ASYMPTOTIC POPULATION ABUNDANCE OF A TWO-PATCH SYSTEM WITH ASYMMETRIC DIFFUSION

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Abstract. This paper considers a two-patch system with asymmetric diffusion rates, in which exploitable resources are included. By using dynamical system theory, we exclude periodic solution in the one-patch subsystem and demonstrate its global dynamics. Then we exhibit uniform persistence of the two-patch system and demonstrate uniqueness of the positive equilibrium, which is shown to be asymptotically stable when the diffusion rates are sufficiently large. By a thorough analysis on the asymptotic population abundance, we demonstrate necessary and sufficient conditions under which the asymmetric diffusion rates can lead to the result that total equilibrium population abundance in heterogeneous environments is larger than that in heterogeneous/homogeneous environments with no diffusion, which is not intuitive. Our result extends previous work to the situation of asymmetric diffusion and provides new insights. Numerical simulations confirm and extend our results.

1. Introduction. There are more and more empirical observations displaying that spatial and temporal heterogeneities have effects on population dynamics [6]. While various effects are observed in both natural environments and experimental tests, an interesting finding is the increase of growth of a population [1, 2]. For example, when species are distributed in heterogeneous environments, spatial diffusion can increase the number of individuals in the global population [13, 14]. Then total realized asymptotic population abundance (abbreviated TRAPA here for convenience) can be larger than the sum of local carrying capacities over every point in the space. Thus, it is important to study mechanisms regarding how the spatial or temporal heterogeneity leads to the increase of TRAPA.

Poggiale et al. [15] theoretically proved the large TRAPA for a two-patch model with asymmetric diffusion:

\[
\begin{align*}
\frac{dN_1}{dt} &= m_{12}N_2 - m_{21}N_1 + \epsilon r_1 N_1 (1 - \frac{N_1}{K}) \\
\frac{dN_2}{dt} &= m_{21}N_1 - m_{12}N_2 + \epsilon r_2 N_2 (1 - \frac{N_2}{K})
\end{align*}
\]  

(1)

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where $r_i$ and $K_i$ respectively represent the maximum per capita growth rate and carrying capacity in patch $i$, and $m_{ij}$ is the displacement rate from patch $j$ to patch $i$ resulting from individuals moving randomly from patch to patch. Since the displacement of individuals is much faster than the demographic process, a small dimensionless parameter $\epsilon$ in the model represents the time scale parameter. When $r_1 > r_2$ and the displacement rates $m_{ij}$ are extremely fast, the total size at a positive equilibrium can be larger than the sum of the carrying capacities of the two patches (i.e., $K^* = N_1^* + N_2^* > 2K$) if

$$1 < \frac{m_{21}}{m_{12}} < \frac{r_1}{r_2},$$

which means that the carrying capacity is enlarged when the ratio of the displacement rate from patch 1 to patch 2 to the displacement rate from patch 2 to patch 1 is lower than the ratio of the local growth rate $r_1$ to the local growth rate $r_2$.

Zhang et al. [18] tested the large TRAPA by laboratory experiments and studied the result by analyzing a two-patch model with exploitable resources and symmetric diffusion. In the experiments, the population was the heterotrophic budding yeast, Saccharomyces cerevisiae, and the resource was the amino acid tryptophan which was the single exploited and renewable nutrient that was spatially varied. The yeast population was spatially distributed in a 96-well microtitre plate, and the wells were linearly arrayed and linked by nearest-neighbor diffusion. In the case of the heterogeneous distribution of resource, the wells with even number had the same high nutrient input, while those with odd number had the same low nutrient input. Thus, the wells can be regarded as two types of patches, which correspond to a two-patch system. In homogeneous distribution, all wells had the same nutrient input, which was the average of the high and low inputs in the heterogeneous distribution. The experimental process was repeated daily over 9 days. First, the initial yeast had 24-hour growth, followed by a diffusion from the original plate (plate 1) to a new empty plate (plate 2), in which 3% volume in each well was transferred to the well on the left in plate 2 and another 3% to the right well of the plate. Then the remaining 94% volume was transferred to the same well in plate 2. After the diffusion and transfer, old media in plate 2 were removed and fresh media were added, and the yeast population underwent another 24-hour growth. It was observed from the experiments that (a) TRAPA in heterogeneous environments can be larger than that in heterogeneous environments with no diffusion, in which the “extra individuals” were observed to reside in the low nutrient patches; (b) TRAPA in heterogeneous environments, even with species diffusion, is less than that in homogeneous environments with no diffusion; and (c) homogeneously distributed resources support the same carrying capacity with or without species diffusion. For additional relevant work, we refer to Hutson et al. [11], Lou [12], Arditi et al. [3, 4], Zhang et al. [19], DeAngelis et al. [8, 9], Ruiz-Herrera and Torres [16], Wang and DeAngelis [17], etc. While Zhang et al. [18] qualitatively exhibited interesting results, the diffusion rates in their work are symmetric. In a natural environment, diffusion is usually asymmetric. Thus, it is necessary to ask if the results obtained by Zhang et al. [18] are effective under asymmetric diffusion.

This paper extends the two-patch mode with symmetric diffusion rates described above to one with asymmetric diffusion rates. By using dynamical system theory, we exhibit nonexistence of periodic solution and display global stability of a unique positive equilibrium in the one-patch subsystem. Then we show uniform persistence of the two-patch system and demonstrate uniqueness of its positive equilibrium.
Also, equilibrium is exhibited to be asymptotically stable when the diffusion rates are sufficiently large. Then, by a thorough analysis on the asymptotic population abundance, we demonstrate mechanisms by which varying the asymmetric diffusion rates can lead to the result that TRAPA in heterogeneous environments is larger than that in heterogeneous environments with no diffusion (see Theorem 4.2), and is larger than that in the same homogeneous environments with no diffusion (see Theorem 4.3). Moreover, we exhibit necessary and sufficient conditions under which TRAPA in heterogeneous environments with no diffusion is larger than that in homogeneous environments with no diffusion (see Theorem 4.4). We also show that TRAPA in homogeneous environments with no diffusion can be larger than that with asymmetric diffusion (see Remark 3). Our result extends previous work to the situation of asymmetric diffusion and provides new insights (see Section 5 and discussions after Theorems 4.2, 4.3, 4.4). Numerical simulations confirm and extend our results.

The paper is organized as follows. In the next section, we describe the two-patch system and show dynamics of the one-patch subsystems. Section 3 exhibits dynamics of the two-patch model, while four TRAPAs are analyzed in Section 4. Discussion and application are in Section 5.

2. The two-patch model. According to their experimental processes with yeast, Zhang et al. [18] established a mechanistic model characterizing a diffusing population of consumers in \( n \) patches with a heterogeneously distributed limiting resource (a nutrient) that is exploited by the consumer (yeast) and externally renewed. The model describing dynamics in patch \( i \) is:

\[
\frac{dN_i}{dt} = N_0 - \eta N_i - \frac{rN_iU_i}{\gamma(k + N_i)}
\]

\[
\frac{dU_i}{dt} = U_i\left(\frac{rN_i}{k + N_i} - m_i - g_iU_i\right) - D(U_i - \frac{1}{2} U_{i-1} - \frac{1}{2} U_{i+1}), i = 1, 2, ..., n
\]

where \( N_i(t) \) is the nutrient concentration, \( U_i(t) \) is the consumer biomass, \( N_0 \) is the nutrient input, \( r \) is the growth rate, \( \gamma \) is the yield, or fraction of nutrient per unit biomass, \( k \) is the half saturation coefficient, \( m_i \) is the mortality rate, \( g_i \) is the density-dependent loss rate, and \( D \) is the symmetric diffusion rate.

In order to provide plausible alternative representations of their experimental nutrient-yeast dynamics, Zhang et al. [18] proposed two special cases, one of which is \( \eta = 0, m_i = 0 \). Then the two-patch system (3) can be extended to one with asymmetric diffusion rates:

\[
\frac{du_1}{dt} = u_{01} - \frac{ru_1v_1}{1 + u_1}
\]

\[
\frac{dv_1}{dt} = v_1\left(\frac{ru_1}{1 + u_1} - g_1v_1\right) - Dv_1 + sDv_2
\]

\[
\frac{du_2}{dt} = u_{02} - \frac{ru_2v_2}{1 + u_2}
\]

\[
\frac{dv_2}{dt} = v_2\left(\frac{ru_2}{1 + u_2} - g_2v_2\right) - sDv_2 + Dv_1
\]

where

\[
s > 0, \quad u_{01} = \frac{N_0}{k}, \quad g_i := k\gamma g_i, \quad u_i = \frac{N_i}{k}, \quad v_i = \frac{U_i}{k\gamma}, \quad i = 1, 2.
\]

\[
(5)
\]
We consider solutions of system (4) with nonnegative initial values $u_i(0) \geq 0, v_i(0) \geq 0, i = 1, 2$.

The model describing dynamics in patch 1 with no diffusion (i.e., $D = 0$) is

$$
\frac{du_1}{dt} = u_0 - \frac{ru_1v_1}{1 + u_1},
$$

$$
\frac{dv_1}{dt} = v_1 \left( \frac{ru_1}{1 + u_1} - g_1v_1 \right).
$$

Theorem 2.1. There is no periodic solution in system (6).

Proof. Let $f_1$ and $f_2$ be the right-hand side of (6). Let $B = 1/v_1$. Then

$$
\frac{\partial (Bf_1)}{\partial u_1} + \frac{\partial (Bf_2)}{\partial v_1} = -\frac{r}{(1 + u_1)^2} - g_1 < 0.
$$

By the Dulac’s Criterion [10], there is no periodic solution in system (6).

Since system (6) has a solution $v_1 = 0$, the $u_1$-axis is an invariant set of (6). From the first equation of (6), solutions of (6) on the $u_1$-axis converge to infinity. On the $v_1$-axis, we have $du_1/dt = u_0 > 0, dv_1/dt = 0$. Since the $u_1$-axis is invariant, solutions of system (6) are nonnegative.

System (6) has two isoclines:

$$
l_1: (v_1 - \frac{u_0}{r})u_1 = \frac{u_0}{r},
$$

$$
l_2: \left( \frac{r}{g_1} - v_1 \right)(1 + u_1) = \frac{r}{g_1}.
$$

Then both isoclines are hyperbolas and $l_1$ has asymptotes $u_1 = 0, v_1 = u_0/r$ while $l_2$ has asymptotes $u_1 = -1, v_1 = r/g_1$.

When $u_0 < r^2/g_1$, system (6) has a unique positive equilibrium, while phase portrait analysis exhibits that solutions of (6) are bounded, as shown in Fig. 1. If $u_0 \geq r^2/g_1$, system (6) has no positive equilibrium and solutions $(u_1(t), v_1(t))$ of (6) with positive initial values satisfies $\lim_{t \to \infty} u_1(t) = \infty$, $\lim_{t \to \infty} v_1(t) = u_0/r$. Thus, in the following discussion, we assume

$$
u_0 < \frac{r^2}{g_1}, u_0 < \frac{r^2}{g_2}.
$$

Let $E_1^+(u_1^+, v_1^+)$ be the positive equilibrium of (6). Then we have

$$
u_1^+ = \frac{rv_1^+}{rv_1^+ - u_0},
$$

$$
v_1^+ = \sqrt{\frac{u_0}{g_1}} < r.
$$

Let $h_1 = 1/(1 + u_1)$. Then the Jacobian matrix of (6) at $E_1^+$ is

$$
J_1^+ = \begin{pmatrix}
-rv_1^+h_1^2 & -ru_1h_1 \\
rv_1^+h_2^2 & -g_1v_1
\end{pmatrix}.
$$

Then $\text{tr}J_1^+ = -rv_1^+h_1^2 - g_1v_1 < 0$ and $\det J_1^+ = rv_1^+h_1^2g_1 + rv_1^+u_1h_1^2 > 0$, which implies that $E_1^+$ is asymptotically stable. By Theorem 2.1, it is globally asymptotically stable.

Therefore, we conclude dynamics of system (6) as follows.

Theorem 2.2. (i) Solutions of system (6) are nonnegative.

(ii) Assume $u_0 < r^2/g_1$. Solutions of system (6) are bounded and there is a unique positive equilibrium $E_1^+(u_1^+, v_1^+)$ in (6), which is globally asymptotically stable as shown in Fig. 1.
(iii) If $u_{01} \geq r^2/g_1$, solutions $(u_1(t), v_1(t))$ of (6) with nonnegative initial values satisfy $\lim_{t \to \infty} v_1(t) = \infty$, $\lim_{t \to \infty} v_1(t) = u_{01}/r$.

Since dynamics of the species in patch 2 can be described by a statement similar to that in Theorem 2.2, we omit the details.

3. The stable equilibrium. Now we consider existence of a stable positive equilibrium in system (4), which is basic for analyzing TRAPAs in the next section.

Assume that $\epsilon_0 > 0$ is sufficiently small. Denote

$$g_m = \min\{g_1, g_2\}, \quad g_M = \max\{g_1, g_2\}, \quad v_M = \frac{2r}{g_m} + \epsilon_0,$$

$$u_{im} = \frac{u_{0i}}{rv_M - u_{0i}}, \quad u_m = \min_{i=1,2}\{u_{im}\}, \quad v_m = \frac{ru_m}{g_M(1 + u_m)} - \epsilon_0,$$

$$v_i^0 = \frac{ru_m}{1 + u_m} - (1 + s)D + \sqrt{(\frac{ru_m}{1 + u_m} - (1 + s)D)^2 + 4g_isDv_m} - \epsilon_0,$$

$$u_i^0 = \frac{u_{0i}}{ru_i^0 - u_{0i}} + \epsilon_0, \quad i = 1, 2.$$

First, we show that when the input rates $u_{0i}$ are small, solutions of system (4) are bounded.

**Theorem 3.1.** (i) Solutions of system (4) are nonnegative.

(ii) If there is $\epsilon_0 > 0$ such that $v_m > 0, v_i^0 > 0$ and $u_{0i} < \min\{rv_M, rv_i^0\}, i = 1, 2$, then solutions of system (4) are bounded.

**Proof.** (i) On the boundary $u_1 = 0$, from the first equation of (4) we have $du_1/dt = u_{01} > 0$. Then $u_1(t) > 0$ as $t > 0$. Similarly, $u_2(t) > 0$ as $t > 0$.

On the boundary $v_1 = 0$, from the second equation of (4) we have $dv_1/dt = sDv_2$. If $v_2 > 0$, then $dv_1/dt > 0$, which implies that $v_1(t)$ is nonnegative as $t$ increases. Assume $v_2 = 0$. Since $v_1 = 0$ is an invariant set of system (4) as $v_2 = 0$, no orbit could pass through the invariant set, which implies that $v_1(t)$ is nonnegative. Thus $v_1(t) \geq 0$ as $t > 0$. Similarly, $v_2(t) \geq 0$ as $t > 0$.

(ii) Boundedness of the solutions is shown as follows. From the second and fourth equations of (4), we have

$$\frac{d(v_1 + v_2)}{dt} < \sum_{i=1}^{2} v_i(r - g_i v_i) < r(v_1 + v_2) - \frac{g_m}{2}(v_1 + v_2)^2$$

which implies $\limsup_{t \to \infty} v_1(t) + v_2(t) \leq \frac{2r}{g_m}$ by the comparison theorem [7]. Thus, when $t$ is sufficiently large, we have $v_1 + v_2 < v_M$, which implies

$$\frac{du_1}{dt} > u_{01} - \frac{ru_1v_M}{1 + u_1}.$$

Then $\limsup_{t \to \infty} u_1(t) \geq u_{1m}$. Thus, when $t$ is sufficiently large, we obtain $u_1(t) > u_{1m} - \epsilon_0 > 0$. Similarly, we have $u_2(t) > u_{2m} - \epsilon_0 > 0$ when $t$ is sufficiently large.

From the second and fourth equations of (4), we have

$$\frac{d(v_1 + v_2)}{dt} > \frac{ru_m}{1 + u_m}(v_1 + v_2) - g_M(v_1 + v_2)^2$$

when $t$ is sufficiently large. Then we have $v_1(t) + v_2(t) > v_m > 0$ when $t$ is sufficiently large, i.e., $v_2 > v_m - v_1$. From the second equation of (4) we have
\[ \frac{dv_1}{dt} > -g_1 v_1^2 + \frac{ru_m}{1 + u_m} - (1 + s)Dv_1 + sDv_m. \]

The righthand side of the above equation is a parabola and convex downward. Thus, \( v_1(t) > v^0_1 > 0 \) when \( t \) is sufficiently large. Similarly, we obtain \( v_2(t) > v^0_2 \) when \( t \) is sufficiently large. Then from the first equation of (4), we have

\[ \frac{du_1}{dt} < u_{01} - \frac{ru_1 v^0_1}{1 + u_1} \]

which implies \( u_1(t) < u^0_1 \) when \( t \) is sufficiently large. Similarly, we obtain \( u_2(t) < u^0_2 \) when \( t \) is sufficiently large. This completes the proof. \( \square \)

**Theorem 3.2.** Under the conditions in Theorem 3.1(ii), system (4) is uniformly persistent and has at least one positive equilibrium.

**Proof.** Since

\[ \frac{du_i}{dt}|_{u_i=0} = u_{0i} > 0, \quad \frac{dv_1}{dt}|_{v_1=0, v_2>0} = sDv_2 > 0, \quad \frac{dv_2}{dt}|_{v_2=0, v_1>0} = Dv_1 > 0, \quad i = 1, 2 \]

all solutions of (4) will not converge to the plane \( u_i = 0, v_i = 0, i = 1, 2 \). Let \( v_1(0) = v_2(0) = 0 \). Then we obtain a nonnegative solution \( v_i(t) \equiv 0 \) and \( u_i(t) = u_i(0) \exp(u_i t) \) for \( t > 0, i = 1, 2 \). From the Acyclic Theorem by Butler et al. [5], system (4) is uniformly persistent and has at least one positive equilibrium. \( \square \)

Uniqueness of the positive equilibrium \( E(u_1, v_1, u_2, v_2) \) of (4) is shown as follows. From the first and third equations of (4) we obtain

\[ u_1 = \frac{u_{01}}{rv_1 - u_{01}}, \quad u_2 = \frac{u_{02}}{rv_2 - u_{02}}. \] (7)

Then from the second and fourth equations of (4) we have

\[ L_1 : v_2 = f_2(v_1) = \frac{g_1}{sD} v_1^2 + \frac{1}{s} v_1 - \frac{u_{01}}{sD}, \]
\[ L_2 : v_1 = f_1(v_2) = \frac{g_2}{D} v_2^2 + s v_2 - \frac{u_{02}}{D}. \] (8)

The curve \( L_1 \) is a parabola with \( f_2(0) < 0 \) and is convex downward, while the curve \( L_2 \) is a parabola with \( f_1(0) < 0 \) and is convex leftward. Thus, there is a unique intersection point \((v^*_1, v^*_2)\) of parabolas \( L_1 \) and \( L_2 \) in the first quadrant of the \((v_1, v_2)\)-plane.

From (8), \((v^*_1, v^*_2)\) satisfies

\[ f_{12}(v_1) = f_1(f_2(v_1)) - v_1 = \frac{g_2}{D} (\frac{g_1}{sD} v_2^2 + \frac{1}{s} v_1 - \frac{u_{01}}{sD})^2 + \frac{g_1}{D} v_1^2 - \frac{u_{01} + u_{02}}{D} = 0, \]
\[ f_{21}(v_2) = f_2(f_1(v_2)) - v_2 = \frac{g_1}{sD} (\frac{g_2}{D} v_2^2 + s v_2 - \frac{u_{02}}{D})^2 + \frac{g_2}{sD} v_2^2 - \frac{u_{01} + u_{02}}{sD} = 0. \] (9)

Stability of equilibrium \( E^* \) is shown as follows. Let \( h_i = 1/(1 + u_i), i = 1, 2 \). The Jacobian matrix of (5) at \( E^* \) is

\[ J^* = \begin{pmatrix} J_{11} & J_{12} & 0 & 0 \\ -J_{11} & J_{22} & 0 & sD \\ 0 & 0 & J_{33} & J_{34} \\ 0 & D & -J_{33} & J_{44} \end{pmatrix} \]
where
\[ J_{11} = -r v_1 h_1^2, \quad J_{12} = -r v_1 h_1, \quad J_{22} = -g_1 v_1 - s D \frac{v_2}{v_1}, \]
\[ J_{33} = -r v_2 h_2^2, \quad J_{34} = -r v_2 h_2, \quad J_{44} = -g_2 v_2 - D \frac{v_1}{v_2}. \]

Then \( J_{ij} < 0 \) and the characteristic equation of \( J^* \) is
\[ \lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0 \]
where
\[ a_1 = -J_{11} - J_{22} - J_{33} - J_{44} > 0, \]
\[ a_2 = J_{11} J_{12} + J_{11} J_{22} + J_{33} J_{34} + J_{33} J_{44} - s D^2 + (J_{11} + J_{22})(J_{33} + J_{44}), \]
\[ a_3 = -J_{11} (J_{12} + J_{22})(J_{33} + J_{44}) - J_{33} (J_{34} + J_{44})(J_{11} + J_{22}) + (J_{11} + J_{33}) s D^2, \]
\[ a_4 = J_{11} J_{33} [(J_{12} + J_{22})(J_{34} + J_{44}) - s D^2] \]
\[ = \frac{J_{11} J_{33}}{v_1 v_2} [(g_1 v_1^2 + u_01)(g_2 v_2^2 + u_02) + (g_1 v_1^2 + u_01)Dv_1 + (g_2 v_2^2 + u_02)Dv_2] > 0. \]

Recall that it is guaranteed that there is at least one positive equilibrium \( E^* \) in (4) by Theorem 3.2. Thus, we conclude the following result by the Hurwitz Criterion [10].

**Theorem 3.3.** Under the condition in Theorem 3.1(ii), there exists a unique positive equilibrium \( E^* \) in system (4). \( E^* \) is asymptotically stable if
\[ a_1 a_2 - a_3 > 0, \quad a_1 a_2 a_3 - a_3^2 - a_1^2 a_4 > 0. \]

When \( D \to \infty \), equations in (9) imply
\[ \lim_{D \to \infty} f_{12}(v_1)D = g_2 \left( \frac{v_1}{s} \right)^2 + g_1 v_1^2 - \frac{u_01 + u_02}{s}, \]
\[ \lim_{D \to \infty} f_{21}(v_2)D = g_1 \left( \frac{sv_2}{s} \right)^2 + g_2 v_2^2 - \frac{u_01 + u_02}{s}. \]

Let
\[ \lim_{D \to \infty} f_{12}(v_1)D = \lim_{D \to \infty} f_{21}(v_2)D = 0, \]
we obtain
\[ v_1^* = sv_2^* = s \sqrt{\frac{u_01 + u_02}{s^2 g_1 + g_2}}. \]

When \( D \to \infty \), a direct computation shows
\[ a_1 \propto \left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right)D > 0, \]
\[ a_2 \propto -\left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right)(J_{11} + J_{33})D > 0, \]
\[ a_3 \propto [J_{11} J_{33} \left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right) + J_{11} J_{12} \frac{v_1}{v_2} + J_{33} J_{34} \frac{sv_2}{v_1}]D > 0, \]
\[ a_4 \propto -J_{11} J_{33} \left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right)D > 0, \]
so that
\[ a_1 a_2 - a_3 \propto -\left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right)^2 (J_{11} + J_{33})D^2 > 0, \]
\[ a_1 a_2 a_3 - a_3^2 - a_1^2 a_4 = a_3 (a_1 a_2 - a_3) - a_1^2 a_4 \]
\[ \propto -\left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right)^2 [J_{11} J_{33} (J_{11} + J_{33}) \left( \frac{v_1}{v_2} + \frac{sv_2}{v_1} \right) + J_{11} J_{12} \frac{v_1}{v_2} + J_{33} J_{34} \frac{sv_2}{v_1}]D^3 > 0, \]
which implies that the positive equilibrium $E^*$ is asymptotically stable.
Therefore, we conclude the following result.

**Theorem 3.4.** Under the condition in Theorem 3.1(ii), system (4) has a unique positive equilibrium $E^*(u_1^*, v_1^*, u_2^*, v_2^*)$, which is asymptotically stable when $D$ is sufficiently large (i.e., $D \to \infty$).

**Remark 1.** While the unique positive equilibrium $E^*$ of system (4) is shown to be locally asymptotically stable in Theorems 3.3 and 3.4, it may be globally asymptotically stable in int$R_+^4$ as shown by numerical simulations in Section 5.

4. **Asymptotic population abundance.** In this section, we compute four types of TRAPA and provide comparisons between them. Denote

$T_0 = TRAPA_{\text{heterogeneous, no diffusion}}, T_1 = TRAPA_{\text{heterogeneous, diffusion}},$

$T_2 = TRAPA_{\text{homogeneous, no diffusion}}, T_3 = TRAPA_{\text{homogeneous, diffusion}}.$

Zhang et al. [18] studied the case of symmetric diffusion rates (i.e., $s = 1$) and obtained the following result.

**Theorem 4.1.** [18] Assume $u_{01} \neq u_{02}, s = 1$.

(i) If $g_1 = g_2$, then $T_1 > T_0$.

(ii) If $g_1 \neq g_2$, then $T_2 > T_1$.

Now we consider the case of asymmetric diffusion rates (i.e., $s \neq 1$). Without loss of generality, we assume $g \geq 1$. Let $u_{\text{mean}} = (u_{01} + u_{02})/2$. When there is no diffusion (i.e., $D = 0$), subsystem (6) for patch 1 has a unique positive equilibrium $E^+_1 (u_1^*, v_1^*)$, which is globally asymptotically stable. A similar discussion can be given for patch 2. Thus, we obtain

$T_0 = v_1^* + v_2^* = \sqrt{\frac{u_{01}}{g_1}} + \sqrt{\frac{u_{02}}{g_2}}, T_2 = \sqrt{\frac{u_{\text{mean}}}{g_1}} + \sqrt{\frac{u_{\text{mean}}}{g_2}}.$

When there is diffusion and the diffusion rate approaches very large values (i.e., $D \to \infty$), we have the following result by (10)

$T_1 = v_1^* + v_2^* = (1 + s)\sqrt{\frac{u_{01} + u_{02}}{s^2 g_1 + g_2}}, T_3 = T_1.$

Denote

$u_0 = \frac{u_{01}}{u_{02}}, g = \frac{g_1}{g_2}, a = -1 + g + 2\sqrt{u_0 g} > 0, b = -2(u_0 + 1) < 0,$

$c = \frac{1 - g}{g} u_0 + 2\sqrt{\frac{u_0}{g}}, \Delta = b^2 - 4ac, s = \frac{-b \pm \sqrt{\Delta}}{2a}, \bar{u}_0 = \frac{4g}{(g-1)^2}$ as $g \neq 1.$

**Theorem 4.2.** Assume $g \geq 1$. Then $T_1 > T_0$ if and only if one of the following conditions is satisfied: (i) $g = 1, u_0 \neq 1$ and $s_- < s < s_+$; (ii) $g > 1, u_0 \geq \bar{u}_0$ and $s < s_+; (iii) g > 1, u_0 < \bar{u}_0, \Delta > 0$ and $s_- < s < s_+$.

**Proof.** Let

$f(s) = T_1(s)^2 - T_0(s)^2 = \frac{-1}{s^2 g + 1}(as^2 + bs + c).$

Then the function $f(s)$ is a parabola and is convex upward.

(i) When $g = 1$, we have

$f(s) = \frac{-2}{s^2 g + 1}(\sqrt{u_0 s} - (u_0 + 1)s + \sqrt{u_0})$. 

Then \( s_+ = (\sqrt{u_0})^{\pm 1} \). When \( u_0 \neq 1 \), we obtain the result in (i).

(ii) When \( u_0 \geq u_0 \), we have \( c \leq 0 \) and \( s_- \leq 0 \), which implies the result in (ii).

(iii) When \( u_0 < \bar{u}_0 \), we have \( c > 0 \), which implies the result in (iii). \( \square \)

From the proof of Theorem 4.2, we have the following result.

**Corollary 1.** Assume \( g \geq 1 \). Then \( T_1 < T_0 \) if and only if one of the following conditions is satisfied: (i) \( g = 1, u_0 \neq 1 \), \( s < s_- \) or \( s > s_+ \); (ii) \( g = 1, u_0 = 1 \) and \( s \neq 1 \); (iii) \( g > 1, u_0 \geq \bar{u}_0 \) and \( s > s_+ \); (iv) \( g > 1, u_0 < \bar{u}_0, \Delta \geq 0 \), \( s < s_- \) or \( s > s_+ \); (v) \( g > 1, u_0 < \bar{u}_0, \Delta < 0 \).

Theorem 4.2 makes sense biologically. Recall that \( g = g_1/g_2 > 1 \) means that intraspecific competition in patch 1 is stronger than that in patch 2 (i.e., \( g_1 > g_2 \)), and \( u_0 = u_{01}/u_{02} \geq u_0 \) means that the nutrient input in patch 1 is relatively larger than that in patch 2 (i.e., \( u_{01} \geq u_{02} u_0 \)). (a) As shown in Theorem 4.2(i), we obtain \( T_1 > T_0 \) when \( g = 1, u_0 \neq 1 \) and \( s_- < s < s_+ \). Here, the two patches have the same intraspecific competition degrees, but have different nutrient inputs. Thus, weak asymmetric diffusion (i.e., \( s_- < s < s_+ \)) can sufficiently utilize the nutrient input in each patch and increase species’ population density (i.e., \( T_1 > T_0 \)). On the contrary, strong asymmetric (i.e., \( s > s_+ \) or \( s < s_- \)) will result in wasting resources in one of the patches, which leads to \( T_1 < T_0 \). (b) As shown in Theorem 4.2(ii), we obtain \( T_1 > T_0 \) when \( g > 1, u_0 > \bar{u}_0 \) and \( s < s_+ \). The reason is that although the nutrient input in patch 1 is relatively large, the intraspecific competition in it is strong. Thus, small asymmetric diffusion from patch 2 to 1 (i.e., \( s < s_+ \)) would lead to \( T_1 > T_0 \). (c) As shown in Theorem 4.2(iii), we obtain \( T_1 > T_0 \) when \( u_0 < \bar{u}_0 \) and \( s_- < s < s_+ \). \( \Delta > 0 \). The reason is that under a combination of the condition \( \Delta > 0 \) and the low nutrient input in patch 1 (i.e., \( u_0 < \bar{u}_0 \)), weak asymmetric diffusion (i.e., \( s_- < s < s_+ \)) would lead to \( T_1 > T_0 \).

The following result exhibits conditions for \( T_2 > T_1 \). Denote

\[
a_1 = g + 2\sqrt{g} - 1, \quad b_1 = -4, \quad c_1 = \frac{1}{g} + \frac{2}{\sqrt{g}} - 1, \quad \bar{s}_+ = \frac{-b_1 \pm \sqrt{b_1^2 - 4a_1c_1}}{2a_1}.
\] (11)

Then \( b_1^2 - 4a_1c_1 = \frac{4}{g}(g - 1)^2 \geq 0 \).

**Theorem 4.3.** \( T_2 > T_1 \) if and only if one of the following conditions is satisfied: (i) \( \sqrt{g} \geq \sqrt{2} + 1, s > \bar{s}_+ \); (ii) \( \sqrt{2} - 1 < \sqrt{g} < \sqrt{2} + 1, s < \bar{s}_- \) or \( s > \bar{s}_+ \); (iii) \( \sqrt{g} = \sqrt{2} - 1, s < c_1/4 \); (iv) \( \sqrt{g} < \sqrt{2} - 1, s < \bar{s}_+ \).

**Proof.** Let \( T_2 > T_1 \). Then we have

\[
F(s) = T_2^2 - T_1^2 = \frac{1}{(s^2g + 1)g_2}(a_1s^2 + b_1s + c_1) > 0,
\]

where the function \( F(s) \) is a parabola. It is obvious that \( a_1 > 0 \) can be written as \( \sqrt{g} > \sqrt{2} - 1, c_1 > 0 \) can be written as \( \sqrt{g} < \sqrt{2} + 1 \).

If \( \sqrt{g} \geq \sqrt{2} + 1, i.e., a_1 > 0, c_1 \leq 0, we have s > \bar{s}_+ \). If \( \sqrt{2} - 1 < \sqrt{g} < \sqrt{2} + 1, i.e., a_1 > 0, c_1 > 0 \), then \( s < \bar{s}_- \) or \( s > \bar{s}_+ \). If \( \sqrt{g} = \sqrt{2} - 1, i.e., a_1 = 0, c_1 > 0 \), then \( s < c_1/4 \). If \( \sqrt{g} < \sqrt{2} - 1, i.e., a_1 < 0, c_1 > 0 \), then \( s < \bar{s}_+ \). \( \square \)

From the proof of Theorem 4.3, we have the following result.

**Corollary 2.** \( T_2 < T_1 \) if and only if one of the following conditions is satisfied: (i) \( \sqrt{g} \geq \sqrt{2} + 1, s < \bar{s}_+ \); (ii) \( \sqrt{2} - 1 < \sqrt{g} < \sqrt{2} + 1, \bar{s}_- < s < \bar{s}_+ \); (iii) \( \sqrt{g} = \sqrt{2} - 1, s > c_1/4 \); (iv) \( \sqrt{g} < \sqrt{2} - 1, s > \bar{s}_+ \).
Theorem 4.3 makes sense biologically. (I) As shown in Theorem 4.3(i), we obtain $T_2 > T_1$ when $\sqrt{g} \geq \sqrt{2} + 1$ and $s > \bar{s}_+$. Here, $\sqrt{g} = \sqrt{g_1/g_2} \geq \sqrt{2} + 1$ means that the intraspecific competition in patch 1 is strong. Thus, large asymmetric diffusion from patch 2 to 1 (i.e., $s < \bar{s}_+$) would lead to $T_2 > T_1$. (II) As shown in Theorem 4.3(iv), we obtain $T_2 > T_1$ when $\sqrt{g} < \sqrt{2} - 1$ and $s < \bar{s}_+$. Here, $\sqrt{g} < \sqrt{2} - 1$ means that the intraspecific competition in patch 1 is weak. Thus, a large diffusion from patch 1 to 2 (i.e., $s < \bar{s}_+$) would lead to $T_2 > T_1$. A similar discussion can be given for Theorem 4.3(iii). (III) As shown in Theorem 4.3(ii), we obtain $T_2 > T_1$ when $\sqrt{2} - 1 < \sqrt{g} < \sqrt{2} + 1$, $s < \bar{s}_-$ or $s > \bar{s}_+$. Here, $\sqrt{2} - 1 < \sqrt{g} < \sqrt{2} + 1$ means that the intraspecific competition in patch 1 is intermediate when compared with that in patch 2. Thus, strong asymmetric diffusion (i.e., $s < \bar{s}_-$ or $s > \bar{s}_+$) would lead to $T_2 > T_1$.

Remark 2. When $g = 1$, i.e., $g_1 = g_2$, a direct computation shows that

$$T_2 - T_3 = \sqrt{\frac{u_{\text{mean}}}{g_1}} \left[ 2 - \frac{\sqrt{2}(s+1)}{s^2+1} \right] = \sqrt{\frac{u_{\text{mean}}}{g_1}} \frac{2(s-1)^2}{\sqrt{s^2+1} \left[ 2\sqrt{s^2+1} + \sqrt{2}(s+1) \right]} \geq 0,$$

which implies $T_2 > T_3$ as $s \neq 1$. The reason is that when the two patches are symmetric, asymmetric diffusion rates will lead to asymmetric population densities in the patches, which results in the decrease of population abundance because of wasting resources.

The following result exhibits conditions for $T_2 > T_0$. Without loss of generality, we assume $g \geq 1$. Denote

$$u_0^+ = 1, \quad u_0^- = \left[ \frac{2\sqrt{g} - (g-1)}{2\sqrt{g} + g - 1} \right]^2.$$

Theorem 4.4. Assume $g \geq 1$. Then $T_2 > T_0$ if and only if one of the following conditions is satisfied: (i) $g = 1, u_0 \neq 1$; (ii) $1 < \sqrt{g} \leq 1 + \sqrt{2}$, $u_0 > u_0^+$ or $u_0 < u_0^-$; (iii) $\sqrt{g} > 1 + \sqrt{2}$ and $u_0 > u_0^+$.

Proof. Denote

$$G(u_0) = T_2^2(u_0) - T_0^2(u_0) = \frac{u_{02}}{2g_1} (a_2u_0 + b_2\sqrt{u_0} + c_2)$$

where

$$a_2 = 2\sqrt{g} + g - 1 > 0, \quad b_2 = -4\sqrt{g} < 0, \quad c_2 = 2\sqrt{g} - (g-1).$$

Then the function $G(u_0)$ is a parabola and is convex upward.

(i) When $g = 1$, we have

$$G(u_0) = \frac{1}{g} (\sqrt{u_{01}} - \sqrt{u_{02}})^2 \geq 0,$$

which implies the result in (i). When $u_0 = 1$, we have $T_2 = T_0$.

(ii) When $1 < \sqrt{g} \leq 1 + \sqrt{2}$, we have $c_2 \geq 0$, which implies the result in (ii).

(iii) When $\sqrt{g} > 1 + \sqrt{2}$, we have $c_2 < 0$, which implies the result in (iii). \qed

From the proof of Theorem 4.4, we have the following result.

Corollary 3. Assume $g \geq 1$. Then $T_2 < T_0$ if and only if one of the following conditions is satisfied:

(i) $1 < \sqrt{g} \leq 1 + \sqrt{2}$ and $u_0^- < u_0 < u_0^+$.

(ii) $\sqrt{g} > 1 + \sqrt{2}$ and $u_0 < u_0^+$. 


Theorem 4.4 makes sense biologically. (a) As shown in Theorem 4.4(i), we obtain $T_2 > T_0$ when $g = 1$, $u_0 \neq 1$. Here, $g = 1$ means that the two patches have the same intraspecific competition degree, while $u_0 \neq 1$ means that they have different nutrient inputs. Since the total nutrient input is fixed, we obtain $u_0 = u_0 \neq 1$.

(b) As shown in Theorem 4.4(ii), we obtain $T_2 > T_0$ when $1 < \sqrt{g} \leq 1+\sqrt{2}$, $u_0 > u_0^+$ or $u_0 < u_0^-$. Here, $1 < \sqrt{g} \leq 1+\sqrt{2}$ means that the intraspecific competition in patch 1 is intermediate. Thus, if the nutrient input in patch 1 is extremely large or extremely small, we have $T_2 > T_0$.

(c) As shown in Theorem 4.4(iii), we obtain $T_2 > T_0$ when $\sqrt{g} > 1+\sqrt{2}$ and $u_0 > u_0^+$. Here, $\sqrt{g} > 1+\sqrt{2}$ means that the intraspecific competition in patch 1 is strong. Thus, if the nutrient input in patch 1 is large (i.e., $u_0 > u_0^+$), we have $T_2 > T_0$.

**Remark 3.** Theorem 4.2(i) is an extension of Theorem 4.1(i), which is shown as follows. Without loss of generality, we assume $u_0 > 1$. Let $g = 1$. A direct computation shows

$$s_- = \frac{1}{\sqrt{u_0}} < 1, \quad s_+ = \sqrt{u_0} > 1.$$  

Then we obtain $s_- < 1 < s_+$, which implies that $T_1 > T_0$ by Theorem 4.2(i). Thus, in the symmetric diffusion $s = 1$, we have $T_1 > T_0$, which is the result in Theorem 4.1(i).

5. Discussion and application. This paper considers dynamics of a consumer-resource system with asymmetric diffusion, which demonstrates necessary and sufficient conditions under which populations diffusing in heterogeneous environments can reach higher total size ($T_1$) than those ($T_0$, $T_2$) in heterogeneous/homogeneous environments if non-diffusing. The results extend previous theory with symmetric diffusion and provide new insights.

Asymmetric diffusion rates can lead to the result that asymptotic population abundance (TRAPA) in heterogeneous environments is larger than that in homogeneous environments with no diffusion (i.e., $T_2 < T_1$). When the diffusion is symmetric (i.e., $s = 1$), Zhang et al. [18] exhibited $T_2 > T_1$ in both experimental observation and theoretical proof as shown in Theorem 4.1(ii). However, when the diffusion is asymmetric (i.e., $s \neq 1$), we demonstrate necessary and sufficient conditions for $T_2 < T_1$, as shown in Corollary 2. Thus, it can be expected that we would have $T_2 < T_1$ in experiments with asymmetric diffusion. For example, as shown in Corollary 2(i), when the intraspecific competition in patch 1 is strong (i.e., $\sqrt{g_1/g_2} \geq \sqrt{2}+1$), we would have $T_2 < T_1$ if the diffusion from patch 2 to 1 is small (i.e., $s < s_-$). For additional analysis on $T_2 < T_1$, we refer to the discussion after Corollary 2.

Asymmetric diffusion rates can also lead to the result that TRAPA in heterogeneous environments with diffusion is less than that in heterogeneous environments with no diffusion (i.e., $T_1 < T_0$). When the diffusion is symmetric (i.e., $s = 1$), Zhang et al. [18] exhibited $T_1 > T_0$ in both experimental observation and theoretical proof as shown in Theorem 4.1(i). However, when the diffusion is asymmetric (i.e., $s \neq 1$), we demonstrate necessary and sufficient conditions for $T_1 < T_0$ as shown in Corollary 1. For example, as shown in Corollary 1(i), when the two patches have the same intraspecific competition degree (i.e., $g_1 = g_2$) and the nutrient input in patch 1 is relatively larger than that in patch 2 (i.e., $u_{01} \geq u_{02}$), an extremely large or extremely small diffusion from patch 2 to 1 (i.e., $s > s_+$ or $s < s_-$) will result in $T_1 < T_0$. For additional analysis on $T_1 < T_0$, we refer to the
discussion after Corollary 1. Moreover, asymmetric diffusion rates can lead to the result that TRAPA in homogeneous environments with no diffusion is larger than that with asymmetric diffusion (see Remark 3).

Asymmetric diffusion rates in two-patch systems including exploitable resources lead to different results from those in systems that do not include such resources as variables. For example, as shown in Theorem 4.2(ii), when the intraspecific competition in patch 1 is strong (i.e., \( g_1 > g_2 \)), we have \( T_1 > T_0 \) if many individuals diffuse from patch 1 to 2 (i.e., \( s < \bar{s}_+ \)), which is different from condition (2) for system (1) in which the ratio of the displacement rate from patch 1 to patch 2 over the displacement rate from patch 2 is larger than a positive value (i.e., \( \frac{m_{12}}{m_{21}} > \frac{r_2}{r_1} \)).

For additional analysis on \( T_1 > T_0 \), we refer to the discussion after Theorem 4.2.

Numerical simulations confirm and extend our results. Let \( r = 0.1, u_{01} = 0.0002, g_1 = 0.001, g_2 = 0.0005, D = 100 \). Then \( u_0 = 300, \bar{u}_0 = 8, g = 2, s_+ = 4.95, \text{ and } u_{\text{mean}} = 0.0301, s_0 = 0.3292, \bar{s}_+ = 0.7158 \). As shown in Fig. 2, when \( s = 0.1 \) (i.e., \( s < s_+ \)), we obtain \( T_1 = 11.9531 > 8.5095 = T_0 \), which is consistent with Theorem 4.2(ii). As shown in Fig. 3, when \( s = 0.5 \) (i.e., \( s_0 < s < \bar{s}_+ \)), we obtain \( T_1 = 13.4364 > 13.2452 = T_2 \), which is consistent with Corollary 4.3(ii). Moreover, numerical simulations in Fig. 4 display that the unique positive equilibrium of (4) is globally asymptotically stable in int\( R^*_+ \), which extend the results in Theorems 3.2 and 3.3.

It is worth mentioning that the analysis method in this paper can be applied to the \( n \)-patch model though our analysis uses the simplest two-patch system. The properties of the \( n \)-patch model are left to be revealed in the future.

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**Figure 1.** Phase-plane diagram of system (6). Stable equilibrium is displayed by solid circle. Vector fields are shown by gray arrows. Isoclines of nutrient $u_1$ and consumer $v_1$ are represented by red and blue lines, respectively. According to parameter values in experiments by Zhang et al. (2017), let $N_{01} = 0.02$, $r = 0.1$, $k_1 = 0.1$, $\gamma = 0.01$, $g_1 = 0.0001$. Then $u_{01} = 0.2 < r^2/g_1$. Numerical simulations show that all positive solutions of (6) converge to equilibrium $E_1^+$, which is consistent with Theorem 2.1(ii).
Figure 2. Numerical simulations for comparison of $T_1$ and $T_0$ when $s$ varies. Let $r = 0.1, u_{01} = 0.06, u_{02} = 0.0002, g_1 = 0.001, g_2 = 0.0005, D = 100$. When $s = 0.1$, we obtain $T_1 = 11.9531 > 8.5095 = T_0$ by numerical computations on (4).

Figure 3. Numerical simulations for comparison of $T_1$ and $T_2$ when $s$ varies. Let $r = 0.1, u_{01} = 0.06, u_{02} = 0.0002, g_1 = 0.001, g_2 = 0.0005, D = 100$. Then $u_{\text{mean}} = 0.0301$. When $s = 0.1$, we obtain $T_1 = 13.4364 > 13.2452 = T_2$ by numerical computations on (4).
Figure 4. Numerical simulations for comparison of $T_1$ and $T_2$ when $s$ varies. Let $r = 0.1, u_{01} = 0.06, u_{02} = 0.0002, g_1 = 0.001, g_2 = 0.0005, D = 100$. When the initial values are $(1.4, 1.4, 1.4, 1.4), (3.4, 3.4, 3.4, 3.4), (4, 4, 4, 4), (7, 7, 7, 7)$ and $(8, 8, 8, 8)$, numerical computations on (4) show that all solutions converge to the same equilibrium $(0.1549, 4.4737, 0.0002, 8.9457)$, while the component $v_1(t)$ is displayed in this figure.