e_2}{k_2} < 1$, i.e., species 2 does not die out in itself.

Theorem 3.3. I. *The equilibrium* $P_2 = \left(0, 1 - \frac{e_2}{k_2}\right)$ *exists and nontrivial if* $\frac{e_2}{k_2} < 1$.

II. *In addition,* P_2 *is locally asymptotically stable if* $\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} < \frac{e_1}{k_1}$.

III. *In the special case* $\max(0, k_1 - k_2) < c$, P_2 *is locally asymptotically stable if* $\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} \leq \frac{e_1}{k_1}$.

IV. *Otherwise,* P_2 *is unstable.*

Proof. For the existence and the stability of the boundary equilibrium P_2 the proof is similar to P_1. The Jacobian matrix of the system at P_2 is $\begin{pmatrix} \frac{ck_2 - e_1k_2 + e_2k_1 - e_2c}{k_2} & 0 \\ \frac{(e_2 - k_2)(k_2 + c)}{k_2} & e_2 - k_2 \end{pmatrix}$ with eigenvalues $\frac{ck_2 - e_1k_2 + e_2k_1 - e_2c}{k_2}$ and $e_2 - k_2$. The second one is negative as $\frac{e_2}{k_2} < 1$. The first one is negative provided $\frac{e_2(k_1 - c)}{k_2} < e_1 - c$, what is equivalent with the condition of the theorem.

The special case $\frac{e_1}{k_1} = \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$ can be considered similarly to Theorem 3.2. Expressing e_1 from this equality and substituting into (2.1), we obtain that the equilibria O, P_1, P_2 may exist (P_1 exists only if $c < k_1$). Since $e_2 < k_2$, O is unstable. The eigenvalues of the Jacobian at P_1 are $\frac{(c-k_1)(k_2-e_2)}{k_2}$ and $\frac{c(k_2-e_2)(c-k_1+k_2)}{k_1k_2}$. The first one is negative, but the second one is positive provided $c > 0$ and $c > k_1 - k_2$. As the region D is invariant, the Poincaré-Bendixson theorem and Lemma 2.1 implies that at least one of the equilibria, namely P_2 must be asymptotically stable. Consequently, if $c > \max(0, k_1 - k_2)$, $\frac{e_1}{k_1} < 1$ and $\frac{e_1}{k_1} = \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$, P_2 is asymptotically stable. ☐

Remember that species 2 is weaker than species 1 in overcolonization. Hence, reordering condition $\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} < \frac{e_1}{k_1}$, we have $\frac{e_2}{k_2} + \left(1 - \frac{e_2}{k_2}\right)\frac{c}{k_1} < \frac{e_1}{k_1}$ that shows that its relative extinction ratio $\frac{e_2}{k_2}$ must be definitely smaller than that of species 1 to survive (even win in the competition).

4. INTERIOR EQUILIBRIUM

The interior equilibrium of system (2.1) is the solution of the linear system

$$k_1(1 - p_1 - p_2) - e_1 + cp_2 = 0,$$

$$k_2(1 - p_1 - p_2) - e_2 - cp_1 = 0,$$

and it takes the form

$$P^* = (p_1^*, p_2^*) = \left(\frac{c(k_2 - e_2) + e_2k_1 - e_1k_2}{c(c - k_1 + k_2)}, \frac{c(e_1 - k_1) - e_2k_1 + e_1k_2}{c(c - k_1 + k_2)}\right) \tag{4.1}$$

The following theorem holds.

Theorem 4.1. I. *If,* $\max(0, k_1 - k_2) < c$, *and* $\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$ *then the interior equilibrium* $P^* = (p_1^*, p_2^*)$ *exists (satisfies* $p_1^* > 0$, $p_2^* > 0$*) and is locally asymptotically stable.*

II. *If* $0 < c < k_1 - k_2$ *and* $\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} < \frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$ *then* P^* *exists and unstable.*

Proof.

Existence: Assume that $c > 0$ and $c > k_1 - k_2$. Now to have $p_1^* > 0$, $p_2^* > 0$ and $p_1^* + p_2^* \leq 1$ the conditions $e_2k_1 - e_1k_2 + c\,(-e_2 + k_2) > 0$, $c\,(e_1 - k_1) - e_2k_1 + e_1k_2 > 0$ and $\frac{(e_1-k_1)-(e_2-k_2)}{c-(k_1-k_2)} \leq 1$ must hold. These inequalities become $\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1}$, $\frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$, and $e_1 \leq c + e_2$, respectively.

Remember that the first two inequalities appear as conditions for instability of P_1 and P_2.

Using $c > k_1 - k_2$, we obtain $\frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} = \frac{e_2}{k_2}\left(\frac{k_1-c}{k_1}\right) + \frac{c}{k_1} < \frac{e_2}{k_2}\frac{k_2}{k_1} + \frac{c}{k_1} = \frac{e_2+c}{k_1}$, and hence the inequality $e_1 \leq c + e_2$ is needless.

In case of $c < k_1 - k_2$ the proof is similar.

Stability: The Jacobian of the system at P^* is

$$J_{P^*} = \begin{pmatrix} \frac{k_1(c(e_2-k_2)-e_2k_1+e_1k_2)}{c(c-k_1+k_2)} & \frac{(c-k_1)(c(k_2-e_2)+e_2k_1-e_1k_2)}{c(c-k_1+k_2)} \\ \frac{(c+k_2)(c(k_1-e_1)+e_2k_1-e_1k_2)}{c(c-k_1+k_2)} & \frac{k_2(c(k_1-e_1)+e_2k_1-e_1k_2)}{c(c-k_1+k_2)} \end{pmatrix} \tag{4.2}$$

(calculations are done with Wolfram *Mathematica*). It is quite difficult to directly estimate the real part of the eigenvalues. Instead, take the benefit of the fact that $\det(J_{P^*}) = v_1v_2$ and $\operatorname{tr}(J_{P^*}) = v_1 + v_2$. Obviously, if $\det(J_{P^*}) > 0$ and $\operatorname{tr}(J_{P^*}) < 0$ then the real parts of both eigenvalues are negative. If any of these inequalities turns to the opposite direction, the real part of at least one of the eigenvalues is positive. Note that this idea is generalized in [8, 9] using the so called second compound matrices.

The determinant of the Jacobian (4.2) is

$$\frac{-\left(e_2k_1 - e_1k_2 + c\,(k_1 - e_1)\right)\left(e_2k_1 - e_1k_2 + c\,(k_2 - e_2)\right)}{c\,(c - k_1 + k_2)}, \tag{4.3}$$

and the trace is

$$\frac{e_2k_1 - e_1k_2}{c}.$$

Case $\max(0, k_1 - k_2) < c$: The determinant (4.3) is negative if

$$\left(e_2k_1 - e_1k_2 + c\,(k_1 - e_1)\right)\left(e_2k_1 - e_1k_2 + c\,(k_2 - e_2)\right) < 0.$$

Thus either $c\,(e_1 - k_1) < e_2k_1 - e_1k_2 < c\,(e_2 - k_2)$ or $c\,(e_2 - k_2) < e_2k_1 - e_1k_2 < c\,(e_1 - k_1)$, that is $\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} < \frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$ or $\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$ must hold. The first inequality contradicts to the conditions of the existence of the equilibrium thus $\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$ hold.

The trace of the Jacobian is negative if $\frac{e_2}{k_2} < \frac{e_1}{k_1}$, but this follows from the previous enequality. If $\frac{e_1}{k_1} \leq 1$, then $\frac{c+e_2}{c+k_2} < 1$ what implies $\frac{e_2}{k_2} < \frac{c+e_2}{c+k_2}$ and hence $\frac{e_2}{k_2} < \frac{e_1}{k_1}$. If $\frac{e_1}{k_1} > 1$, then $1 < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$, and hence $k_1 - c < \frac{e_2}{k_2}(k_1 - c)$. If $k_1 > c$, then $\frac{e_2}{k_2} > 1$ would hold. However it is impossible, since $\frac{e_1}{k_1}, \frac{e_2}{k_2} > 0$ contradicts to the existence of P^*. Hence $k_1 < c$ and $1 > \frac{e_2}{k_2}$ hold, what implies $\frac{e_2}{k_2} < \frac{e_1}{k_1}$.

Case $0 < c < k_1 - k_2$: The conditions of stability become $(e_2k_1 - e_1k_2 + c\,(k_1 - e_1))$ $(e_2k_1 - e_1k_2 + c\,(k_2 - e_2)) > 0$ and $\frac{e_2}{k_2} < \frac{e_1}{k_1}$. Thus $\max\{c\,(e_1 - k_1)\,, c\,(e_2 - k_2)\} < e_2k_1 - e_1k_2$ or $e_2k_1 - e_1k_2 < \min\{c\,(e_1 - k_1)\,, c\,(e_2 - k_2)\}$ must hold. These inequalities contradict to the conditions of the existence of the equilibrium. Thus in case of $0 < c < k_1 - k_2$ the equilibrium P^* exists but unstable. □

5. GLOBAL DYNAMICS

We can see that in the case $\max(0, k_1 - k_2) < c$, the conditions of asymptotic stability of equlibria are disjoint, and they cover the whole positive quadrant of the $\left\{\frac{e_1}{k_1}, \frac{e_2}{k_2}\right\}$ parameter space. Hence, at a given parameter combination, exactly one of the equilibria is asymptotically stable on the simply connected domain D. Since we excluded the existence of periodic solutions for system (2.1), the Poincaré-Bendixson theorem implies that the asymptotic stability of this equilibrium is global.

On the other hand, if $0 < c < k_1 - k_2$ the asymptotic stability conditions for P_1 and P_2 overlap each other. There is a domain where both are asymptotically stable and both the trivial and the interior equilibrium is unstable. Hence the following corollary holds:

Corollary 5.1. I. *Case* $\max(0, k_1 - k_2) < c$*: one of the equilibria* O, P_1, P_2, P^* *is globally asymptotically stable and the others are unstable.*

II. *Case* $0 < c < k_1 - k_2$*: if the interior equilibrium* P^* *exists, then it is unstable,* O *is unstable and both* P_1 *and* P_2 *equilibria are locally asymptotically stable. If* P^* *does not exists, one of* O, P_1, P_2 *is globally asymptotically stable.*

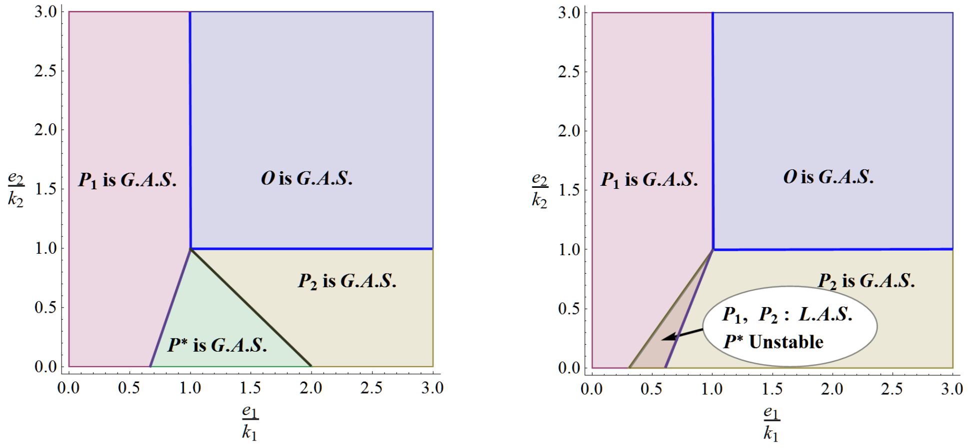
The attractivity conditions can be shown on the parameter space $\left\{\frac{e_1}{k_1}, \frac{e_2}{k_2}\right\}$. Obviously, the attractivity domains (except for $O = (0, 0)$) change according to the values of k_1, k_2 and c.

Asymptotic stability in the case $\max(0, k_1 - k_2) < c$ can be seen in Fig. 4 (a) and Table 3. Observe that due to the stronger overcolonization strategy, species 1 can coexist with species 2 even if $\frac{e_1}{k_1} \geq 1$.

Asymptotic stability properties in the case $0 < c < k_1 - k_2$ are similar to the case with absence of overcolonization, but the dynamics is more complex. It can be seen in Fig. 4 (b) and Table 4. In most cases only the boundary equilibria O, P_1, P_2 exist and one of them is G.A.S., but on a narrow parameter domain an unstable P^* appears and then the result of the competition depends on the initial values.

6. EXAMPLES AND COMPUTER EXPERIMENTS

To verify the conditions and investigate the properties of the system interactively, we have prepared a dynamic application in Wolfram *Mathematica* (available at our website [1]). Here we show some snapshots to illustrate different cases.



(a) (b)

FIGURE 4. Parameter space with the stability of coexistence: (a) The case $\max(0, k_1 - k_2) < c$ with stable coexistence ($k_1 = 0.2, k_2 = 0.2, c = 0.4$); (b) The case $0 < c < k_1 - k_2$ with unstable coexistence ($k_1 = 1, k_2 = 0.2, c = 0.3$)

Equilibrium	*Exists*	*G.A.S.*	*Unstable*
O	always	$1 \le \frac{e_1}{k_1}$ and $1 \le \frac{e_2}{k_2}$	otherwise
P_1	$\frac{e_1}{k_1} < 1$	$\frac{e_1}{k_1} \le \frac{c+e_2}{c+k_2}$	otherwise
P_2	$\frac{e_2}{k_2} < 1$	$\frac{e_1}{k_1} \ge \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$	otherwise
P^*	$\frac{c+e_2}{c+k_2} < \frac{e_1}{k_1} < \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$	when P^* exists	never

TABLE 3. Summary of attractivity properties in the case $\max(0, k_1 - k_2) < c$

Equilibrium	*Exists*	*A.S.*	*G.A.S.*	*Unstable*
O	always	$1 \le \frac{e_1}{k_1}$ and $1 \le \frac{e_2}{k_2}$	if A.S.	otherwise
P_1	$\frac{e_1}{k_1} < 1$	$\frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$	$\nexists P^*$	otherwise
P_2	$\frac{e_2}{k_2} < 1$	$\frac{e_1}{k_1} > \frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1}$	$\nexists P^*$	otherwise
P^*	$\frac{e_2}{k_2}\left(1 - \frac{c}{k_1}\right) + \frac{c}{k_1} < \frac{e_1}{k_1} < \frac{c+e_2}{c+k_2}$	–	–	always

TABLE 4. Summary of attractivity properties in the case $0 < c < k_1 - k_2$

First consider, the case of large overcolonization $c > 0$, $k_1 - k_2 < c$, see Fig. 5. The parameter space $\left\{\frac{e_1}{k_1}, \frac{e_2}{k_2}\right\}$ contains four disjoint domains. Let us present parameter combinations with different development. It is obvious that although species 1 is weaker both at dispersal and survivor than species 2, however species 1 can survive

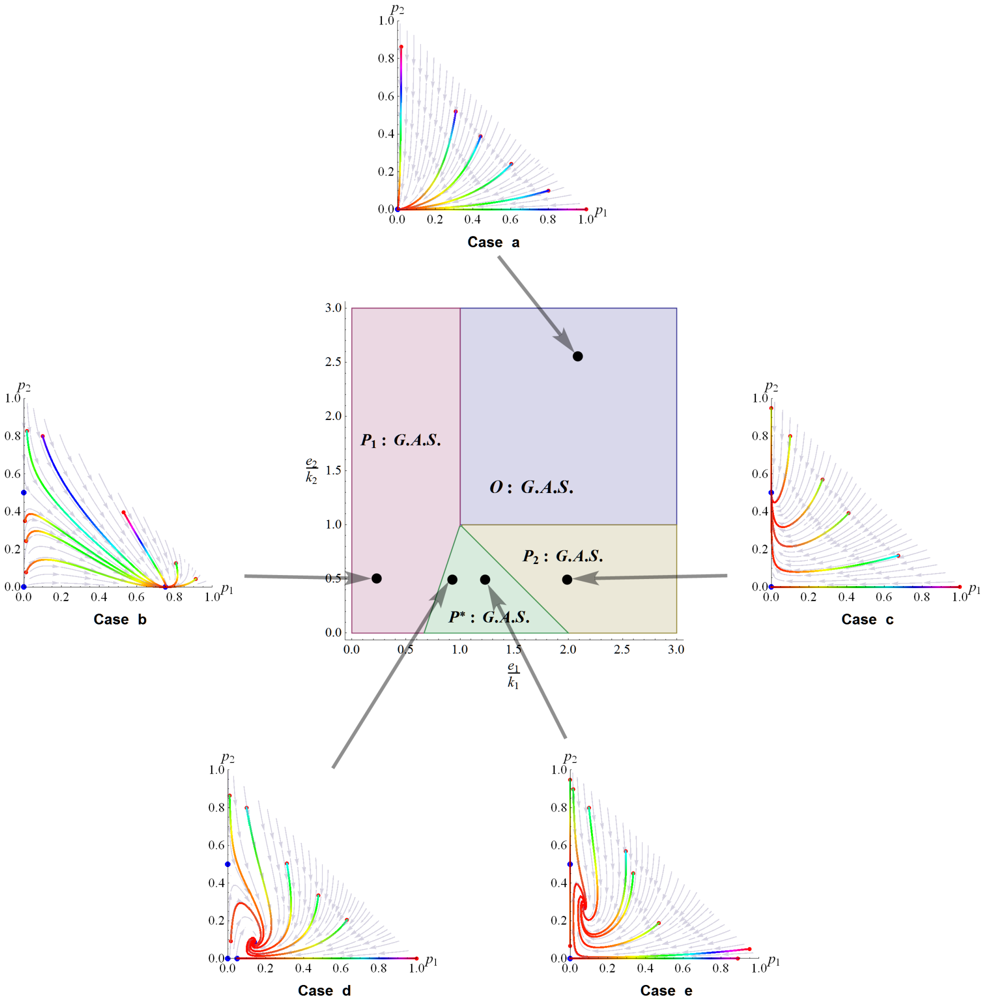
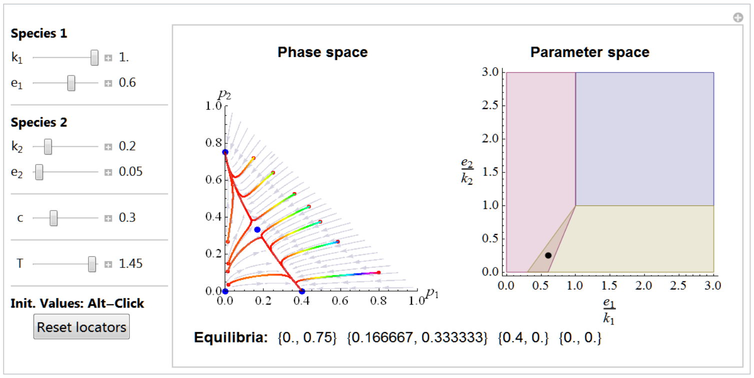


FIGURE 5. Large overcolonization $k_1 = k_2 = 0.2, c = 0.4$: Case a: $e_1 = 0.4, e_2 = 0.5$; Case b: $e_1 = 0.4, e_2 = 0.1$; Case c: $e_1 = 0.05, e_2 = 0.1$; Case d: $e_1 = 0.18, e_2 = 0.1$; Case e: $e_1 = 0.24, e_2 = 0.1$.

because of its dominance in overcolonization. In *Case a* both species die out. In *Case b* species 1 wins the competition as a result of effective overcolonization. Without overcolonization the species 2 would win the competition (as in Fig. 1). In *Case c* species 2 wins the competition. In *Case e* the competing species coexist, although species 1 would die out without species 2. Observe that P_1 does not exists in this example. A similar behavior with existing unstable P_1 can be seen at *Case d*.

Finally, consider the case of small overcolonization $0 < c < k_1 - k_2$. Here we present only the case where the interior equilibrium is unstable. The other cases are similar to the corresponding ones at large overcolonization. Fig. 6 contains the full view of the dynamic demonstration prepared in Wolfram *Mathematica*.



Species 1

k1 1.

e1 0.6

Species 2

k2 0.2

e2 0.05

c 0.3

T 1.45

Init. Values: Alt–Click

Equilibria: {0., 0.75} {0.166667, 0.333333} {0.4, 0.} {0., 0.}

FIGURE 6. Small overcolonization with unstable coexistence: $k_1 = 1, k_2 = 0.2, c = 0.3, e_1 = 0.6, e_2 = 0.05$.

7. SUMMARY

Our metapopulation model with overcolonization can be considered as the most general extension of Levins model for two species. In the cases $c = 0$ or $c = k_1$ we obtain the known models (see the Introduction (1.2) and (1.3)).

We have shown that a stable interior equilibrium can exist only if there is large enough asymmetric interaction between species. Otherwise, it either does not exist or is unstable and the outcome of the system depends on the density of the competing species. Relation of difference in ability of empty patch colonization $k_1 - k_2$ and the net overcolonization plays important role in determining existence of G.A.S. equilibria in parameter space.

Metapopulation based models have been being successfully used in several conservation biological and ecological problems, henceforward they still provide opportunities to further investigation and applications. A general n species model, where $n \geq 2$, the competition can be described as follows:

$$p_i' = k_i p_i \left(1 - \sum_{j=1}^{n} p_j\right) + \sum_{j \neq i} c_i p_i p_j - \sum_{j \neq i} c_j p_i p_j - e_i p_i, (i = 1, 2, ..., n),$$

where $p_i = p_i(t)$ is the proportion of occupied patches at time t for species i where $0 \leq p_i$, $i = 1, \ldots, n$; $\sum_{i=1}^{n} p_i \leq 1$; $k_i, c_i, e_i \geq 0$, are the global colonization, overcolonization and extinction rates of species i, respectively $(i = 1, \ldots, n)$.

Based on previous works [13, 14], our further research will concern the generalizations to n-species as well as spatial explicit analogues, e.g. cellular automata and partial differential equations.

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