Coexistence of competitors in deterministic and stochastic patchy environments

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The spatial component of ecological interactions plays an important role in shaping ecological communities. A crucial ecological question is how do habitat disturbance and fragmentation affect species persistence and diversity? In this paper, we develop a deterministic metapopulation model that takes into account a time-dependent patchy environment, thus our model and analysis take into account environmental changes. We investigate the effects that spatial variations have on persistence and coexistence of two competing species. In particular, we study the local behaviour of the model, and we provide a rigorous proof for the global analysis of our model. Also, we compare the results of the deterministic model with simulations of a stochastic version of the model.

Keywords: metapopulation; patch dynamics; species competition; coexistence; stochasticity

1. Introduction

Understanding the impact of space on species coexistence is a major topic in theoretical and experimental ecology studies [23]. Over the past decades, lots of mathematical models have been used to study the impact of spatial heterogeneity on population dynamics of systems of interacting species (see, e.g. [6,8,14,30,35]). These studies have demonstrated that spatial structure is at least as important as birth and death processes, competition, or predation [35]. For example, spatial structure is known to allow two competing species to coexist [30]; stabilize predator–prey dynamics [9,14], and influence the evolution of cooperative behaviour [24].

There are several ways of incorporating spatial heterogeneity or patchiness into population models [6]. Space is implicitly included in spatially structured metapopulation models, such as the Levins model [16]. These models focus on changes in patch occupancy as a function of

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rates of patch colonization and extinction. However, these models have no spatial dimension and portray patches as equally accessible to one another [26]. More recently, the spatially structured metapopulation models have been used extensively in studies of formation and conservation of biodiversity. Furthermore, extensions of these models have been used to describe multi-species intraspecific competition in patchy environments [6–8,30,35]. Metapopulation models are known to have many characteristics that are similar to those of epidermic models [4,5,20] if empty and occupied 'patches' are represented as susceptible and infected individuals, respectively. Therefore, some typical results and terminologies in epidemiology will be used in this paper.

In 1983, Hanski and Ranta [8] formulated a two-species model to study intraspecific competition in water fleas of the genus *Daphnia*. In their model, the rate of appearance of new habitable patches is assumed to be constant, and the dynamic process of patch destruction and recreation is ignored. In real systems, however, habitable patches may be destroyed while destroyed patches may become habitable again. The rates at which these events occur may depend on many factors including climate changes, environmental conditions, or human activities. Thus, to capture this biological reality, we include patch dynamics into our deterministic metapopulation model. Another major contribution of our study is that we provide a detailed analysis for the global stability of the system. Our analysis provides significant insights into the outcomes of species competition. The local stability analysis in Hanski and Ranta [8] is only applicable to special cases, and the stability conditions (based on the Routh–Hurwitz criteria) do not provide biological insights, and the conditions for coexistence are only verified by numerical simulations instead of a rigorous mathematical proof. It should be noted that the approaches used in this paper are very general and can be used to analyse the global dynamics of the model formulated in Hanski and Ranta [8].

Real biological systems are inevitably subject to stochastic interference. Demographic stochasticity and environmental stochasticity are two familiar types of stochasticity that may significantly affect a biological system. Demographic stochasticity is the temporal variance in population density caused by randomness in the reproduction and mortality of individuals [30], and environmental stochasticity is the stochastic variation in the physical and biological environment and thereby in the parameters affecting the system. Many epidemiological and ecological models with demographic or environmental stochasticity have been studied in the past few decades (see, e.g. [1,17–19,32]). In this paper, we incorporate such stochastic factors in our model and examine how these factors may influence the persistence and coexistence of two competing species.

The paper is organized as follows. In Section 2, we formulate the deterministic model. The model describes changes in the state of patches. Section 3 is focused on stability analysis of the deterministic model. We prove in Section 3, the local dynamics of the boundary steady states. Furthermore, we prove that under certain conditions on the 'invasion reproductive number' the model is uniformly persistent. That is, we obtain conditions that guarantee the coexistence of competing species in a deterministic patchy environment. In addition, we prove a global stability result for the deterministic model. In Section 4, we introduce two stochastic models that are based on the deterministic model. We investigate the impact of environmental stochasticity and demographic stochasticity on the persistence and coexistence of two competing species. We compare the dynamics of the deterministic model with that of two stochastic models. The paper ends with a brief discussion of our results in Section 5.

2. Deterministic model

Our deterministic model follows Levin's framework for metapopulation model, which in the case of a single species has the form

101
102

$$\frac{\mathrm{d}p(t)}{\mathrm{d}t} = cp(t)(1 - p(t)) - ep(t),$$

103 where $p(t)$ denotes the proportion of occupied patches at time t, c is the per capita colonization rate
104 of empty patches, and e is the per capita extinction rate of occupied patches. This model assumes
105 an infinite network of homogeneous patches and is spatially implicit. A classic result provided
106 by this model is that metapopulation persistence is possible if and only if the colonization rate
107 exceeds the critical threshold set by the extinction rate. This model has been extended to include
108 two interacting species [8,12,15,21,22] or multiple species [10,11,15,30].

109   Although our model has a similar structure as that in Hanski and Ranta [8], there are some key
110 differences between the two models. One of the most significant differences between their study
111 and ours lies in the biological insights obtained from the analytical results of the models. In terms
112 of the model structure, their model includes a per capita rate (ν) of pool (patch) disappearance
113 and a constant rate q of appearance of new pools (patches). Under this assumption, the total
114 number of pools (N) satisfies the equation $N'(t) = q - \nu N(t)$, and is asymptotically a constant
115 (q/ν). Our model assumes a constant per capita patch destruction rate d (i.e. the rate at which a
116 habitable patch becomes nonhabitable) and a constant per capita patch recreation rate r (i.e. the
117 rate at which an nonhabitable patch becomes habitable). Under this assumption, the number of
118 nonhabitable and habitable patches are time-dependent while the total number of patches remain
119 constant for all time.

120   The analytic results of the model in Hanski and Ranta [8] and our model include the stability
121 analysis of the nontrivial boundary equilibria (i.e. equilibria at which only one species is present).
122 It is pointed out in Hanski and Ranta [8] that the local stability conditions expressed by (6c) and
123 (6d) can be written down using the model parameters but they are uninformative. Consequently,
124 they considered only some special cases of the expression. Our model allows us to derive general
125 stability conditions for the system equilibria and are much more informative. Particularly, our
126 results can be used to compute the criteria for one species to invade a metapopulation in which
127 the other species has already established itself, as well as to examine the role of patch dynamics
128 (destruction and recreation) on species invasion and coexistence. Moreover, our analytical results
129 include both the local and the global stabilities of the nontrivial boundary equilibria as well as the
130 uniform persistence of the metapopulations of both species.

131   In our two-species metapopulation model, we divide the total number of patches into five
132 subtypes of patches. The fractions of these five types of patches are denoted by: u_0 for nonhabitable
133 patches (or destroyed); u_1 for habitable but empty (i.e. not colonized by either species); x for
134 patches occupied by species 1 only; y for patches occupied by species 2 only; and z for doubly
135 occupied patches (i.e. occupied by both species 1 and species 2). The transition diagram between
136 patch states is shown in Figure 1. Patch destruction occurs at a constant per capita rate d, and
137 nonhabitable patches can become habitable at a constant per capita rate r. Species i ($i = 1, 2$)
138 colonizes an empty patch at the per capita rate c_i, and it goes extinct in a patch absent of the
139 other species at the per capita rate e_i. A patch that is occupied by species i can be colonized by
140 species j ($j \neq i$) at the per capita rate $k_j c_i$ with $k_j \leq 1$ (which represents the assumption that the
141 colonization of a patch occupied by the other species is more difficult than the colonization of an
142 empty patch). If a patch is doubly occupied, then there may be an extra extinction rate $\epsilon_i \geq 0$ for
143 species i so that the total extinction rate is $e_i + \epsilon_i$. All our model parameters are nonnegative. The
144 definitions of all variables and parameters are summarized in Table 1. The model is described by
145 the following system of differential equations:

146

147      $$u_0' = -ru_0 + d(1 - u_0),$$

148

149      $$u_1' = ru_0 - c_1(x + z)u_1 - c_2(y + z)u_1 + e_1 x + e_2 y - du_1,$$

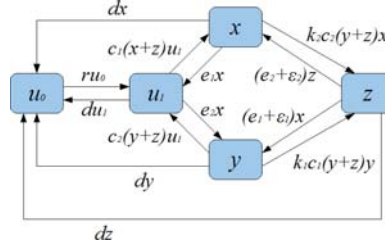150 $$x' = c_1(x + z)u_1 - (e_1 + d)x - k_{21}(y + z)x + (e_2 + \epsilon_2)z,$$

Figure 1.   Transition diagram between patch states. Nonhabitable patches and empty habitable patches correspond to u_0 and u_1, respectively. Patch dynamics are governed by destruction and creation rates d and r, respectively. Metapopulation dynamics are governed by colonization rates c_i and k_{ij} and extinction rates e_i and ϵ_i.

Table 1.   Model parameters.

Parameter	Description
c_i	Species i colonization rate of an empty patch
e_i	Species i extinction rate in a patch occupied by a single species
$e_i + \epsilon_i$	Species i extinction rate in a patch occupied by two species
$k_{ij} \in (0, 1)$	Species i colonization rate of a patch occupied by species j
d	Constant rate of patch destruction
r	Constant rate of patch creation

$$y' = c_2(y + z)u_1 - (e_2 + d)y - k_{12}(x + z)y + (e_1 + \epsilon_1)z,$$
$$z' = k_{21}c_2(y + z)x + k_{12}c_1(x + z)y - (e_1 + \epsilon_1 + e_2 + \epsilon_2 + d)z. \tag{1}$$

Using the fact that $u_0 + u_1 + x + y + z = 1$, we can ignore the u_0 equation in system (1) and consider the following equivalent four-dimensional system:

$$u_1' = r(1 - u_1 - x - y - z) - c_1(x + z)u_1 - c_2(y + z)u_1 + e_1x + e_2y - du_1,$$
$$x' = c_1(x + z)u_1 - (e_1 + d)x - k_{21}(y + z)x + (e_2 + \epsilon_2)z,$$
$$y' = c_2(y + z)u_1 - (e_2 + d)y - k_{12}(x + z)y + (e_1 + \epsilon_1)z,$$
$$z' = k_{21}c_2(y + z)x + k_{12}c_1(x + z)y - (e_1 + \epsilon_1 + e_2 + \epsilon_2 + d)z. \tag{2}$$

Our analytical results will be conducted using system (2).

Adding all the equations in system (2) yields

$$(u_1 + x + y + z)' = r - (r + d)(u_1 + x + y + z).$$

From the above equation, we know that $u_1(t) + x(t) + y(t) + z(t) \to p$ as $t \to +\infty$, where

$$p = \frac{r}{r + d} \tag{3}$$

represents the long-term proportion of habitable patches. Assume that the system has reached the asymptotic state, i.e.

$$u_1(t) + x(t) + y(t) + z(t) = p.$$

Then, the biologically feasible region for system (2) is

$$\Gamma = \{(u_1, x, y, z) : 0 \le u_1, x, y, z \le 1, \ u_1 + x + y + z = p\}.$$

It can be verified that Γ is positively invariant, and that the usual results on the existence and uniqueness of solutions as well as the continuation results hold. In the following sections, we restrict our analysis to solutions with initial conditions in Γ.

201 ## 3. Stability analysis
202
203 System (2) always has the trivial (species-free) equilibrium
204
205 $$E_0 = (p, 0, 0, 0).$$
206
207 There are two possible nontrivial boundary equilibria at which only one species is present:
208
209 $$E_1 = (\bar{u}_1, \bar{x}, 0, 0) \quad \text{and} \quad E_2 = (\tilde{u}_1, 0, \tilde{y}, 0),$$
210
211 where
212
213 $$\bar{u}_1 = \frac{e_1 + d}{c_1}, \quad \bar{x} = p - \frac{e_1 + d}{c_1}, \tag{4}$$
214
215 and
216
217 $$\tilde{u}_1 = \frac{e_2 + d}{c_2}, \quad \tilde{y} = p - \frac{e_2 + d}{c_2}. \tag{5}$$
218 Clearly, E_i is biologically feasible (i.e. the components are between 0 and 1) only if the following
219 quantities
220
221 $$\mathcal{R}_i = \frac{pc_i}{e_i + d} \quad \text{for } i = 1, 2, \tag{6}$$
222
223 are sufficiently large or more specifically, if the following conditions hold
224
225 $$\mathcal{R}_i > 1 \quad \text{for } i = 1, 2.$$
226
227 Note that c_i is the rate at which species i colonizes a habitable and empty patch, $1/(e_i + d)$ is
228 the mean time of patch occupancy by species i (in the absence of the other species), and p is
229 the long-term fraction of habitable patches. Thus, $\mathcal{R}_i$ gives the long-term expected 'reproduction
230 number' of species i in a landscape where the proportion of habitable patches is p.
231
232 ### 3.1. *Local stability and invasion criterion*
233
234 The following results show that the reproduction numbers $\mathcal{R}_1$ and $\mathcal{R}_2$ also determine the stabilities
235 of the equilibria E_i, $i = 0, 1, 2$.
236
237 THEOREM 1 *Let $\mathcal{R}_i$ be defined as in Equation (6). Then*
238
239 (i) *E_0 is globally asymptotically stable (g.a.s.) if $\mathcal{R}_i < 1$ for $i = 1, 2$, and it is unstable if*
240   *$\mathcal{R}_1 > 1$ or $\mathcal{R}_2 > 1$;*
241 (ii) *E_i is g.a.s. if and only if $\mathcal{R}_i > 1$ and $\mathcal{R}_j < 1$ for $i, j = 1, 2$ and $j \neq i$.*
242
243 *Proof* Proof of part (i). Since $k_1 < 1$, adding the second and fourth equations of system (2) gives
244
245 $$(x + z)' < (x + z)(c_1 p - (e_1 + d_1)).$$
246
247 From the above inequality and $\mathcal{R}_1 < 1$, we have $x(t) + z(t) \to 0$ as $t \to +\infty$; and thus, $x(t) \to 0$
248 and $z(t) \to 0$ as $t \to +\infty$. Similarly, it can be shown that if $\mathcal{R}_2 < 1$ then $y(t) \to 0$ and $z(t) \to 0$
249 as $t \to +\infty$. Therefore, if $\mathcal{R}_i < 1$ for $i = 1, 2$, then E_0 is globally asymptotically stable. This
250 completes the proof of part (i).

251   For the proof of part (ii), noticing the mathematical symmetry between species 1 and 2, we
252   only need to prove the results for the case of $i = 1$. From the proof of part (i), we know that if
253   $\mathcal{R}_2 < 1$ then $y(t) \to 0$ and $z(t) \to 0$ as $t \to +\infty$. Thus, the limiting system of (2) is

$$u_1' = r(1 - u_1 - x) - c_1 x u_1 + e_1 x - d u_1,$$
$$x' = c_1 x u_1 - (e_1 + d)x. \tag{7}$$

260   Let $E_{1l} = (\bar{u}_1, \bar{x})$ denote the nontrivial equilibrium of system (7). Then the stability of E_{1l} is
261   equivalent to the stability of E_1 for system (2). It is easy to show that E_{1l} is locally asymptotically
262   stable (l.a.s.) when $\mathcal{R}_1 > 1$. For the global stability of E_{1l}, let (f_1, f_2) be the vector field defined
263   by system (7). Then using the Dulac function $D(u_1, x) = u_1 x$ and noticing that $x < 1$, we have

$$\frac{\partial D f_1}{\partial u_1} + \frac{\partial D f_2}{\partial x} = -\frac{r}{u_1^2}\left(\frac{1}{x} - 1\right) - \frac{e}{u_1^2} < 0.$$

269   Thus, system (7) does not have a limit cycle. Notice that the trivial equilibrium $(u_1, x) = (0, 0)$
270   of system (7) is unstable as $\mathcal{R}_1 > 1$, and that E_{1l} is the only nontrivial equilibrium of system (7).
271   Therefore, E_{1l} is g.a.s. It follows that the boundary equilibrium E_1 of system (2) is g.a.s. Using
272   a similar argument, we can show that E_2 is g.a.s. when $\mathcal{R}_1 < 1$ and $\mathcal{R}_2 > 1$. This completes the
273   proof.   ∎

276   Next, we consider system (2) in the case of $\mathcal{R}_1 > 1$ and $\mathcal{R}_2 > 1$. In this case, both E_1 and E_2
277   exist. However, their stabilities will now depend on other conditions. In fact, these conditions can
278   be written in terms of the following quantities:

$$\mathcal{R}_{12} = \frac{1}{\Delta_1}((c_2 \bar{u} + k_2 c_2 \bar{x})(e_1 + e_2 + \epsilon_1 + d + k_1 c_1 \bar{x}) + \epsilon_2 c_2 \bar{u}), \tag{8}$$

$$\mathcal{R}_{21} = \frac{1}{\Delta_2}((c_1 \tilde{u} + k_1 c_1 \tilde{y})(e_1 + e_2 + \epsilon_2 + d + k_2 c_2 \tilde{y}) + \epsilon_1 c_1 \tilde{u}), \tag{9}$$

286   where

$$\Delta_1 = (e_2 + d)(e_1 + e_2 + \epsilon_1 + \epsilon_2 + d + k_1 c_1 \bar{x}) + \epsilon_2 k_1 c_1 \bar{x},$$
$$\Delta_2 = (e_1 + d)(e_1 + e_2 + \epsilon_1 + \epsilon_2 + d + k_2 c_2 \tilde{y}) + \epsilon_1 k_2 c_2 \tilde{y}.$$

292   The biological interpretations of the quantities $\mathcal{R}_{12}$ and $\mathcal{R}_{21}$ are given in Section 3.3.
293   The local stability results for E_i ($i = 1, 2$) are described in the following theorems.

296   THEOREM 2   *Let $\mathcal{R}_{12}$ and $\mathcal{R}_{21}$ be as defined in Equations (8) and (9), respectively.*

299   (a) *If $\mathcal{R}_{12} < 1$ ($\mathcal{R}_{12} > 1$) then the boundary equilibrium E_1 is l.a.s. (unstable).*
300   (b) *If $\mathcal{R}_{21} < 1$ ($\mathcal{R}_{21} > 1$) then the boundary equilibrium E_2 is l.a.s. (unstable).*

301 *Proof* Due to the mathematical symmetry between the two species, we only need to present a
302 proof for Part (a) of this theorem. The Jacobian matrix of system (2) at E_1 is

303
304
305 $$J_1 = \begin{pmatrix} -(r+d+c_1\bar{x}) & -(r+d) & -r-c_2\bar{u}_1+e_2 & -(r+c_1\bar{u}_1+c_2\bar{u}_1) \\ c_1\bar{x} & 0 & -k_2c_2\bar{x} & c_1\bar{u}_1-k_2c_2\bar{x}+e_2+\epsilon_2 \\ 0 & 0 & c_2\bar{u}_1-e_2-d-k_1c_1\bar{x} & c_2\bar{u}_1+e_1+\epsilon_1 \\ 0 & 0 & k_2c_2\bar{x}+k_1c_1\bar{x} & k_2c_2\bar{x}-(e_1+\epsilon_1+e_2+\epsilon_2+d) \end{pmatrix}.$$
306
307

308 The top-left 2×2 block matrix has two negative eigenvalues
309

310
311 $$\frac{1}{2}[-(r+d+c_1\bar{x}) \pm |r+d-c_1\bar{x}|].$$
312

313 For the bottom-right 2×2 block matrix, the trace is

314
315 $$A = c_2[p-(1-k_2)\bar{x}] - e_2 - d - k_1c_1\bar{x} - (e_1+\epsilon_1+e_2+\epsilon_2+d),$$

316 and the determinant is
317

318
319 $$B = [c_2(p-\bar{x}) - e_2 - d - k_1c_1\bar{x}][k_2c_2\bar{x} - (e_1+\epsilon_1+e_2+\epsilon_2+d)].$$

320 It can be shown that if $A > 0$ then $B < 0$. Thus, $B > 0$ implies that $A < 0$. We can also verify
321 (with extensive algebraic calculations) that $B > 0$ if and only if $\mathcal{R}_{12} < 1$. Therefore, E_1 is l.a.s.
322 if $\mathcal{R}_{12} < 1$, and it is unstable if $\mathcal{R}_{12} > 1$. This completes the proof of Part (a) of Theorem 2. Part
323 (b) can be proved in a similar way. ∎
324

325 The following theorem provides a result concerning the uniform persistence of both species,
326 i.e. there exists a constant $\delta > 0$, which is independent of initial data, such that
327

328 $$\liminf_{t\to+\infty} x(t) > \delta, \quad \liminf_{t\to+\infty} y(t) > \delta, \quad \liminf_{t\to+\infty} z(t) > \delta.$$
329

330 THEOREM 3 *If $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$, then system (2) is uniformly persistent and has a positive*
331 *equilibrium.*
332

333 *Proof* Define
334

335 $$X = \{(u_1, x, y, z) : u_1 \geq 0, \ x \geq 0, \ y \geq 0, \ z \geq 0\},$$

336
337 $$X_0 = \{(u_1, x, y, z) : u_1 > 0, \ x > 0, \ y > 0, \ z > 0\},$$

338 $$\partial X_0 = X \setminus X_0.$$
339

340 It suffices to show that system (2) is uniformly persistent with respect to $(X_0, \partial X_0)$ [34]. It is
341 easy to see that both X and X_0 are positively invariant. Clearly, ∂X_0 is relatively closed in X and
342 system (2) is point dissipative. Set
343

344 $$M_\partial = \{(u_1(0), x(0), y(0), z(0)) | (u_1(t), x(t), y(t), z(t)) \in \partial X_0, \ \forall t \geq 0\}$$

345 with $u_1(t), x(t), y(t), z(t)$ also satisfying Equation (2).
346 We first show that
347

348 $$M_\partial = B_1 \cup B_2, \tag{10}$$

349 where $B_1 = \{(u_1, x, y, z) \in \partial X : y \equiv 0, z \equiv 0\}$ and $B_2 = \{(u_1, x, y, z) \in \partial X : x \equiv 0, z \equiv 0\}$.
350 Let $(u_1(0), x(0), y(0), z(0)) \in M_\partial$. To show that Equation (10) holds, it suffices to show that

we have either $x(t) = 0$ and $z(t) = 0$, or $y(t) = 0$ and $z(t) = 0$ for all $t \geq 0$. Suppose this is not true. Then there exists a $t_0 \geq 0$ such that, without loss of generality, $x(t_0) > 0$, $y(t_0) > 0$, and $z(t_0) = 0$ (other cases can be discussed in the same way). Assume that $u_1(0) > 0$ (a reasonable assumption), then it follows that $u_1(t) > 0$ for all $t > 0$. Since

$$z'(t_0) \geq k_2 c_2 x(t_0) y(t_0) + k_1 c_1 x(t_0) y(t_0) > 0,$$

it follows that there is an ε_0 such that $z(t) > 0$ for $t_0 < t < t_0 + \varepsilon_0$. Clearly, we can restrict ε_0 to be small enough so that $x(t) > 0$, $y(t) > 0$, $z(t) > 0$, and $u_1(t_0) > 0$ for $t_0 < t < t_0 + \varepsilon_0$. This means that $(u_1(t), x(t), y(t), z(t)) \notin \partial X_0$ for $t_0 < t < t_0 + \varepsilon_0$, which contradicts the assumption that $(u_1(0), x(0), y(0), z(0)) \in M_\partial$. Hence, this shows that Equation (10) holds.

Using the same argument as in the proof of Theorem 1, we know that E_i is a global attractor in $B_i \setminus \{(p, 0, 0, 0)\}$ for system (2) $(i = 1, 2)$. It then follows that the set $\{E_0, E_1, E_2\}$ is isolated and is an acyclic covering in ∂X_0. By Theorem 4.6 in Thieme [29], we only need to show that $W^s(E_0) \cap X_0 = \emptyset$, $W^s(E_1) \cap X_0 = \emptyset$, and $W^s(E_2) \cap X_0 = \emptyset$ when $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$.

To show that $W^s(E_0) \cap X_0 = \emptyset$, we notice that the conditions $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$ imply that $\mathcal{R}_1 > 1$ and $\mathcal{R}_2 > 1$. Thus, we can choose δ small enough such that

$$c_1(p - \delta) - (e_1 + d) - 2k_2 c_2 \delta > 0. \tag{11}$$

Assume that $W^s(E_0) \cap X_0 \neq \emptyset$. Then there exists a positive solution $(\check{u}_1(t), \check{x}(t), \check{y}(t), \check{z}(t))$ with $(\check{u}_1(0), \check{x}(0), \check{y}(0), \check{z}(0)) \in X_0$ such that $(\check{u}_1(t), \check{x}(t), \check{y}(t), \check{z}(t)) \to E_0$ as $t \to +\infty$. Then, for t sufficiently large, we have $p - \delta < \check{u}_1(t) < p + \delta$, $0 < \check{x}(t) < \delta$, $0 < \check{y}(t) < \delta$, $0 < \check{z}(t) < \delta$, and

$$\check{x}'(t) = c_1(\check{x}(t) + \check{z}(t))\check{u}_1(t) - (e_1 + d)\check{x} - k_2 c_2(\check{y} + \check{z})\check{x} + (e_2 + \epsilon_2)\check{z}(t)$$

$$> (c_1(p - \delta) - (e_1 + d) - 2k_2 c_2 \delta)\check{x}(t).$$

Since $c_1(p - \delta) - (e_1 + d) - 2k_2 c_2 \delta > 0$ (from the inequality (11)), by the comparison principle [27] we have $\check{x}(t) \to +\infty$ as $t \to +\infty$. This contradicts $\check{x}(t) \to 0$ as $t \to +\infty$, implying that $W^s(E_0) \cap X_0 = \emptyset$.

We now show that $W^s(E_1) \cap X_0 = \emptyset$ when $\mathcal{R}_{12} > 1$. Since $\mathcal{R}_{12} > 1$ and hence $B < 0$, we can choose $\eta > 0$ small enough such that

$$\begin{vmatrix} c_2(\bar{u}_1 - \eta) - e_2 - d - k_1 c_1(\bar{x} + 2\eta) & c_2(\bar{u}_1 - \eta) + e_1 + \epsilon_1 \\ k_2 c_2(\bar{x} - \eta) + k_1 c_1(\bar{x} - \eta) & k_2 c_2(\bar{x} - \eta) - (e_1 + e_2 + \epsilon_1 + \epsilon_2 + d) \end{vmatrix} < 0. \tag{12}$$

Assume that $W^s(E_1) \cap X_0 \neq \emptyset$. Then there exists a positive solution $(\hat{u}_1(t), \hat{x}(t), \hat{y}(t), \hat{z}(t))$ with $(\hat{u}_1(0), \hat{x}(0), \hat{y}(0), \hat{z}(0))) \in X_0$ such that $(\hat{u}_1(t), \hat{x}(t), \hat{y}(t), \hat{z}(t)) \to E_1(\bar{u}_1, \bar{x}, 0, 0)$ as $t \to +\infty$. Thus, for t sufficiently large we have $\bar{u}_1 - \eta < \hat{u}_1(t) < \bar{u}_1 + \eta, 0 < \hat{x}(t) < \eta$, $0 < \hat{y}(t) \leq \eta$, $0 < \hat{z}(t) < \eta$, and

$$\hat{y}' \geq c_2(\hat{y} + \hat{z})(\bar{u}_1 - \eta) - (e_2 + d)\hat{y} - k_1 c_1(\bar{x} + \eta)\hat{y} + (e_1 + \epsilon_1)\hat{z},$$

$$\hat{z}' \geq k_2 c_2(\bar{x} - \eta)(\hat{y} + \hat{z}) + k_1 c_1(\bar{x} - \eta)\hat{y} - (e_1 + \epsilon_1 + e_2 + \epsilon_2 + d)\hat{z}.$$

Consider the following auxiliary system

$$y' = c_2(y + z)(\bar{u}_1 - \eta) - (e_2 + d)y - k_1 c_1(\bar{x} + \eta)y + (e_1 + \epsilon_1)z,$$

$$z' = k_2 c_2(\bar{x} - \eta)(y + z) + k_1 c_1(\bar{x} - \eta)y - (e_1 + \epsilon_1 + e_2 + \epsilon_2 + d)z. \tag{13}$$

The coefficient matrix $\hat{J}$ of system (13) is given by

$$\hat{J} = \begin{pmatrix} c_2(\bar{u}_1 - \eta) - e_2 - d - k_1c_1(\bar{x} + 2\eta) & c_2(\bar{u}_1 - \eta) + e_1 + \epsilon_1 \\ k_2c_2(\bar{x} - \eta) + k_1c_1(\bar{x} - \eta) & k_2c_2(\bar{x} - \eta) - (e_1 + e_2 + \epsilon_1 + \epsilon_2 + d) \end{pmatrix}.$$

Since $\hat{J}$ has positive off-diagonal elements, from the Perron–Frobenius theorem we know that there is a positive eigenvector v_m corresponding to the maximum eigenvalue λ_m of $\hat{J}$. After extensive computations, we have $\lambda_m > 0$ since Equation (12) holds. Using linear systems theory, we can show that all positive solutions of Equation (13) tend to infinity as $t \to \infty$. Then, applying the standard comparison principle we have $\hat{y}(t) \to +\infty$ and $\hat{z}(t) \to +\infty$ as $t \to +\infty$. This contradicts $\hat{y}(t) \to 0$, $\hat{z}(t) \to 0$ as $t \to +\infty$, implying that $W^s(E_1) \cap X_0 = \emptyset$. The case $W^s(E_2) \cap X_0 = \emptyset$ for $\mathcal{R}_{21} > 1$ can be proved in a similar way.

Finally, from $W^s(E_0) \cap X_0 = \emptyset$, $W^s(E_1) \cap X_0 = \emptyset$, $W^s(E_2) \cap X_0 = \emptyset$, and the fact that the set $\{E_0, E_1, E_2\}$ is acyclic in ∂X_0, we can apply Theorem 4.6 in Thieme [29] and conclude that system (2) is uniformly persistent with respect to $(X_0, \partial X_0)$. Using Theorem 1.3.7 in Zhao [36] as applied to the solution semiflow of systems (2), we can immediately obtain that the system has a positive equilibrium. This completes the proof of Theorem 3. ∎

3.2. *Global analysis of the coexistence equilibrium*

In this section, we mainly consider the case when the extra extinction rates in doubly occupied patches are ignored, i.e. $\epsilon_1 = \epsilon_2 = 0$. In this case, it is convenient to use the variables $n_1 = x + z$ and $n_2 = y + z$ (in stead of x and y). Note that n_i represents the total proportion of patches with species i ($i = 1, 2$). System (2) can be rewritten as

$$u_1' = r(1 - u_1 - n_1 - n_2 + z) - c_1n_1u_1 - c_2n_2u_1 + e_1(n_1 - z) + e_2(n_2 - z) - du_1,$$

$$n_1' = c_1n_1u_1 - (e_1 + d)n_1 + k_1c_1n_1(n_2 - z),$$

$$n_2' = c_2n_2u_1 - (e_2 + d)n_2 + k_2c_2n_2(n_1 - z),$$

$$z' = k_2c_2n_2(n_1 - z) + k_1c_1n_1(n_2 - z) - (e_1 + e_2 + d)z. \tag{14}$$

Noting that

$$u_1(t) + n_1(t) + n_2(t) - z(t) \to p$$

as $t \to +\infty$, we can consider the limiting system of Equation (14):

$$n_1' = c_1n_1(p - n_1 - n_2 + z) - (e_1 + d)n_1 + k_1c_1n_1(n_2 - z),$$

$$n_2' = c_2n_2(p - n_1 - n_2 + z) - (e_2 + d)n_2 + k_2c_2n_2(n_1 - z),$$

$$z' = k_2c_2n_2(n_1 - z) + k_1c_1n_1(n_2 - z) - (e_1 + e_2 + d)z. \tag{15}$$

For system (15), the trivial equilibrium and the two nontrivial boundary equilibria are

$$E_0 = (0, 0, 0), \quad E_1 = (\bar{x}, 0, 0), \quad E_2 = (0, \tilde{y}, 0),$$

where $\bar{x} = p - (e_1 + d)/c_1$ and $\tilde{y} = p - (e_2 + d)/c_2$. Notice that these equilibria are the same as the corresponding ones for system (2), and we have used the same notation E_i ($i = 0, 1, 2$). From Theorem 1, we can easily see that the global asymptotic behaviours of system (15) remain

the same for the case of $\mathcal{R}_1 < 1$ or $\mathcal{R}_2 < 1$. Thus, for the remaining analysis in this section, we assume that $\mathcal{R}_1 > 1$ and $\mathcal{R}_2 > 1$, i.e.

$$p > \max\left\{\frac{e_1 + d}{c_1}, \frac{e_2 + d}{c_2}\right\}.$$

Notice that for $\epsilon_i = 0$ the invasion reproduction numbers $\mathcal{R}_{12}$ and $\mathcal{R}_{21}$ (given in Equations (8) and (9)) now simplify to

$$\mathcal{R}_{12} = \frac{c_2}{e_2 + d}(\bar{u}_1 + k_2\bar{x})$$

$$= \frac{c_2}{e_2 + d}\left(\frac{e_1 + d}{c_1} + k_2\left(p - \frac{e_1 + d}{c_1}\right)\right) \tag{16}$$

and

$$\mathcal{R}_{21} = \frac{c_1}{e_1 + d}(\tilde{u}_1 + k_1\tilde{y})$$

$$= \frac{c_1}{e_1 + d}\left(\frac{e_2 + d}{c_2} + k_1\left(p - \frac{e_2 + d}{c_2}\right)\right). \tag{17}$$

Let

$$\Gamma = \{(n_1, n_2, z) : \ 0 \le z, n_1, n_2 \le 1\}.$$

It is easy to verify that all solutions of system (15) starting in Γ will remain in Γ for all $t \ge 0$. Hence, Γ is positively invariant. Thus, in this section, our analysis will be carried out for system (15) in Γ. Since $\mathcal{R}_i > 1$ for $i = 1, 2$, it follows that

$$\mathcal{R}_{12}\mathcal{R}_{21} > 1.$$

Therefore, we must have either $\mathcal{R}_{12} > 1$ or $\mathcal{R}_{21} > 1$.

Let $E^* = (n_1^*, n_2^*, z^*)$ denote a positive equilibrium of system (15), i.e. $n_1^* > 0$, $n_2^* > 0$, and $z^* > 0$. We can find E^* by solving the following algebraic equations:

$$n_1 + (1 - k_1)n_2 - (1 - k_1)z - p + \frac{e_1 + d}{c_1} = 0,$$

$$(1 - k_2)n_1 + n_2 - (1 - k_2)z - p + \frac{e_2 + d}{c_2} = 0,$$

$$k_2c_2n_2(n_1 - z) + k_1c_1n_1(n_2 - z) - (e_1 + e_2 + d)z = 0. \tag{18}$$

Using the first and second equations in (18) we have

$$n_1 = \frac{k_1p - (e_1 + d)/c_1 + (1 - k_1)((e_2 + d)/c_2) + k_2(1 - k_1)z}{k_1 + k_2 - k_1k_2},$$

$$n_2 = \frac{k_2p - (e_2 + d)/c_2 + (1 - k_2)((e_1 + d)/c_1) + k_1(1 - k_2)z}{k_1 + k_2 - k_1k_2}. \tag{19}$$

From Equation (19) and the third equation of (18) we know that z^* satisfies the following quadratic equation

$$f(z) = B_1z^2 + B_2z + B_3 = 0, \tag{20}$$

501 where

$$B_1 = -\frac{k_1 k_2}{(k_1 + k_2 - k_1 k_2)^2}(c_2 k_1(1 - k_2) + c_1 k_2(1 - k_1)) < 0,$$

$$B_2 = \frac{k_1 k_2}{(k_1 + k_2 - k_1 k_2)^2}\left[(c_2(1 - k_2) - c_1)\left(k_1 p - \frac{e_1 + d}{c_1} + (1 - k_1)\frac{e_2 + d}{c_2}\right)\right.$$

$$\left. + (c_1(1 - k_1) - c_2)\left(k_2 p - \frac{e_2 + d}{c_2} + (1 - k_2)\frac{e_1 + d}{c_1}\right)\right] - (e_1 + e_2 + d),$$

$$B_3 = \frac{k_2 c_2 + k_1 c_1}{(k_1 + k_2 - k_1 k_2)^2}\frac{e_1 + d}{c_1}\frac{e_2 + d}{c_2}(\mathcal{R}_{12} - 1)(\mathcal{R}_{21} - 1). \tag{21}$$

513 Thus, the components of E^* are given by

$$n_1^* = \frac{k_1 p - (e_1 + d)/c_1 + (1 - k_1)((e_2 + d)/c_2) + k_2(1 - k_1)z^*}{k_1 + k_2 - k_1 k_2},$$

$$n_2^* = \frac{k_2 p - (e_2 + d)/c_2 + (1 - k_2)((e_1 + d)/c_1) + k_1(1 - k_2)z^*}{k_1 + k_2 - k_1 k_2},$$

$$z^* = \frac{-B_2 - \sqrt{B_2^2 - 4B_1 B_3}}{2B_1}, \tag{22}$$

523 where B_1, B_2, B_3 are defined in Equation (21).
524   The existence (or nonexistence) condition of E^* is described in the following theorem.

526 THEOREM 4   *Let $E^* = (n_1^*, n_2^*, z^*)$ denote a positive equilibrium of system* (15). *Then*

528 (i) *E^* does not exist if $\mathcal{R}_{12} < 1$ and $\mathcal{R}_{21} > 1$, or if $\mathcal{R}_{21} < 1$ and $\mathcal{R}_{12} > 1$;*
529 (ii) *E^* exists and is unique if $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$. Moreover, $n_1^*, n_2^*,$ and z^* are given by*
530   *Equation (22).*

532 *Proof*   For the proof of part (i), we only pick up the case $\mathcal{R}_{12} < 1$, $\mathcal{R}_{21} > 1$ to prove the theorem.
533 If $\mathcal{R}_{21} < 1$, $\mathcal{R}_{12} > 1$, the theorem can be proved in a similar way. If $\mathcal{R}_{12} < 1$, $\mathcal{R}_{21} > 1$ we have
534 $B_3 < 0$ and

$$(1 - k_{12})\frac{e_2 + d}{c_2} + k_{12}p > \frac{e_1 + d}{c_1},$$

$$(1 - k_{21})\frac{e_1 + d}{c_1} + k_{21}p < \frac{e_2 + d}{c_2}.$$

541 It follows that

$$\frac{1}{k_{21}}\frac{e_2 + d}{c_2} - \frac{1 - k_{21}}{k_{21}}\frac{e_1 + d}{c_1} > p > \max\left\{\frac{e_1 + d}{c_1}, \frac{e_2 + d}{c_2}, \frac{1}{k_{12}}\frac{e_1 + d}{c_1} - \frac{1 - k_{12}}{k_{12}}\frac{e_2 + d}{c_2}\right\}$$

545 and

$$\frac{e_2 + d}{c_2} > \frac{e_1 + d}{c_1}.$$

549 We claim that $B_2 < 0$. In order to prove the claim, we consider three cases, i.e. $c_2 \leq (1 - k_{12})c_1$,
550 $(1 - k_{12})c_1 < c_2 < (c_1/(1 - k_{21}))$ and $c_1 > (c_2/(1 - k_{12}))$.

Case 1 $c_2 \leq (1 - k_{12})c_1$. In this case, it is easy to see that $B_2 < 0$ since

$$(c_2(1 - k_{21}) - c_1)\left(k_{12}p - \frac{e_1 + d}{c_1} + (1 - k_{12})\frac{e_2 + d}{c_2}\right) < 0$$

and

$$(c_1(1 - k_{12}) - c_2)\left(k_{21}p - \frac{e_2 + d}{c_2} + (1 - k_{21})\frac{e_1 + d}{c_1}\right) < 0.$$

Case 2 $(1 - k_{12})c_1 < c_2 < (c_1/(1 - k_{21}))$. In this case, since

$$(c_2(1 - k_{21}) - c_1)\left(k_{12}p - \frac{e_1 + d}{c_1} + (1 - k_{12})\frac{e_2 + d}{c_2}\right) < 0,$$

we have

$$B_2 \leq \frac{k_{12}k_{21}}{(k_{12} + k_{21} - k_{12}k_{21})^2}(c_1(1 - k_{12}) - c_2)$$

$$\times \left(k_{21}p - \frac{e_2 + d}{c_2} + (1 - k_{21})\frac{e_1 + d}{c_1}\right) - (e_1 + e_2 + d)$$

$$\leq \frac{k_{12}k_{21}}{(k_{12} + k_{21} - k_{12}k_{21})^2}(c_2 - c_1(1 - k_{12}))(1 - k_{21})\left(\frac{e_2 + d}{c_2} - \frac{e_1 + d}{c_1}\right) - (e_1 + e_2 + d)$$

$$\leq \frac{k_{12}k_{21}}{(k_{12} + k_{21} - k_{12}k_{21})^2}(1 - k_{21})(e_2 + d) - (e_1 + e_2 + d) < 0.$$

Case 3 $c_1 > (c_2/(1 - k_{12}))$. In this case, we have

$$B_2 \leq \frac{k_{12}k_{21}}{(k_{12} + k_{21} - k_{12}k_{21})^2}\left((c_2(1 - k_{21}) - c_1)\left(\frac{k_{12} + k_{21} - k_{12}k_{21}}{k_{21}}\left(\frac{e_2 + d}{c_2} - \frac{e_1 + d}{c_1}\right)\right)\right.$$

$$+ (c_2 - c_1(1 - k_{12}))\left(\frac{k_{12} + k_{21} - k_{12}k_{21}}{k_{12}}\left(\frac{e_2 + d}{c_2} - \frac{e_1 + d}{c_1}\right)\right) - (e_1 + e_2 + d)$$

$$= (c_2 - c_1)\left(\frac{e_2 + d}{c_2} - \frac{e_1 + d}{c_1}\right) - (e_1 + e_2 + d)$$

$$\leq -e_1 < 0.$$

Since $B_i < 0$, $i = 1, 2, 3$, it is easy to see that Equation (20) has no positive solution. Therefore, when $\mathcal{R}_{12} < 1$, $\mathcal{R}_{21} > 1$, system (15) has no positive equilibrium. This finishes the proof of part (i).

Proof of Part (ii). As $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$, we have $B_1 < 0$ and $B_3 > 0$. It then follows that Equation (20) has at most one positive solution

$$z^* = \frac{-B_2 - \sqrt{B_2^2 - 4B_1B_3}}{2B_1}.$$

Consequently, system (15) has at most one positive equilibrium $E^* = (n_1^*, n_2^*, z^*)$. On the other hand, system (20) is uniformly persistent for $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$. This implies that system (15) has at least one positive equilibrium. Therefore, when $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$, system (15) has a

601 unique positive equilibrium $E^* = (n_1^*, n_2^*, z^*)$, where n_1^*, n_2^* and z^* are given by Equation (22).
602 This finishes the proof of part (ii). The proof of Theorem 4 is completed. ∎

604 The next result concerns the global stabilities of the nontrivial equilibria E_1 and E_2. For these
605 global dynamics of system (15), we need to first mention some results from Jiang *et al.* [13]
606 concerning three-dimensional K-competitive dynamical systems.
607 Consider the system of differential equations:

$$\dot{x} = f(x), \quad x \in \mathbb{R}_+^3. \tag{23}$$

610 It follows from Smith [27] that a matrix A is called *type K-competitive* and *irreducible* if A has
611 the following form

$$\begin{pmatrix} * & - & + \\ - & * & + \\ + & + & * \end{pmatrix},$$

615 where the '$*$' represents an arbitrary element. System (23) is called *type K-competitive* and
616 *irreducible* if the Jacobian $Df(x)$ of f is type K-competitive and irreducible for each $x \in \mathbb{R}_+^3$.
617 Set

$$K = \{(x, y, z)|\ x \geq 0,\ y \geq 0,\ z \leq 0\}.$$

620 It follows from the Perron–Frobenius theorem that A has a real eigenvalue, which has a unique
621 unit eigenvector in Int K, and the real parts of the other two eigenvalues are strictly greater than
622 this real eigenvalue if A is type K-competitive and irreducible.
623 We also need to introduce the following concepts. A vector x is called *K-positive* if $x \in K$, and
624 it is called *strictly K-positive* if $x \in$ Int K. Two distinct points $u, v \in \mathbb{R}^3$ are *K-related* if either
625 $u - v$ or $v - u$ is strictly K-positive. A set S is called *K-balanced* if no two distinct points of S
626 are related.
627 Notice that the Jacobian of system (15) is

$$\begin{pmatrix} c_1(p - 2n_1 - n_2 + z) & -(1 - k_1)c_1 n_1 c_2 & (1 - k_1)c_1 n_1 \\ -(e_1 + d) + k_1 c_1(n_2 - z) & (p - n_1 - 2n_2 + z) & (1 - k_2)c_2 n_2 \\ -(1 - k_2)c_2 n_2 \times k_2 c_2 n_2 & -(e_2 + d) + k_2 c_2(n_1 - z) & -k_2 c_2 n_2 - k_1 c_1 n_1 \\ +k_1 c_1(n_2 - z) & k_2 c_2(n_1 - z) + k_1 c_1 n_1 & -(e_1 + e_2 + d) \end{pmatrix}.$$

633 It can be verified that system (15) is K-competitive in Γ. From the expressions of $n_1^*, n_2^*, z^*, \bar{x}$,
634 and $\tilde{y}$, it is not difficult to see that the equilibria E_1 and E_2 (or $E_1, E_2,$ and E^*) are unordered in the
635 K-order. It follows from Proposition 3.2 in Wang and Jiang [33] and Proposition 1.3 in Takac [28]
636 that there exists a two-dimensional compact Lipschitz submanifold Σ such that $E_1, E_2 \in$ IntΣ, or
637 $E^* \in$ IntΣ and $E_1, E_2 \in \partial\Sigma$. Moreover, Σ is K-balanced. Since Σ is a two-dimensional compact
638 Lipschitz submanifold and homeomorphic to a compact domain in the plane, it is obvious that
639 the Poincare–Bendixson theorem holds for the dynamics of system (15) on Σ.
640 Notice that system (15) has only two boundary equilibria E_1 and E_2, and from Theorems 2
641 and 3 we know that E_1 is stable and E_2 is unstable when $\mathcal{R}_{12} < 1$ and $\mathcal{R}_{21} > 1$. Since there is
642 no positive equilibrium, from the Poincare–Bendixson theorem we know that E_1 is g.a.s. Using
643 a similar way, we show that E_2 is g.a.s. if $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} < 1$. Therefore, the following result
644 holds.

645 THEOREM 5 *If $\mathcal{R}_{ij} < 1$ and $\mathcal{R}_{ji} > 1$ ($i, j = 1, 2, j \neq i$) then the nontrivial boundary equilib-*
646 *rium E_i of system (15) is g.a.s.*

648 Although we do not have an analytic result for the stability of the interior equilibrium E^*, the results
649 in Theorems $1 - 6$ suggest that E^* is l.a.s. when $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$. Biological interpretations
650 of these results are provided in the next section.

3.3. *Biological interpretations of the results*

In the previous sections, we proved several results regarding the local and global dynamics of system (2) including the existence and stability of the equilibria E_0, E_1, E_2, and E^*. We point out that these results have been described using the quantities $\mathcal{R}_i$ and $\mathcal{R}_{ij}$ ($i, j = 1, 2$ and $i \neq j$), which are defined in Equations (6), (8), and (9). These quantities have clear biological meanings. For example, $\mathcal{R}_i = pc_i/(e_i + d)$ is the product of c_i (the rate that species i colonize a habitable and empty patch), $1/(e_i + d)$ (the mean time that a patch is occupied by species i in the absence of the other species), and p (the fraction of habitable patches). Thus, $\mathcal{R}_i$ gives the expected 'reproduction number' of species i in a landscape where the proportion of habitable patches is p. If a landscape is completely habitable, i.e. if $p = 1$, then the 'basic reproduction number' of species i is

$$\mathcal{R}_{0i} = \frac{c_i}{e_i + d}, \quad i = 1, 2. \tag{24}$$

To see the meaning of $\mathcal{R}_{ij}$ more easily, we ignore the extra extinction rate for doubly occupied patches (i.e. $\epsilon_i = 0$). In this case, from Equations (8) and (9) we can simplify the expressions for $\mathcal{R}_{12}$ and $\mathcal{R}_{21}$ as

$$\mathcal{R}_{12} = \frac{c_2(\bar{u} + k_2\bar{x})}{e_2 + d} = \mathcal{R}_2(\bar{u}_1 + k_2\bar{x}),$$

$$\mathcal{R}_{21} = \frac{c_1(\tilde{u} + k_1\tilde{y})}{e_1 + d} = \mathcal{R}_1(\tilde{u}_1 + k_1\tilde{y}), \tag{25}$$

where $\bar{u}_1$, $\bar{x}$, $\tilde{u}_1$, and $\tilde{y}$ are given in Equations (4) and (5). Notice that $E_1 = (\bar{u}_1, \bar{x}, 0, 0)$ is the species 1-only equilibrium and $E_2 = (\tilde{u}_1, 0, \tilde{y}, 0)$ is the species 2-only equilibrium. Thus, $\mathcal{R}_{ij}$ gives the reproduction number of species j in a landscape in which only species i ($j \neq i$) is present. We term $\mathcal{R}_{ij}$ the 'invasion reproduction number' of species j. The result in Theorem 2 implies that species 2 can invade the metapopulation of species 1 only if the invasion reproduction number $\mathcal{R}_{12}$ exceeds 1.

Combining the results in Theorems 1–5, we can draw the following conclusions for the competition outcomes of the two species:

(i) Only species i will be present if $\mathcal{R}_i > 1$ and $\mathcal{R}_{ij} < 1$ ($i, j = 1, 2$ and $i \neq j$).

(ii) Both species will coexist if $\mathcal{R}_i > 1$ ($i = 1, 2$) and $\mathcal{R}_{ij} > 1$ ($i, j = 1, 2$ and $i \neq j$).

(iii) Both species will go extinct if $\mathcal{R}_i < 1$ for $i = 1, 2$. $\tag{26}$

These conditions make clear biological sense from the meaning of $\mathcal{R}_i$ and $\mathcal{R}_{ij}$. Comparing with the corresponding results in Hanski [6] in which the conditions for nontrivial equilibria cannot provide explicit biological interpretations due to the complexity of the expressions, our results are more useful in terms of gaining biological insights.

It is also helpful to rewrite the invasion condition $\mathcal{R}_{ij} > 1$ in Equation (25) in terms of $\mathcal{R}_1$ and $\mathcal{R}_2$:

$$\mathcal{R}_{12} > 1 \quad \text{if and only if} \quad \mathcal{R}_2 > \frac{1}{1 - (1 - k_2)(1 - 1/\mathcal{R}_1)} =: H_1(\mathcal{R}_1) \tag{27}$$

and

$$\mathcal{R}_{21} > 1 \quad \text{if and only if} \quad \mathcal{R}_2 < \frac{1}{1 - (1/(1 - k_1))(1 - 1/\mathcal{R}_1)} =: H_2(\mathcal{R}_1). \tag{28}$$
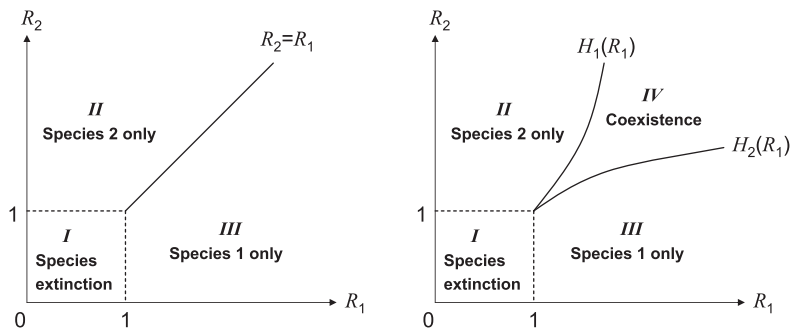
Figure 2. $(\mathcal{R}_1, \mathcal{R}_2)$ plane. The left figure is for the case when there is no doubly occupied patches ($k_1 = k_2 = 0$) and the right figure is for the case $k_1 > 0$ and $k_2 > 0$. The two curves $\mathcal{R}_2 = H_1(\mathcal{R}_1)$ and $\mathcal{R}_2 = H_2(\mathcal{R}_1)$ are determined by the invasion conditions $\mathcal{R}_{ij} > 1$ ($i, j = 1, 2, i \neq j$). Both species will go extinct if $\mathcal{R}_i < 1$ ($i = 1, 2$), i.e. if $(\mathcal{R}_1, \mathcal{R}_2)$ is in Region I. Only species 1 will be present if $(\mathcal{R}_1, \mathcal{R}_2)$ is in Region II, and only species 2 will be present if $(\mathcal{R}_1, \mathcal{R}_2)$ is in Region III. Both species will coexist if $(\mathcal{R}_1, \mathcal{R}_2)$ is in Region IV.

Since the equilibrium E_i exists if and only if $\mathcal{R}_i > 1$ ($i = 1, 2$), and from $0 \leq k_i \leq 1, \bar{u}_1 + k_2\bar{x} < 1$ and $\tilde{u}_1 + k_1\tilde{y} < 1$, we know that the curve $H_1(\mathcal{R}_1)$ is above the curve $H_2(\mathcal{R}_1)$ for $\mathcal{R}_1 > 1$, except that $H_1(\mathcal{R}_1) = H_2(\mathcal{R}_1) = \mathcal{R}_1$ in the case of $k_1 = k_2 = 0$ (i.e. no doubly occupied patches). Moreover, the two curves intersect at $\mathcal{R}_1 = 1$. Bifurcation diagrams for these two cases are shown in Figure 2. It is shown in Figure 2 that coexistence is very unlikely if no patches can be cooccupied by both species (the left figure), and there are three regions (labelled by I, II, and III) formed by the lines $\mathcal{R}_i = 1$ and by the curves $H_i(\mathcal{R}_i)$ ($i = 1, 2$) representing species extinction (Region I), species 1 only (Region II), and species 2 only (Region III). If double occupancy is allowed, then there is a region for coexistence (Region IV).

These results can be used to examine the role of various ecological factors play in the competitive outcomes of metapopoulation. For example, from the threshold value $\mathcal{R}_i = 1$ we can derive a threshold value of colonization rate c_i^*,

$$c_i^* = \frac{(e_i + d)(r + d)}{r}, \tag{29}$$

such that $\mathcal{R}_i > (<)1$ if and only if $c_i > (<)c_i^*$. Similarly, the conditions $\mathcal{R}_{12} > 1$ and $\mathcal{R}_{21} > 1$ are equivalent to, respectively,

$$c_2 > \frac{e_2 + d}{p} \frac{1}{1 - (1 - k_2)(1 - ((e_1 + d)/pc_1))} =: F(c_1) \tag{30}$$

and

$$c_2 < \frac{e_2 + d}{p} \frac{1}{1 - (1/(1 - k_1))(1 - ((e_1 + d)/pc_1))} =: G(c_1), \tag{31}$$

where $p = r/(r + d)$ is the long-term proportion of habitable patches.

Using Equations (29)–(31), we can draw a bifurcation diagram in the (c_1, c_2) plane. Moreover, these conditions allow us to examine how the model parameters such as p (the long-term proportion of habitable patches) and e_i (patch extinction) may affect the competition outcomes. For example, the effect of p is illustrated in Figure 3, in which the three plots are for the values of $p = 1$ (left), $p = 0.75$ (middle), and $p = 0.6$ (right). We observe that as p decreases (i.e. as the fraction of
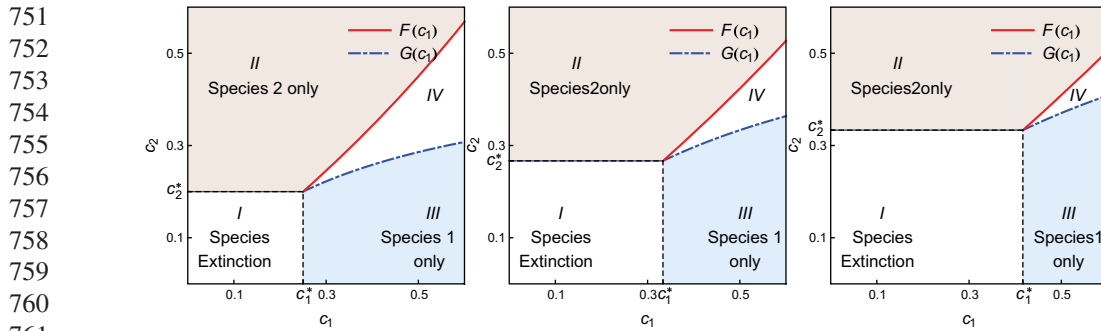
Figure 3.   Regions of competition outcomes in the first quadrant of the (c_1, c_2) plane for different values of p, the long-term proportion of habitable patches. The four regions are: (i) species extinction if $c_i < c_i^*$ for $i = 1, 2$, where the threshold values c_1^* and c_2^* are given in Equation (29), i.e. if (c_1, c_2) is in Region I; (ii) species 1 only if (c_1, c_2) is in Region II; (iii) species 2 only if (c_1, c_2) is in Region III; and (iv) coexistence of both species if (c_1, c_2) is in Region IV. The left figure is for the case $p = 1$ (i.e. all patches are habitable). The middle and right figures are for the cases $p = 0.8$ and $p = 0.5$, respectively. It shows that as p decreases, the region of extinction increases significantly while the region of coexistence becomes much smaller. It also suggests that the negative impact of decreasing p is higher on species 1 than on species 2.

habitable patches decreases), the region for the extinction of both species increases significantly while the coexistence of two species becomes much less likely. It also suggests that the negative impact of decreasing p is higher on species 1 than on species 2. The parameter values used in this figure are $e_1 = 0.15$, $e_2 = 0.1$, $k_1 = 0.1$, and $k_2 = 0.4$.

4.   Stochastic simulations

To explore the impact of stochastic factors on the system behaviours, we conducted stochastic simulations of the system, and the results from the deterministic model and stochastic simulations are compared. Guided by the theoretical results from the deterministic model, we consider stochasticity in several parameters that may have important influence on the dynamics of the system. For example, the effect of environmental stochasticity is examined by considering random parameters including the species i, $i = 1, 2$ colonization rate of empty patch c_i, the extinction rate e_i, the colonization rates of occupied patch k_{12} and k_{21}, and the rates of patch destruction d and recreation r. For simplicity, our basic model describes the dynamics of a metapopulation without keeping track of the local population dynamics for species within each patch. That is, a habitable patch is considered either empty or occupied, and there is no detailed description for the population growth within an occupied patch. Consequently, there is no demographic stochasticity.

   In this section, we present three scenarios based on the competitive outcomes of the two species identified from the analysis of the deterministic model. There scenarios correspond to the three cases are listed in Equation (26). We first consider the case when the rates of colonization (c_i) and extinction (e_i) are random parameters, which are assumed to be uniformly distributed.

   In Figure 4, $\mathcal{R}_2 > 1$ and $\mathcal{R}_{21} < 1$, which corresponds to the case (i) described in Equation (26) with $i = 2$ and $j = 1$. Thus, the deterministic outcome is that only species 2 will be present. Time variations of the variables x, y, z, u_1 are presented in these figures. Figure 4 shows the average of 500 stochastic runs (the dashed curve) and the solution curve of the deterministic model (the solid curve), whereas Figure 4 illustrates four individual stochastic runs (thin curves) together
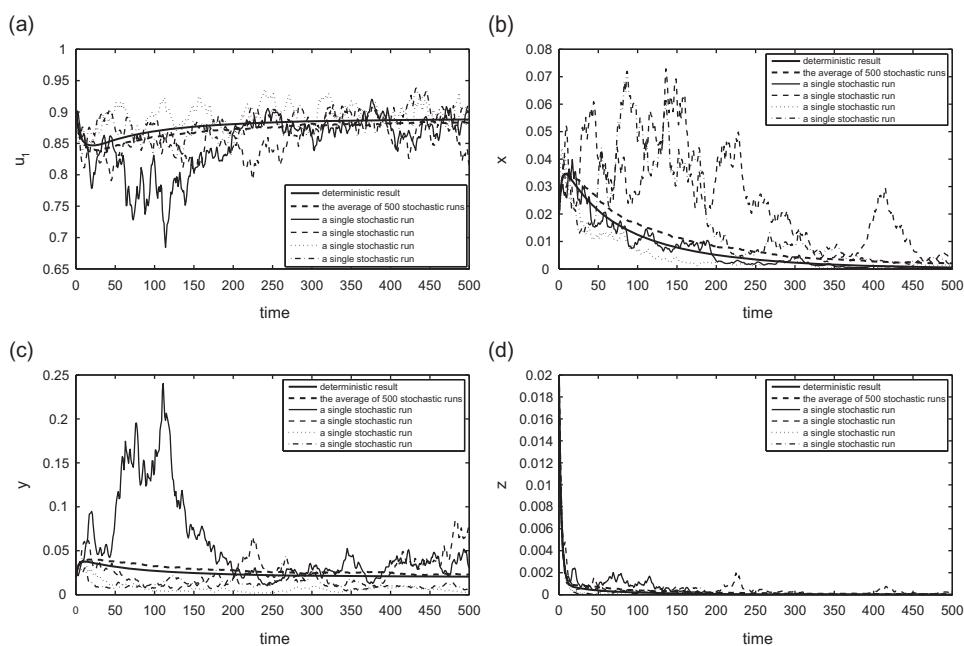
Figure 4. Stochastic simulations with c_i and e_i as random parameters (see the text for more detailed explanations). (a) The fraction of habitable but empty patches; (b) the fraction of patches occupied by the species 1 only; (c) the fraction of patches occupied by the species 2 only; (d) the fraction of patches occupied by both species 1 and 2. The random parameters are again $c_i, e_i, i = 1, 2, k_{12}, k_{21}, d$, and r. The solid curve represents the solution curve of the deterministic model and the dash thick curve shows the average of 500 stochastic runs. The thin (solid, dashed, dot, dashed, and dot) curves show four individual stochastic runs. The parameter values used for the deterministic simulation, which are the mean values of the random variables in the stochastic runs, are: $c_1 = 0.17, c_2 = 0.18, e_1 = e_2 = 0.15, r = 0.1, d = 0.01, \epsilon_1 = \epsilon_2 = 0.01$. For this set of parameter values, $\mathcal{R}_1 = 0.9659$, $\mathcal{R}_2 = 1.0227$, $\mathcal{R}_{12} = 1.0408$, and $\mathcal{R}_{21} = 0.9552$. This corresponds to the case (i) listed in Equation (26). In this case, the deterministic outcome is that only species 2 will be present. We observe that the average behaviours of stochastic simulations is very similar to the behaviour of the deterministic model. The outcomes of some individual runs, for example the solid thin curves, may be very different from the average outcome in some relative short time periods.

with the deterministic curve (the solid curve). We see from Figure 4 that the average behaviour of the stochastic simulations is very similar to that of the deterministic simulation. More diverse outcomes can also be observed in Figure 4. There are individual runs that exhibit coexistence of the two species (e.g. see the solid blue curve), and other runs show that both species go extinct (see the solid red curve).

Figure 5 is similar to Figure 4, but for the case (ii) described in Equation (26). That is, $\mathcal{R}_i > 1$ $(i = 1, 2)$ and $\mathcal{R}_{ij} > 1$ $(i, j = 1, 2$ and $i \neq j)$. In this case, the deterministic outcome is coexistence of both species. We see from Figure 5 again that the average behaviour of the stochastic simulations is very similar to that of the deterministic simulation. The individual runs shown in Figure 4 include both the case when species 1 out-competes species 2 (blue solid curve) and the case when species 2 out-competes species 1 (red solid curve).

Figure 6 is also similar to Figure 4 except that it corresponds to the case (iii) given in Equation (26), i.e. $\mathcal{R}_i < 1$ for $i = 1, 2$. The deterministic outcome for this case is that both species will go extinct. Figure 6 shows again that the behaviour of average stochastic simulations is similar to that of the deterministic model. We also observe from Figure 6 that all individual runs also show extinction of both species, although it may take a very long time in some individual runs.
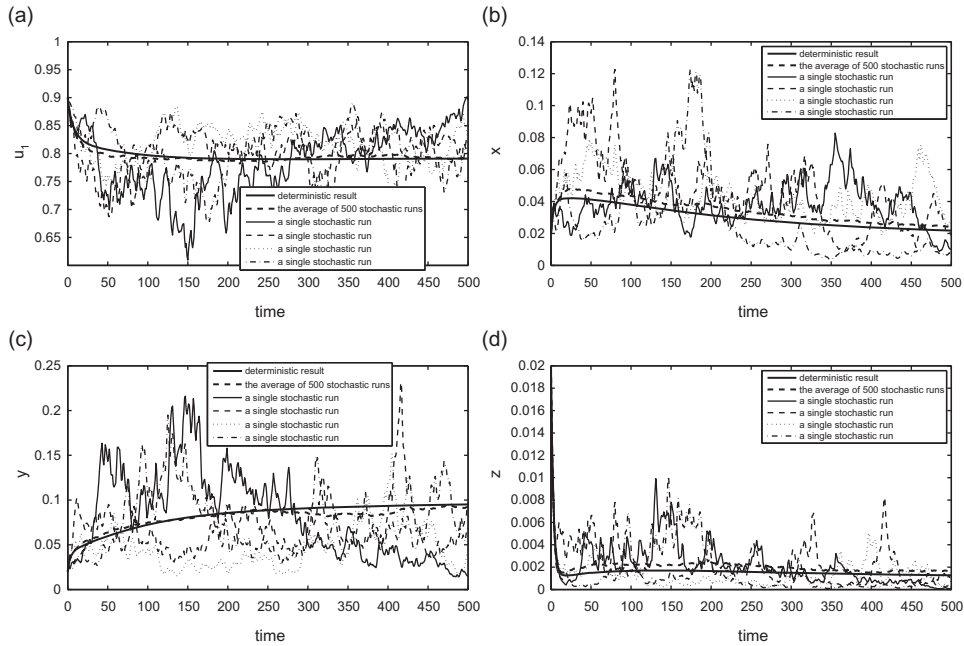
Figure 5.   (a) The fraction of habitable but empty patches; (b) the fraction of patches occupied only by the species 1; (c) the fraction of patches occupied only by the species 2; (d) the fraction of patches occupied by both species 1 and 2. Similar to Figure 4 but for a set of parameter values that correspond to the case (ii) given in Equation (26). The random parameters are again c_i, e_i, $i = 1, 2$, k_{12}, k_{21}, d, and r. The solid curve represents the solution curve of the deterministic model and the dash thick curve shows the average of 500 stochastic runs. The thin (solid, dashed, dot, dashed, and dot) curves show four individual stochastic runs. The parameter values used for the deterministic simulation are the same as these in Figure 4 except the colonization rates are increased as: $c_1 = 0.19$, $c_2 = 0.2$. For this set of parameter values, $\mathcal{R}_1 = 1.0795$, $\mathcal{R}_2 = 1.1364$, $\mathcal{R}_{12} = 1.0945$, and $\mathcal{R}_{21} = 1.0148$. In this case, the deterministic outcome is that the two species will coexist. We observe again that the average behaviours of stochastic simulations is very similar to the behaviour of the deterministic model.

5.   Conclusion

In this paper, we studied a two-species metapopulation model in a competitive dynamic landscape. We considered both a deterministic and stochastic versions of the model. For the deterministic system, we presented detailed stability analysis including the local and global stabilities of the nontrivial boundary equilibria (the equilibria at which only one species is present). These analytical results provide threshold conditions for the invasion of a species into an environment in which the other species has already established, and the conditions are expressed in terms of the 'invasion reproduction numbers', $\mathcal{R}_{12}$ and $\mathcal{R}_{21}$ [23,31]. These invasion reproduction numbers are shown to have clear ecological interpretations in terms of their dependence on parameters representing patch colonization and extinction (c_i and e_i), species competition (k_{ij}), and landscape dynamics (d).

The analytical results can be used to examine the impact of various factors on species coexistence. For example, from the invasion condition $\mathcal{R}_{ij} > 1$ ($i, j = 1, 2$), we derived the threshold level c_i^* of colonization rate c_i for species i, such that the species i can invade into a population of species j if and only if $c_i > c_i^*$. Moreover, coexistence of the two species can be expected when $c_i > c_i^*$ for $i = 1, 2$. Similarly, the invasion and coexistence conditions can be expressed using other model parameters including the rates of patch extinction, patch destruction and recreation, and species competition. These types of results may provide useful information for management.
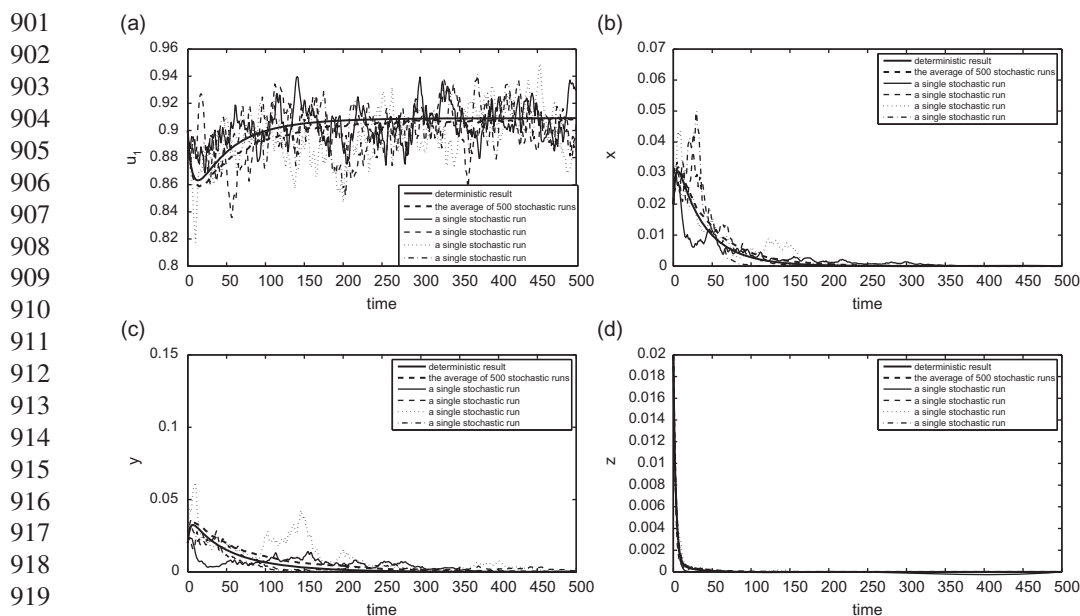
Figure 6. (a) The fraction of habitable but empty patches; (b) the fraction of patches occupied only by the species 1; (c) the fraction of patches occupied only by the species 2; (d): the fraction of patches occupied by both species 1 and 2. Similar to Figure 4 but for a set of parameter values that correspond to the case (iii) listed in Equation (26). The random parameters are again c_i, e_i, $i = 1, 2$, k_{12}, k_{21}, d, and r. The solid curve represents the solution curve of the deterministic model and the dash thick curve shows the average of 500 stochastic runs. The thin (solid, dashed, dot, dashed, and dot) curves show four individual stochastic runs. The parameter values used for the deterministic simulation are the same as these in Figure 4 except the colonization rates are decreased as: $c_1 = 0.15$, $c_2 = 0.16$. For this set of parameter values, $\mathcal{R}_1 = 0.8523$, $\mathcal{R}_2 = 0.9091$, $\mathcal{R}_{12} = 0.9879$, and $\mathcal{R}_{21} = 0.8949$. In this case, the deterministic outcome is that the both species will go extinct. We observe again that the average behaviour of stochastic simulations is very similar to the behaviour of the deterministic model. The outcomes of some individual runs may be very different from the average outcome in some relative short time periods.

The analytical results also provided helpful guidance for the simulations of the system with and without stochastic factors. Our simulations suggest that stochastic factors such as environmental fluctuations do not alter qualitative behaviours of metapopulation systems. That is, stochasticity does not alter species coexistence or competitive exclusion.

Acknowledgements

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