DYNAMICS OF A CHEMOSTAT SYSTEM WITH TWO PATCHES

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Abstract. This paper studies a diffusion model with two patches, which is derived from experiments and includes exploitable resources. Our aim is to provide theoretical proof for experimental observations and extend previous theory to consumer-resource systems with external resource inputs. First, we exhibit nonnegativeness and boundedness of solutions of the model. For one-patch subsystems, we demonstrate the global dynamics by excluding periodic solutions. For the two-patch system, we exhibit uniform persistence of the system and asymptotic stability of the positive equilibria, while the equilibria converge to a unique positive point as the diffusion tends to infinity. Then we demonstrate that homogeneously distributed resources support higher total population abundance than heterogeneously distributed resources with diffusion, which coincides with empirical observation but refutes previous theory. Meanwhile, we exhibit new conditions under which populations diffusing in heterogeneous environments can reach higher total size than if non-diffusing. A new finding of our study is that these results hold even with source-sink populations, and varying the diffusion rate can result in survival/extinction of the species. Our results are consistent with experimental observations and provide new insights.

1. Introduction. Carrying capacities in diffusion systems have puzzled researchers for years (Freedman and Waltman 1977; Zhang et al. 2017). The carrying capacity of an ecological system is the steady-state upper limit on a population’s abundance. It is fixed in the Pearl-Verhulst logistic equation with homogeneous environments, while it is not fixed in heterogeneous environments. When a species is distributed heterogeneously, spatial diffusion can increase the amount of the global population. Thus, total realized asymptotic population abundance (i.e., TRAPA, by Arditi et al. 2015) can be larger than the sum of local carrying capacities over every point in the space.

The fact that TRAPA can be larger than the total carrying capacity has been proven for a two-patch model with Pearl-Verhulst logistic growth (Freedman and
Waltman 1977; Holt 1985):
\[
\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) + D(N_2 - N_1)
\]
\[
\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) + D(N_1 - N_2)
\]
where \(r_i\) and \(K_i\) respectively represent the maximum per capita growth rate and carrying capacity in patch \(i\), and \(D\) is the diffusion rate between patches, \(i = 1, 2\). When the diffusion rate is extremely high, the total size at the stable positive equilibrium can be larger than the sum of the carrying capacities of the two patches, (i.e., \(N_1^+ + N_2^+ > K_1 + K_2\)) if and only if
\[
(K_1 - K_2) \left(\frac{r_1}{K_1} - \frac{r_2}{K_2}\right) > 0
\]
which means that the slope of patch growth rate to carrying capacity has a positive relationship with the carrying capacity. This result was shown even with source-sink populations in which one patch (the sink) is not self-sustaining (Holt 1985; Crowder et al. 2010). For example, in an experiment described by Watkinson (1995), the plant seeds of \(Cakile edentula\) were manipulated along a sand dune gradient. On the gradient, the seaward end was a source and the landward site was a sink, in which mortality was higher than reproduction. Experimental observations exhibited that the plants were abundant in the sink site because the seeds can migrate from the source to the sink site. Thus, the overall population in the heterogeneous environment with diffusion can exceed that with no diffusion. These “somewhat paradoxical” results are extended to a continuous spatial setting by Lou (2006) via a reaction-diffusion model. For further relevant works, we refer to Hutson et al. (2005), Zhang et al. (2015), DeAngelis et al. (2016), Wang and DeAngelis (2018), etc.

To test these results in real situations, Zhang et al. (2017) included exploitable resources in the previous theory, and conducted laboratory experiments in spatially distributed, single-strain populations of yeast. In their experiments, the consumer is the heterotrophic budding yeast, \(Saccharomyces cerevisiae\), while the resource is the amino acid tryptophan which is the single exploited and renewable nutrient. Varying sublethal doses of the macrolide eukaryotic antibiotic cycloheximide (i.e., Cyh) was applied to the growth media to manipulate growth rates independently of the resource level. The yeast population is spatially distributed in a 96-well microtitre plate, and the wells are linearly arrayed and linked by nearest-neighbor diffusion, while no diffusion is assumed between the two end wells. In heterogeneous distribution of resources, the wells with even number have nutrient input larger than those with odd number. In homogeneous distribution, all wells have the same nutrient input.

The experimental diffusion process conducted by Zhang et al. (2017) is as follows. First, the initial yeast had 24 h 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 h growth. This process was repeated over 9 days, and experimental data in the interior wells (i.e., not the end wells) were recorded. The empirical observations displayed a surprising
result that homogeneously distributed resources support higher total population abundance than heterogeneously distributed resources, even with species diffusion. Meanwhile, homogeneously distributed resources support the same total population abundance with or without species diffusion. The observations also exhibited that populations diffusing in heterogeneous environments can reach higher total size than if non-diffusing, in which the “extra individuals” were observed to reside in the low nutrient patches. Difference between the total sizes increases when the difference between the growth rates increases by decreasing $C_Y$ in the growth media.

Motivated from the experiments, Zhang et al. (2017) established a pair of new equations to model the chemostat system. Based on assuming nonnegativeness of solutions and existence of stable positive equilibria in the model, they confirmed the experimental observations by comparing four TRAPAs in heterogeneous/homogeneous environments with or without species diffusion, while the confirmation is not a theoretically proof (see Remarks 1 and 2). Thus, it is necessary to analyze basic properties of the model, give theoretically proof for the experimental observations and exhibit underlying reasons, and provide new insights.

The paper is organized as follows. In the next section, we describe the model, exhibit nonnegativeness and boundedness of the solutions, and display global dynamics of one-patch subsystems. Section 3 exhibits uniform persistence of the system and existence of stable positive equilibria, while relationships between four TRAPAs are proven in Section 4. Discussion and application are in Section 5.

2. Model. In this section, we describe the consumer-resource model with diffusion, exhibit nonnegativeness and boundedness of the solutions, and demonstrate global dynamics of its subsystems. Since experimental observations by Zhang et al. (2017) focused on the interior wells that can be divided into two types (i.e., low and high nutrient inputs), we focus on the model with two patches in this work.

A pair of equations for a consumer-resource system with external resource input established by Zhang et al. (2017) is, for consumer, $u(x,t)$, nutrient, $n(x,t)$

$$\frac{dn(x,t)}{dt} = N_{input}(x) - n(x,t) - \frac{r(x)n(x,t)u(x,t)}{\gamma(k + n(x,t))}$$

$$\frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u(x,t)}{\partial x^2} + \frac{r(x)n(x,t)u(x,t)}{k + n(x,t)} - m(x)u(x,t) - g(x)u(x,t)^2$$

where $n(x,t)$ is the nutrient concentration, $u(x,t)$ is the consumer biomass, $N_{input}(x)$ is the nutrient input, $r(x)$ is the growth rate, $\gamma$ is the yield, or fraction of nutrient per unit biomass, $k$ is the half saturation coefficient, $m(x)$ is the mortality rate, $g(x)$ the density-dependent loss rate, and $D$ is the diffusion rate.

According to their experiments, Zhang et al. (2017) rewrote the above equations as a spatially discrete, or patch version, along one dimension, of this model with $g_i = 0$, so the equations for multiple patches are

$$\frac{dN_i}{dt} = N_{input,i} - N_i - \frac{r_i N_i U_i}{\gamma(k + N_i)}$$

$$\frac{dU_i}{dt} = U_i \left( \frac{r_i N_i}{k + N_i} - m_i \right) - D \left( U_i - \frac{1}{2} U_{i-1} - \frac{1}{2} U_{i+1} \right)$$

where $1 \leq i \leq n$. Let

$$x_0i = \frac{N_{input,i}}{k}, \quad x_i = \frac{N_i}{k}, \quad y_i = \frac{U_i}{k\gamma}, \quad i = 1, 2, \ldots, n.$$
Then the above system for two patches can be written as
\[
\begin{align*}
\frac{dx_1}{dt} &= x_{01} - x_1 - \frac{r_1 x_1 y_1}{1 + x_1} \\
\frac{dy_1}{dt} &= y_1\left(\frac{r_1 x_1}{1 + x_1} - m_1\right) + D(y_2 - y_1) \\
\frac{dx_2}{dt} &= x_{02} - x_2 - \frac{r_2 x_2 y_2}{1 + x_2} \\
\frac{dy_2}{dt} &= y_2\left(\frac{r_2 x_2}{1 + x_2} - m_2\right) + D(y_1 - y_2).
\end{align*}
\]
(2)

We consider solutions of system (2) with nonnegative initial values.

When there is no diffusion (i.e., \(D = 0\)), model (2) becomes two subsystems. We focus on the dynamics in patch 1, while a similar discussion can be given for patch 2. The model on patch 1 is
\[
\begin{align*}
\frac{dx_1}{dt} &= x_{01} - x_1 - \frac{r_1 x_1 y_1}{1 + x_1} \\
\frac{dy_1}{dt} &= y_1\left(\frac{r_1 x_1}{1 + x_1} - m_1\right).
\end{align*}
\]
(3)

**Lemma 2.1.** There is no periodic solution in system (3).

**Proof.** Let \(G_1\) and \(G_2\) be the right-hand side of (3). Let \(F = 1/y_1\). Then

\[
\frac{\partial(FG_1)}{\partial x_1} + \frac{\partial(FG_2)}{\partial y_1} = -\frac{1}{y_1} - \frac{r_1}{(1 + x_1)^2} < 0.
\]

By the Dulac’s Criterion, there is no periodic solution in (3). \(\square\)

**Theorem 2.2.**

(i) Solutions of system (3) are nonnegative and bounded.

(ii) If \(r_1 > m_1\) and \(x_{01} > \frac{m_1}{r_1 - m_1}\), system (3) has a unique positive equilibrium \(E^+(x_1^+, y_1^+)\), which is globally asymptotically stable as shown in Fig. 1.

(iii) If \(r_1 > m_1\), \(x_{01} \leq \frac{m_1}{r_1 - m_1}\) or \(r_1 \leq m_1\), equilibrium \(E_1(x_{01}, 0)\) is globally asymptotically stable in (3).

**Proof.** From \(r_1 \leq m_1\) we have \(dy_1/dt < 0\), which implies that \(y_1 \to 0, x_1 \to x_{01}\). Thus we assume \(r_1 > m_1\) in the following discussion.

Since \(y_1 = 0\) is a solution, the \(x_1\)-axis is an invariant set of (3). System (3) has two isoclines:

\[
l_1: y_1 = f_1(x_1) = \frac{1}{r_1}(x_{01} - x_1)(1 + \frac{1}{x_1}), \quad l_2: x_1^+ = \frac{m_1}{r_1 - m_1}.
\]

Thus \(l_2\) is a vertical line and

\[
f_1(x_{01}) = 0, \quad \lim_{x_1 \to 0^+} f_1(x_1) = \infty, \quad \frac{df_1}{dx_1} = -\frac{1}{r_1}(1 + \frac{x_{01}}{x_1^2}) < 0
\]

which implies that \(l_1\) is monotonically decreasing as shown in Fig. 1. Then system (3) has at most one positive equilibrium and its solutions are nonnegative and bounded by phase portrait analysis.

Stability of equilibria in (3) is shown as follows. Let \(h_1 = 1/(1 + x_1)\). Then the Jacobian matrix of (3) is

\[
J = \begin{pmatrix}
-1 - r_1 y_1 h_1^2 & -r_1 x_1 h_1 & \\
r_1 y_1 h_1^2 & r_1 x_1 h_1 - m_1
\end{pmatrix}.
\]
There is a boundary equilibrium of (3), namely, $E_1(x_{01},0)$. $E_1$ has eigenvalues $\lambda_1^{(1)} = -1$, $\lambda_1^{(2)} = \frac{r_1x_{01}}{1 + x_{01}} - m_1$. When $\lambda_1^{(2)} > 0$, i.e., $x_{01} > \frac{m_1}{r_1 - m_1}$, there is a unique positive equilibrium $E^+(x_1^+, y_1^+)$ of (3) with

$$x_1^+ = \frac{m_1}{r_1 - m_1}, \quad y_1^+ = \frac{1}{r_1}(x_{01} - x_1^+)(1 + \frac{1}{x_1^+}).$$

(4)

The Jacobian matrix of (3) at $E^+$ is

$$J^+ = \begin{pmatrix} -1 - r_1y_1h_1^2 & -r_1x_1h_1 \\ r_1y_1h_1^2 & 0 \end{pmatrix}.$$ 

Then $\text{tr}J^+ = -1 - r_1y_1h_1^2 < 0$ and $\det J^+ = r_1^2x_1y_1h_1^3 > 0$, which implies that $E^+$ is asymptotically stable. By Lemma 2.1, $E^+$ is globally asymptotically stable. When $\lambda_1^{(2)} \leq 0$, i.e., $x_{01} \leq \frac{m_1}{r_1 - m_1}$, there is no positive equilibrium in (3), and $E_1$ is globally asymptotically stable. $\blacksquare$

Now we consider the two-patch system (2).

**Lemma 2.3.** Solutions of system (2) are nonnegative and bounded with

$$\lim \sup_{t \to \infty} \sum_{i=1}^2 (x_i(t) + y_i(t)) \leq (x_{01} + x_{02})/s, \ s = \min\{m_1, m_2, 1\}.$$

**Proof.** Assume $x_1(t_0) = 0$ for some $t_0 > 0$. From the first equation of (2) we have $dx_1/dt|_{t_0} = x_{01} > 0$. Then $x_1(t) > 0$ if $t_0 < t < t_0 + \epsilon$ for some $\epsilon > 0$. Thus $x_1(t)$ cannot be negative. By the third equation of (2), we obtain that $x_2(t)$ is nonnegative in a similar way. Thus, $x_1(t)$ and $x_2(t)$ are nonnegative.

Let $y_1(t_0) = 0$ for some $t_0 > 0$. From the second equation of (2) we have $dy_1/dt|_{t_0} = Dy_2(t_0)$. When $y_2(t_0) > 0$, we have $dy_1/dt|_{t_0} > 0$, which implies that $y_1(t)$ is nonnegative if $t$ increases. Assume $y_2(t_0) = 0$. Since $y_1(t)$ is an invariant set of system (2) if $y_2 = 0$, no orbit could pass through the invariant set, which implies that $y_1(t)$ is nonnegative. Thus $y_1(t)$ is nonnegative if $t > 0$. By the fourth equation of (2), we obtain that $y_2(t)$ is nonnegative in a similar way. Therefore, solutions of system (2) are nonnegative.

Boundedness of solutions of (2) are shown as follows. From (2) we have

$$\frac{d(x_1 + y_1 + x_2 + y_2)}{dt} = x_{01} + x_{02} - (x_1 + x_2) - (m_1y_1 + m_2y_2) \leq x_{01} + x_{02} - s(x_1 + x_2 + y_1 + y_2).$$

By the comparison theorem (Cosner, 1996), we have $\lim \sup_{t \to \infty} \sum_{i=1}^2 (x_i(t) + y_i(t)) \leq (x_{01} + x_{02})/s$. Thus there are $\delta_0 > 0$ and $T > 0$ such that when $t > T$, we have $x_i(t) \leq (x_{01} + x_{02})/s + \delta_0, y_i(t) \leq (x_{01} + x_{02})/s + \delta_0, i = 1, 2$. Therefore, solutions of (2) are bounded. $\blacksquare$

3. Uniform persistence. In this section, we show uniform persistence of system (2), which guarantees existence of a positive equilibrium. Then we exhibit that the positive equilibrium is asymptotically stable when the diffusion rate $D$ is large, and demonstrate that the limit point of the equilibrium is positive and unique if $D \to \infty$. Denote

$$D_0 = -\prod_{i=1}^2 \frac{r_i}{1 + x_{0i}} - m_i \prod_{i=1}^2 \frac{r_i}{1 + x_{0i}} - m_i.$$
Theorem 3.1.

(i) Assume \( r_i > m_i, x_{01} > \frac{m_i}{r_i - m_i}, x_{02} \leq \frac{m_i}{r_i - m_i}, i = 1, 2 \). If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) > 0 \), system (2) is uniformly persistent. If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) < 0 \), system (2) is uniformly persistent when \( 0 < D < D_0 \) and is not persistent when \( D > D_0 \).

(ii) Assume \( r_i > m_i, x_{0i} > \frac{m_i}{r_i - m_i}, i = 1, 2 \). Then system (2) is uniformly persistent.

(iii) Assume \( r_i > m_1, r_2 \leq m_2 \). If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) > 0 \), system (2) is uniformly persistent. If \( x_{01} > \frac{m_1}{r_1 - m_1} \) and \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) < 0 \), system (2) is uniformly persistent when \( 0 < D < D_0 \) and is not persistent when \( D > D_0 \).

(iv) Assume \( r_i > m_i, x_{0i} = \frac{m_i}{r_i - m_i}, i = 1, 2 \), or \( r_i \leq m_i, i = 1, 2 \). Then system (2) is not persistent, and equilibrium \( P_1(x_{01}, 0, x_{02}, 0) \) is globally asymptotically stable.

Proof. (i) On the boundary \( x_i = 0 \) for \( i = 1, 2 \), we have \( dx_i/dt = x_{0i} > 0 \), which implies that no positive solutions of (2) would approach the boundary \( x_i = 0 \).

On the boundary \( y_1 = 0 \), we have \( dy_1/dt = D y_2 \geq 0 \). If \( y_2 > 0 \), then \( dy_1/dt > 0 \), which implies that no positive solutions of (2) would approach the boundary \( y_1 = 0 \). Assume \( y_2 = 0 \). On the \((x_1, x_2)\)-plane, we can see all solutions of (2) converge to equilibrium \( P_1 \). \( P_1 \) has no stable manifold in \( \text{int} R_+^2 \), which is shown as follows. Let \( H_i = 1/(1 + x_i), i = 1, 2 \). The Jacobian matrix of (2) at \( P_1 \) is

\[
J = \begin{pmatrix}
-1 & J_{12} & 0 & 0 \\
0 & J_{22} & 0 & D \\
0 & 0 & -1 & J_{34} \\
0 & D & 0 & J_{44}
\end{pmatrix}
\]

where \( J_{12} = -r_1 x_1 H_1, J_{22} = r_1 x_1 H_1 - m_1 - D, J_{34} = -r_2 x_2 H_2, J_{44} = r_2 x_2 H_2 - m_2 - D \). The characteristic equation of \( J \) is \( (\lambda + 1)^2 \lambda^2 + a \lambda + b = 0 \) with

\[
a = 2D - \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right), \quad b = \prod_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) - D \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right).
\]

If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) > 0 \), then \( b < 0 \) and \( P_1 \) is a saddle point. The matrix \( J \) has eigenvalues \( \lambda_{1,2} = -1 \), which have eigenvectors \( v_1 = (1, 0, 0, 0) \) and \( v_2 = (0, 0, 1, 0) \), respectively. Its other eigenvalues and corresponding eigenvectors are

\[
\lambda_{3,4} = \frac{1}{2} \left[ J_{22} + J_{44} \pm \sqrt{(J_{22} + J_{44})^2 - 4(J_{22} J_{44} - D^2)} \right] \text{ with } \lambda_4 < 0
\]

\( v_3 = (0, -D, 0, J_{22} - \lambda_3), \quad v_4 = (0, -D, 0, J_{22} - \lambda_4) \)

Since \( J_{22} - \lambda_4 = [J_{22} - J_{44} + \sqrt{(J_{22} + J_{44})^2 - 4(J_{22} J_{44} - D^2)}]/2 > 0 \), \( v_4 \) does not direct toward \( \text{int} R_+^4 \), which implies that \( P_1 \) has no stable manifold in \( \text{int} R_+^4 \). Therefore, no positive solutions of (2) would approach the boundary \( y_1 = 0 \). Similarly, no positive solutions of (2) would approach the boundary \( y_2 = 0 \). Since \( P_1 \) is the unique boundary equilibrium and cannot be in a heteroclinic cycle in \( R_+^4 \), we obtain uniform persistence of system (2) by the Acyclicity Theorem of Butler et al. (1986).

If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) < 0 \) and \( 0 < D < D_0 \), then \( b < 0 \) and \( P_1 \) is a saddle point. By a proof similar to the above one, we obtain that system (2) is uniformly persistent.

If \( \sum_{i=1}^{2} \left( \frac{r_i x_{0i}}{1 + x_{0i}} - m_i \right) < 0 \) and \( D > D_0 \), then \( a > 0, b > 0 \) and \( P_1 \) is asymptotically stable. Thus system (2) is not persistent.
(ii) Let \( V = y_1 + y_2 \) and
\[
G = \{ P(x_1, y_1, x_2, y_2) : 0 < |x_i - x_{0i}| < \epsilon_i, y_i > 0 \}, \quad \epsilon_i = \frac{1}{2}(x_{0i} - \frac{m_i}{r_i - m_i}), \quad i = 1, 2.
\]
Then \( G \) is an open neighborhood of equilibrium \( P_1(x_{01}, 0, x_{02}, 0) \) in \( \text{int}R^4_{+} \). When \( P \in G \), we have
\[
\frac{dV}{dt}|_2 = y_1(\frac{r_1 x_1}{1 + x_1} - m_1) + y_2(\frac{r_2 x_2}{1 + x_2} - m_2) > 0
\]
which implies that \( P_1 \) has no stable manifold in \( \text{int}R^4_{+} \) by the Liapunov Theorem (Hofbauer and Sigmund, 1998). Since \( P_1 \) is the unique boundary equilibrium of (2), \( P_1 \) cannot be in a heteroclinic cycle in \( R^4_{+} \). From Lemma 2.3, we obtain uniform persistence of system (2) by the Acyclicity Theorem of Butler et al. (1986).

(iii) The proof is similar to that of (i).

(iv) We focus on the case \( r_i > m_i, x_{0i} < \frac{m_i}{r_i - m_i}, i = 1, 2 \), while a similar proof can be given for \( r_i \leq m_i, i = 1, 2 \).

From the first and third equations of (2) we obtain that \( \limsup_{t \to \infty} x_i(t) \leq x_{0i}, i = 1, 2 \). Let \( \delta_0 = \frac{1}{2}\min_{i=1,2}\{m_i/(r_i - m_i) - x_{0i}\} \). Then for a positive solution of (2), there exists \( T > 0 \) such that when \( t > T \), we have \( 0 < x_i(t) \leq x_{0i} + \delta_0, i = 1, 2 \).

Let \( V = y_1 + y_2 \). Then when \( t > T \), we have \( \frac{dV}{dt}|_2 = y_1(\frac{r_1 x_1}{1 + x_1} - m_1) + y_2(\frac{r_2 x_2}{1 + x_2} - m_2) \leq 0 \)
which implies that \( P_1 \) is globally asymptotically stable in \( \text{int}R^4_{+} \) by the Liapunov Theorem.

Theorem 3.1 makes sense biologically. As shown in Theorem 3.1(i)(iii), the species cannot survive in patch 2 with no diffusion since \( x_{02} \leq \frac{m_2}{r_2 - m_2} \). When the growth rates are intermediate such that \( \frac{r_2 x_{02}}{1 + x_{02}} - m_1 > 0 \) and \( \sum_{i=1}^{2}(\frac{r_i x_{0i}}{1 + x_{0i}} - m_i) < 0 \), the consumer survives in two patches when the diffusion rate is small \( 0 < D < D_0 \), which is consistent with experimental observations by Watkinson (1995). The underlying reason is that the population that diffuses from patch 1, can enhance the population of patch 2, which leads to survival of the species in two patches. However, when the diffusion rate is large \( (D > D_0) \), the species would go to extinction in the patches. The underlying reason is that the population that diffuses from patch 1, will largely go to extinction in patch 2, which results in extinction of the species in two patches. Since the consumer can persist in the system when \( 0 \leq D < D_0 \), it is the large diffusion rate \( (D > D_0) \) that results in the extinction. On the other hand, Theorem 3.1(ii) exhibits that if a species can survive in each patch with no diffusion, then it can persist in both patches with diffusion. Theorem 3.1(iv) displays that if a species cannot survive in each patch with no diffusion, then it cannot persist in both patches with diffusion. These results are consistent with our intuition.

From Theorem 3.1 we conclude the following result.

**Corollary 1.** If \( \sum_{i=1}^{2}(\frac{r_i x_{0i}}{1 + x_{0i}} - m_i) > 0 \), system (2) is uniformly persistent for \( D \in (0, \infty) \).

When system (2) is uniformly persistent, its dissipativity by Lemma 2.3 guarantees that it has a positive equilibrium \( P^* \) (Butler et al. 1986, Smith and Thieme 2010).
Theorem 3.2. Let $P^*$ be the positive equilibrium of system (2). Then $P^*$ is asymptotically stable when $D$ is large.

Proof. Let $H_i = 1/(1 + x_i), i = 1, 2$. The Jacobian matrix of (2) at $P^*$ is

$$
\bar{J}^* = \begin{pmatrix}
-1 - \bar{J}_{21} & \bar{J}_{12} & 0 & 0 \\
\bar{J}_{21} & \bar{J}_{22} & 0 & D \\
0 & 0 & -1 - \bar{J}_{43} & \bar{J}_{34} \\
0 & D & \bar{J}_{43} & \bar{J}_{44}
\end{pmatrix}
$$

where

$$
\bar{J}_{12} = -r_1x_1H_1 < 0, \quad \bar{J}_{21} = r_1y_1H_1^2 > 0, \quad \bar{J}_{22} = -D\frac{y_2}{y_1} < 0,
$$

$$
\bar{J}_{34} = -r_2x_2H_2 < 0, \quad \bar{J}_{43} = r_2y_2H_2^2 > 0, \quad \bar{J}_{44} = -D\frac{y_1}{y_2} < 0.
$$

Then the characteristic equation of $\bar{J}^*$ is $\lambda^4 + \bar{a}_1\lambda^3 + \bar{a}_2\lambda^2 + \bar{a}_3\lambda + \bar{a}_4 = 0$. When $D \to \infty$, we have

$$
\bar{a}_1 = 2 + \bar{J}_{21} + \bar{J}_{43} - \bar{J}_{22} - \bar{J}_{44} \propto D\frac{y_1}{y_2} + \frac{y_2}{y_1} > 0
$$

$$
\bar{a}_2 = -D^2 - \bar{J}_{22}(1 + \bar{J}_{21}) - \bar{J}_{12}\bar{J}_{21} - \bar{J}_{44}(1 + \bar{J}_{43}) - \bar{J}_{34}\bar{J}_{43}
$$

$$
+ (1 + \bar{J}_{21} - \bar{J}_{22})(1 + \bar{J}_{43} - \bar{J}_{44})
$$

$$
\propto D(2 + \bar{J}_{21} + \bar{J}_{43})(\frac{y_1}{y_2} + \frac{y_2}{y_1}) > 0
$$

$$
\bar{a}_3 = [-\bar{J}_{22}(1 + \bar{J}_{21}) - \bar{J}_{12}\bar{J}_{21}](1 + \bar{J}_{43} - \bar{J}_{44})
$$

$$
+ [-\bar{J}_{44}(1 + \bar{J}_{43}) - \bar{J}_{34}\bar{J}_{43}](1 + \bar{J}_{21} - \bar{J}_{22}) - D^2(2 + \bar{J}_{21} + \bar{J}_{43})
$$

$$
\propto D\{\frac{y_2}{y_1}(1 + \bar{J}_{21})(1 + \bar{J}_{43}) - \bar{J}_{34}\bar{J}_{43}\} + \frac{y_1}{y_2}[(1 + \bar{J}_{21})(1 + \bar{J}_{43}) - \bar{J}_{12}\bar{J}_{21}] > 0
$$

$$
\bar{a}_4 = [-\bar{J}_{22}(1 + \bar{J}_{21}) - \bar{J}_{12}\bar{J}_{21}][-\bar{J}_{44}(1 + \bar{J}_{43}) - \bar{J}_{34}\bar{J}_{43}] - D^2(1 + \bar{J}_{21})(1 + \bar{J}_{43})
$$

$$
\propto -D\{\frac{y_2}{y_1}(1 + \bar{J}_{21})\bar{J}_{34}\bar{J}_{43} + \frac{y_1}{y_2}(1 + \bar{J}_{43})\bar{J}_{12}\bar{J}_{21}\} > 0.
$$

Then we have

$$
\begin{vmatrix}
\bar{a}_1 & 1 & 0 \\
\bar{a}_3 & \bar{a}_2 & \bar{a}_3 \\
0 & \bar{a}_4 & \bar{a}_3
\end{vmatrix} \propto D^2(2 + \bar{J}_{21} + \bar{J}_{43})(\frac{y_1}{y_2} + \frac{y_2}{y_1})^2 > 0,
$$

$$
\begin{vmatrix}
\bar{a}_1 & 1 & 0 \\
\bar{a}_3 & \bar{a}_2 & \bar{a}_3 \\
0 & \bar{a}_4 & \bar{a}_3
\end{vmatrix} \propto D^3(\frac{y_1}{y_2} + \frac{y_2}{y_1})^2((\frac{y_1}{y_2} + \frac{y_2}{y_1})(2 + \bar{J}_{21} + \bar{J}_{43})(1 + \bar{J}_{21})(1 + \bar{J}_{43})
$$

$$
- \frac{y_2}{y_1}(1 + \bar{J}_{43})\bar{J}_{34}\bar{J}_{43} - \frac{y_1}{y_2}(1 + \bar{J}_{21})\bar{J}_{12}\bar{J}_{21} > 0.
$$

By the Hurwitz Criterion, $P^*$ is asymptotically stable when $D$ is large.

When there is diffusion and the diffusion rate approaches very large values (i.e., $D \to \infty$), that is, $D \gg y_i(\frac{1}{1 + x_i} - m_i)$, the stable positive equilibrium $P^*(x_1, y_1, x_2, y_2)$, in this limit, satisfies $y_1 \approx y_2 \approx Z$. By Lemma 2.3, equilibria $P^*$ are bounded if $D \to \infty$. Thus the sequence $\{P^* : D \in (0, \infty)\}$ has convergent subsequences, whose limit points can be written as $\bar{P}(x_1, Z, x_2, Z)$.\hfill \Box
By summing the second and fourth equations of (2) and by the first and third equations of (2), we obtain the following equations that the limit point $P(x_1, z, x_2, z)$ satisfies:

$$x_01 - x_1 - \frac{r_1 x_1 z}{1 + x_1} = 0, \quad x_02 - x_2 - \frac{r_2 x_2 z}{1 + x_2} = 0$$

$$\frac{r_1 x_1}{1 + x_1} - m_1 + \frac{r_2 x_2}{1 + x_2} - m_2 = 0.$$  \hspace{2cm} (6)

**Theorem 3.3.** Assume $\sum_{i=1}^{2} \left( \frac{r_i x_{i0}}{1 + x_{i0}} - m_i \right) > 0$. Then equation (6) has a unique positive solution $\bar{P}$.

**Proof.** The point $\bar{P}$ is positive if $\sum_{i=1}^{2} \left( \frac{r_i x_{i0}}{1 + x_{i0}} - m_i \right) > 0$. Indeed, suppose $z = 0$. Then $y_i \rightarrow 0$ if $D \rightarrow \infty$. From (2) we have $x_i \rightarrow x_{i0}$ if $D \rightarrow \infty$, which implies that $\sum_{i=1}^{2} y_i \left( \frac{r_i x_{i0}}{1 + x_{i0}} - m_i \right) > 0$ if $D \rightarrow \infty$. However, from (2), we always have $\sum_{i=1}^{2} y_i \left( \frac{r_i x_{i0}}{1 + x_{i0}} - m_i \right) = 0$ if $D \in (0, \infty)$, which forms a contradiction. Suppose $x_1 = 0$. From the first equation of (2), we have $dx_1/dt \rightarrow x_{i0} > 0$ if $D \rightarrow \infty$, which contradicts with $x_1 = 0$. Thus $x_1 > 0$. Similarly, we have $x_2 > 0$.

The positive point $\bar{P}$ is unique. Indeed, let $F_i = F_i(\Theta, x_j, y_1, x_2, y_2)$ be the left hand of (6), where $\Theta = \{x_{i0}, r_i, m_j, j = 1, 2\}$, $i = 1, 2, 3$. The Jacobian matrix of $F_i$ at $\bar{P}$ satisfies

$$\det \frac{D(F_1, F_2, F_3)}{D(x_1, x_2, z)}|_{\bar{P}} = \det \begin{pmatrix}
-1 - r_1 H_1^2 Z & 0 & -r_1 x_1 H_1 \\
0 & -1 - r_2 H_2^2 Z & -r_2 x_2 H_2 \\
r_1 H_1^2 & r_2 H_2^2 & 0
\end{pmatrix}$$

$$= -r_1^2 x_1 H_1^3 (1 + r_2 H_2^2 Z) - r_2^2 x_2 H_2^3 (1 + r_1 H_1^2 Z) < 0. \hspace{2cm} (7)$$

Let $\Theta_0 = \{x_{i0} = x_0, r_j = r, m_j = m, j = 1, 2\}$. By symmetry in (6) and Theorem 2.2, equation (6) has a unique positive solution $\bar{P}_0$. By (7) and the Implicit Function Theorem, there is a small neighborhood of $\Theta_0$ in which equation (6) has a unique positive solution $\bar{P}$. Since (7) holds for all $\Theta$ and positive solution $\bar{P}$, the Implicit Function Theorem implies that the unique positive solution $\bar{P}$ derived from $\bar{P}_0$ can be extended to all $\Theta$ with $0 < \epsilon < \sum_{i=1}^{2} \left( \frac{r_i x_{i0}}{1 + x_{i0}} - m_i \right) \leq M$, where $0 < \epsilon < M$. Let $\epsilon \rightarrow 0+, M \rightarrow \infty$, we completes the proof. \hfill \Box

4. Total population abundance. In this section, we consider relationships between four TRAPAs in heterogeneous/homogeneous resource distributions with/without consumer diffusion. Denote

$$T_0 = \text{TRAPA}_{\text{heterogeneous, no diffusion}}, \quad T_1 = \text{TRAPA}_{\text{heterogeneous, diffusion}}$$

$$T_2 = \text{TRAPA}_{\text{homogeneous, no diffusion}}, \quad T_3 = \text{TRAPA}_{\text{homogeneous, diffusion}}$$

where $\text{TRAPA}_{\text{heterogeneous, no diffusion}}$ represents the total realized asymptotic population abundance at equilibrium in heterogeneous environments without diffusion, while similar descriptions can be given for the others.

4.1. Source-source populations. This subsection considers source-source populations, in which the species can persist in each patch without diffusion. We exhibit $T_1 > T_0$ under conditions and show $T_3 = T_2 > T_1$. Let

$$x_01 = x_0 + \epsilon, \quad x_02 = x_0 - \epsilon, \quad r_i = r > m, \quad m_i = m, \quad i = 1, 2 \hspace{2cm} (8)$$

where $x_0 - \frac{m}{r - m} = \bar{\epsilon} > 0, |\epsilon| < \bar{\epsilon}$. Then system (2) has homogeneous inputs when $\epsilon = 0$. 

Theorem 4.1. Let (8) hold. Then $T_3 = T_2 > T_1$.

Proof. When there is no diffusion (i.e., $D = 0$), the positive equilibrium $P(\xi_1, \eta_1, \xi_2, \eta_2)$ of (6) satisfies

$$
x_0 + \epsilon - \xi_1 - \frac{r\xi_1\eta_1}{1 + \xi_1} = 0, \quad x_0 - \epsilon - \xi_2 - \frac{r\xi_2\eta_2}{1 + \xi_2} = 0
$$

Thus, $T_0 = \eta_1(\epsilon) + \eta_2(\epsilon), T_2 = \eta_1(0) + \eta_2(0)$.

Assume $\epsilon = 0$. Then $T_3 = 2Z$ where $Z$ is defined by (6). Since equations (6) and (9) have the same solution by Lemma 3.3, we obtain $T_3 = T_2$ because the root is unique by Theorem 2.2.

Assume $\epsilon > 0$. Then $T_1 = 2Z(\epsilon)$ where $Z$ is defined by (6). By Lemma 3.2, system (2) has a stable equilibrium $P^*$ which converges to $P(x_1, Z, x_2, Z)$ if $D \to \infty$. From the analyticity of (6), components of $P(x_1, Z, x_2, Z)$ are differentiable on $\epsilon$.

Let $H_i = 1/(1 + x_i), i = 1, 2$. By subtracting the first and second equations of (6), we have $x_1 - x_2 = \frac{2\epsilon}{1 + rZH_iH_2} > 0$. By differentiating each side of (6) on $\epsilon$, we obtain

$$
rH_1 \frac{dx_1}{d\epsilon} + rH_2 \frac{dx_2}{d\epsilon} = 0
$$

$$
1 - \frac{dx_1}{d\epsilon} - rH_1^2 \frac{dx_1}{dZ} - rx_1H_1 \frac{dZ}{d\epsilon} = 0
$$

$$
-1 - \frac{dx_2}{d\epsilon} - rH_2^2 \frac{dx_2}{dZ} - rx_2H_2 \frac{dZ}{d\epsilon} = 0.
$$

Since $x_1 > x_2$, we have

$$
\frac{dZ}{d\epsilon} = \frac{a}{b}, \quad a = \frac{rH_1^2}{1 + rH_1^2Z} - \frac{rH_2^2}{1 + rH_2^2Z} < 0, \quad b = \frac{r^2x_1H_1^3}{1 + rH_1^2Z} + \frac{r^2x_2H_2^3}{1 + rH_2^2Z} > 0.
$$

Thus $\frac{dZ}{d\epsilon} < 0$ if $\epsilon > 0$, which means $T_2 > T_1$ because $T_1(0) = T_3 = T_2$. A similar discussion could show that $T_2 > T_1$ if $\epsilon < 0$. \hfill \square

Remark. (a) Theorem 4.1 demonstrates that $T_3 = T_2 > T_1$ for general heterogeneous/homogeneous distributions of resources. Indeed, for general nutrient inputs with $x_{01} > x_{02} > \frac{m}{r - m}$, we can rewrite them as $x_{01} = x_0 + \epsilon, x_{02} = x_0 - \epsilon$ with $x_0 = (x_{01} + x_{02})/2, \epsilon = (x_{01} - x_{02})/2$.

(b) Zhang et al. (2017) displayed $T_2 > T_1$ in (2), in which $T_1$ is obtained by letting $x_i = \frac{m}{r_i - m}$ (see (D19), Supporting Information Appendix D, Zhang et al. 2017), which contradicts with (6). This is not appropriate because $x_1 > x_2$ as shown in the above proof. We perform numerical simulations as follows: let $m = 1, r_1 = r_2 = 2, x_{01} = 1.7, x_{02} = 1.3, D = 100$. From (2) we obtain $x_1 = 1.1737, x_2 = 0.8519, 2Z = 0.9744$, which coincides with the roots of (6), but is different from $x_1 = x_2 = 1.2, Z = 1$ obtained by (D19).

Next we exhibit $T_1 > T_0$ under conditions. Let

$$
x_{01} = x_0 + \epsilon, x_{02} = x_0 - \epsilon, r_1 = r + \alpha, r_2 = r - \alpha, \quad m_i = m, \quad i = 1, 2 (10)
$$

where $r > m, x_{01} > \frac{m}{r_1 - m}$ and $\epsilon \geq 0$. 
When there is no diffusion (i.e., \( D = 0 \)), system (2) has a positive equilibrium \( P(\xi_1, \eta_1, \xi_2, \eta_2) \) of (2), which satisfies

\[
x_0 + \epsilon - \xi_1 - \frac{(r + cc)\xi_1\eta_1}{1 + \xi_1} = 0, \quad x_0 - \epsilon - \xi_2 - \frac{(r - cc)\xi_2\eta_2}{1 + \xi_2} = 0
\]

\[
(r + cc)\xi_1 - m = 0, \quad (r - cc)\xi_2 - m = 0
\]

where \( \xi_i = \xi_i(\epsilon), \eta_i = \eta_i(\epsilon) \) are differentiable on \( \epsilon \) by the analyticity of (11), \( i = 1, 2 \). Then \( T_0(\epsilon) = \eta_1(\epsilon) + \eta_2(\epsilon) \).

When there is diffusion (i.e., \( D \to \infty \)), the dissipativity and uniform persistence of (2) by Theorem 3.2 guarantees that it has a positive equilibrium, whose limit point \( \bar{P}(x_1, Z, x_2, Z) \) satisfies

\[
x_0 + \epsilon - x_1 - \frac{(r + cc)x_1Z}{1 + x_1} = 0, \quad x_0 - \epsilon - x_2 - \frac{(r - cc)x_2Z}{1 + x_2} = 0
\]

\[
(r + cc)x_1 + \frac{(r - cc)x_2}{1 + x_1} - 2m = 0
\]

where \( x_i = x_i(\epsilon), Z = Z(\epsilon) \) are differentiable on \( \epsilon \) by the analyticity of (12), \( i = 1, 2 \). Then \( T_1(\epsilon) = 2Z(\epsilon) \).

If \( \epsilon = 0 \), symmetry of equations (11)-(12) implies

\[
\xi_i(0) = x_i(0), \eta_i(0) = Z(0), \quad i = 1, 2.
\]

Let

\[
c_0 = \frac{r\bar{H}_1}{1 + r\bar{H}_1^2Z + x_1(1 + 2r\bar{H}_1^2Z)}, \quad \bar{H}_1 = \frac{1}{1 + x_1}
\]

where \( \bar{x}_1, \bar{Z} \) are roots of (12) if \( \epsilon = 0 \). Then \( c_0 > 0 \).

**Theorem 4.2.** Let (10) hold. There exists \( c_0 > 0 \) such that if \( c > c_0, 0 < |\epsilon| < \epsilon_0 \), then \( T_1 > T_0 \) and \( T_1(\epsilon) - T_0(\epsilon) \) is a monotonically increasing function of \( |\epsilon| \). If \( c < c_0, 0 < |\epsilon| < \epsilon_0 \), then \( T_1 < T_0 \).

**Proof.** Let \( f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) \). From (13) we have \( f(0) = 0 \).

We show \( \frac{df}{d\epsilon}(0) = 0 \) as follows. Let \( h_i = 1/(1 + \xi_i), i = 1, 2 \). By differentiating each side of (11) on \( \epsilon \), we obtain

\[
1 - \frac{d\xi_1}{d\epsilon} - c\xi_1h_1\eta_1 - (r + cc)\xi_1^2h_1^2\eta_1\frac{d\xi_1}{d\epsilon} - (r + cc)\xi_1h_1\frac{d\eta_1}{d\epsilon} = 0
\]

\[
-1 - \frac{d\xi_2}{d\epsilon} + c\xi_2h_2\eta_2 - (r - cc)\xi_2^2h_2^2\eta_2\frac{d\xi_2}{d\epsilon} - (r - cc)\xi_2h_2\frac{d\eta_2}{d\epsilon} = 0
\]

\[
c\xi_1h_1 + (r + cc)\xi_1^2h_1^2\frac{d\xi_1}{d\epsilon} = 0
\]

\[
-c\xi_2h_2 + (r - cc)\xi_2^2h_2^2\frac{d\xi_2}{d\epsilon} = 0.
\]

By summing the first two equations and last two equations of (14) respectively and letting \( \epsilon = 0 \), we have

\[
\left( \frac{d\xi_1}{d\epsilon} + \frac{d\xi_2}{d\epsilon} \right)|_{\epsilon = 0} = -\frac{r\xi_1h_1}{1 + rh_1^2\eta_1} \left( \frac{d\eta_1}{d\epsilon} + \frac{d\eta_2}{d\epsilon} \right)|_{\epsilon = 0}
\]

\[
\left( \frac{d\xi_1}{d\epsilon} + \frac{d\xi_2}{d\epsilon} \right)|_{\epsilon = 0} = 0, \quad \left( \frac{d\eta_1}{d\epsilon} + \frac{d\eta_2}{d\epsilon} \right)|_{\epsilon = 0} = 0.
\]
Let \( H_i = 1/(1 + x_i), i = 1, 2 \). By differentiating each side of (12) on \( \epsilon \), we obtain
\[
1 - \frac{dx_1}{d\epsilon} - cx_1 H_1 Z - (r + ce) H_1^2 Z \frac{dx_1}{d\epsilon} - (r + ce) x_1 H_1 \frac{dZ}{d\epsilon} = 0
\]
\[
-1 - \frac{dx_2}{d\epsilon} + cx_2 H_2 Z - (r - ce) H_2^2 Z \frac{dx_2}{d\epsilon} - (r - ce) x_2 H_2 \frac{dZ}{d\epsilon} = 0
\]
\[
cx_1 H_1 + (r + ce) H_1^2 \frac{dx_1}{d\epsilon} - cx_2 H_2 + (r - ce) H_2^2 \frac{dx_2}{d\epsilon} = 0.
\]
(16)

Let \( \epsilon = 0 \). From the third equation of (16), we obtain \( \frac{dx_1}{d\epsilon} + \frac{dx_2}{d\epsilon} = 0 \). By summing the first and second equations of (16), we have \( \frac{dZ}{d\epsilon} = 0 \). Thus \( \frac{d\xi}{d\epsilon}(0) = 0 \).

We show \( \frac{d\xi}{d\epsilon}(0) > 0 \) as follows. By differentiating each side of (14) on \( \epsilon \) and letting \( \epsilon = 0 \), we obtain
\[
\frac{d^2 \xi_1}{d\epsilon^2} (1 + rh_1^2 \eta_1) + 2 ch_1^2 \eta_1 \frac{d\xi_1}{d\epsilon} + 2 c \xi_1 \frac{d\eta_1}{d\epsilon} - 2 rh_1^3 \eta_1 \frac{d\xi_1}{d\epsilon}^2 \\
+ 2 rh_1 \frac{d\xi_1}{d\epsilon} \frac{d\eta_1}{d\epsilon} + r \xi_1 \frac{d^2 \eta_1}{d\epsilon^2} = 0
\]
\[
\frac{d^2 \xi_2}{d\epsilon^2} (1 + rh_2^2 \eta_2) - 2 ch_2^2 \eta_2 \frac{d\xi_2}{d\epsilon} - 2 c \xi_2 \frac{d\eta_2}{d\epsilon} - 2 rh_2^3 \eta_2 \frac{d\xi_2}{d\epsilon}^2 \\
+ 2 rh_2 \frac{d\xi_2}{d\epsilon} \frac{d\eta_2}{d\epsilon} + r \xi_2 \frac{d^2 \eta_2}{d\epsilon^2} = 0
\]
\[
\frac{d^2 \eta_1}{d\epsilon^2} + \frac{d^2 \eta_2}{d\epsilon^2} = \frac{4}{r h_1 \xi_1} \left( c - h_1 \frac{d\xi_1}{d\epsilon} \right) \frac{d\xi_1}{d\epsilon}.
\]
(17)

By summing the first and second equations of (17) and summing the third and fourth equations of (17) respectively, we have
\[
\frac{d^2 \xi_1}{d\epsilon^2} + \frac{d^2 \xi_2}{d\epsilon^2} = \frac{4}{r} \left( c + rh_1 \frac{d\xi_1}{d\epsilon} \right) \frac{d\xi_1}{d\epsilon}
\]
\[
\frac{d^2 \eta_1}{d\epsilon^2} + \frac{d^2 \eta_2}{d\epsilon^2} = \frac{4}{r h_1 \xi_1} \left( c - h_1 \frac{d\xi_1}{d\epsilon} \right) \frac{d\xi_1}{d\epsilon}.
\]
(18)

By differentiating each side of (16) on \( \epsilon \) and letting \( \epsilon = 0 \), we obtain
\[
- \frac{d^2 x_1}{d\epsilon^2} (1 + r H_1^2 Z) - 2 c H_1^2 Z \frac{dx_1}{d\epsilon} + 2 r H_1^3 Z \frac{dx_1}{d\epsilon}^2 - r H_1 x_1 \frac{d^2 Z}{d\epsilon^2} = 0
\]
\[
- \frac{d^2 x_2}{d\epsilon^2} (1 + r H_2^2 Z) + 2 c H_2^2 Z \frac{dx_2}{d\epsilon} + 2 r H_2^3 Z \frac{dx_2}{d\epsilon}^2 - r H_2 x_2 \frac{d^2 Z}{d\epsilon^2} = 0
\]
\[
\frac{d^2 x_1}{d\epsilon^2} + \frac{d^2 x_2}{d\epsilon^2} = -\frac{4}{r} \left( c - r H_1 \frac{dx_1}{d\epsilon} \right) \frac{dx_1}{d\epsilon}.
\]
(19)

By summing the first and second equations of (19), we obtain
\[
- \left( \frac{d^2 x_1}{d\epsilon^2} + \frac{d^2 x_2}{d\epsilon^2} \right) (1 + r H_1^2 Z) - 4 c H_1^2 Z \frac{dx_1}{d\epsilon} + 4 r H_1^3 Z \frac{dx_1}{d\epsilon}^2 - 2 r H_1 x_1 \frac{d^2 Z}{d\epsilon^2} = 0.
\]
(20)

From the third equation of (19) and (20), we obtain
\[
\frac{d^2 (2Z)}{d\epsilon^2} = \frac{4}{r x_1 H_1} \left( c - H_1 \frac{dx_1}{d\epsilon} \right) \frac{dx_1}{d\epsilon}.
\]
(21)
When \( \epsilon = 0 \), equations (14) and (16) imply

\[
\frac{d\xi_1}{d\epsilon} = -\frac{c\xi_1}{rh_1} < 0, \quad \frac{dx_1}{d\epsilon} = \frac{1-cx_1H_1Z}{1+rH_1^2Z}.
\]

From (13), (18) and (21) we obtain

\[
\frac{d^2(2Z)}{d\epsilon^2} - \left( \frac{d^2\eta_1}{d\epsilon^2} + \frac{d^2\eta_2}{d\epsilon^2} \right) = \frac{4}{rx_1H_1^2} \left[ \frac{c}{r} \left( \frac{dx_1}{d\epsilon} - \frac{d\xi_1}{d\epsilon} \right) - H_1 \left( \left( \frac{dx_1}{d\epsilon} \right)^2 - \left( \frac{d\xi_1}{d\epsilon} \right)^2 \right) \right]
\]

\[
= \frac{4(rH_1 + cx_1)[1 + rH_1^2Z + x_1(1 + 2rH_1^2Z)]}{r^3x_1H_1^2(1 + rH_1^2Z)^2} (c - c_0)
\]

(22)

which implies \( \frac{d^2f(0)}{d\epsilon^2} > 0 \) if \( c > c_0 \).

Since \( f(0) = 0, \frac{df(0)}{d\epsilon} = 0 \) and \( \frac{d^2f(0)}{d\epsilon^2} > 0 \), the function \( f = f(\epsilon) \) is convex downward at \( \epsilon = 0 \). Thus there exists \( 0 < \epsilon_{01} < \epsilon^0 \) such that when \( 0 < |\epsilon| < \epsilon_{01}, c > c_0 \), \( f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) > 0 \) and \( T_1(\epsilon) - T_0(\epsilon) \) is a monotonically increasing function of \( |\epsilon| \).

Similarly, there exists \( 0 < \epsilon_{02} < \epsilon^0 \) such that when \( 0 < |\epsilon| < \epsilon_{02}, c < c_0 \), \( f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) < 0 \) and \( |T_1(\epsilon) - T_0(\epsilon)| \) is a monotonically increasing function of \( |\epsilon| \). Let \( \epsilon_0 = \min\{\epsilon_{01}, \epsilon_{02}\} \), then the proof is completed.

Theorem 4.2 makes sense biologically. The result that \( T_1(\epsilon) - T_0(\epsilon) \) is a monotonically increasing function of \( |\epsilon| \) implies that the larger the difference between the growth rates, the higher the difference between \( T_1 \) and \( T_0 \), which is clearly observed in experiments (see Fig. 4 in Zhang et al. 2017).

**Corollary 2.** Let (10) hold with \( c = 0 \). Then \( T_1 \leq T_0 \).

**Proof.** From \( c = 0 \) and (11), we obtain

\[
\xi_1 = \xi_2 = \frac{m}{r - m}, \quad \eta_1 = \frac{x_0 + \epsilon - \xi_1}{m}, \quad \eta_2 = \frac{x_0 - \epsilon - \xi_2}{m}.
\]

Thus \( T_0 = \eta_1 + \eta_2 = \frac{1}{m}(2x_0 - \xi_1 - \xi_2) \).

From (12), we obtain \( T_1 = 2Z = \frac{1}{m}(2x_0 - x_1 - x_2) \). By the third equation of (12), we obtain

\[
x_1 = \frac{2m - (r - 2m)x_2}{2(r - m)x_2 + r - 2m}.
\]

We focus on the case of \( r < 2m \) while a similar discussion can be given for \( r \geq 2m \).

Since \( r < 2m \) and \( x_1 > 0 \), we have \( 2(r - m)x_2 + r - 2m > 0 \) and

\[
T_1 - T_0 = -\frac{2[m - (r - m)x_2]^2}{m(r - m)[2(r - m)x_2 + r - 2m]} \leq 0.
\]

**Remark 2.** Zhang et al. (2017) exhibits \( T_1 > T_0 \) when (10) holds with \( c = 0 \), which contradicts with Corollary 2. The reason is that they obtained \( T_1 \) by letting \( x_i = \frac{m}{r_i - m_i} \), which is explained in Remark 1.
4.2. Source-sink populations. This subsection considers source-sink populations, in which the species cannot persist in one patch (the sink) without diffusion. We exhibit $T_1 > T_0$ under conditions and show $T_3 = T_2 > T_1$. Let

$$r_i = r, \ m_i = m, \ \sum_{i=1}^{2} \frac{rx_{0i}}{1 + x_{0i}} - m > 0.$$  \hspace{1cm} (23)

Then a direct computation shows $\frac{x_{01} + x_{02}}{2} > \frac{m}{r-m}$. By Corollary 1 and a proof similar to that of Theorem 4.1, we conclude the following result.

**Theorem 4.3.** Let (23) holds. Then $T_3 = T_2 > T_1$ in system (2) with source-sink populations.

Next we exhibit $T_1 > T_0$ in source-sink populations. First, we demonstrate a threshold for $T_1 > T_0$ under condition (e.g., $x_{02} = \frac{m}{r-m}$). Let

$$x_{01} = x_0 + \epsilon c, \ x_{02} = x_0, \ r_1 = r + \epsilon, \ r_2 = r, \ m_i = m, \ i = 1, 2$$  \hspace{1cm} (24)

where $c > 0, \epsilon \geq 0, x_0 = \frac{m}{r-m}$.

Note that $x_{01} > \frac{m}{r_1-m}, x_{02} = \frac{m}{r_2-m}$. Assume $D = 0$. From Theorem 2.2, we obtain that patch 2 is a sink and patch 1 is a source with a steady state $E^+(\xi_1, \eta_1)$ which satisfies

$$\xi_1 = \frac{m}{r + \epsilon - m}, \ \eta_1 = \frac{x_0 + \epsilon c - \xi_1}{m}.$$  \hspace{1cm} (25)

Note that $\sum_{i=1}^{2} \left( \frac{rx_{0i}}{1 + x_0} - m_i \right) > 0$. Then from Corollary 1, Theorems 3.2-3.3, system (2) has a stable positive equilibrium $P(x_1, y_1, x_2, y_2)$, and the limit point $\bar{P}(x_1, Z, x_2, Z)$ of the equilibrium satisfies

$$x_0 + \epsilon c - x_1 - \frac{(r + \epsilon)x_1 Z}{1 + x_1} = 0, \ x_0 - x_2 - \frac{rx_2 Z}{1 + x_2} = 0$$

$$\frac{(r + \epsilon)x_1}{1 + x_1} + \frac{rx_2}{1 + x_2} - 2m = 0$$

where $x_i = x_i(\epsilon), \ Z = Z(\epsilon)$ are differentiable on $\epsilon$ by the analyticity of (26), $i = 1, 2$.

Then $T_1 = 2Z(\epsilon)$.

If $\epsilon = 0$, equations (25)-(26) imply

$$\xi_i(0) = x_i(0) = x_0, \eta_i(0) = Z(0) = 0, \ i = 1, 2.$$  \hspace{1cm} (27)

If $\epsilon < 0$, then $x_0 + \epsilon c < m/(r+\epsilon - m)$, which implies that $\xi_i(\epsilon) = x_i(\epsilon) = x_0, \eta_i(\epsilon) = Z(\epsilon) = 0, i = 1, 2$. Let $\sigma_0 = (1 + \bar{x}_1)^2/r$ where $\bar{x}_1$ is the solution of (26) when $\epsilon = 0$.

**Theorem 4.4.** Let (24) hold. Then there exists $\epsilon_0 > 0$ such that if $0 < \epsilon < \epsilon_0, 0 < c < \sigma_0$, then $T_1 > T_0$. If $0 < \epsilon < \epsilon_0, c > \sigma_0$, then $T_1 < T_0$.

**Proof.** Let $f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) = 2Z(\epsilon) - \eta_1(\epsilon)$. From (27) we have $f(0) = 0$.

We show $\frac{df}{d\epsilon}(0) = 0$ as follows. Let $h_i = 1/(1 + \xi_i), i = 1, 2$. By differentiating each side of (11) on $\epsilon$, we obtain

$$c - \frac{d\xi_1}{d\epsilon} - \xi_1 h_1 \eta_1 - (r + \epsilon) h_1^2 \eta_1 \frac{d\xi_1}{d\epsilon} - (r + \epsilon) \xi_1 h_1 \frac{d\eta_1}{d\epsilon} = 0$$

$$\xi_1 h_1 + (r + \epsilon) h_1^2 \frac{d\xi_1}{d\epsilon} = 0$$

which implies

$$\frac{d\xi_1}{d\epsilon}(0) = -\frac{\xi_1}{r h_1}, \ \frac{d\eta_1}{d\epsilon}(0) = \frac{c r h_1 + \xi_1}{r^2 \xi_1 h_1^2}|_{\epsilon = 0} > 0.$$  \hspace{1cm} (28)
Let $H_i = 1/(1 + x_i), i = 1, 2$. By differentiating each side of (26) on $\epsilon$, we obtain

$$c - \frac{dx_1}{de} - x_1 H_1 y_1 - (r + \epsilon) H_1^2 y_1 \frac{dx_1}{de} - (r + \epsilon) x_1 H_1 \frac{dZ}{de} = 0$$

$$- \frac{dx_2}{de} - r H_2^2 y_2 \frac{dx_2}{de} - r x_2 H_2 \frac{dZ}{de} = 0$$

$$(30)$$

$$x_1 H_1 + (r + \epsilon) H_2 \frac{dx_1}{de} + r H_2^2 \frac{dx_2}{de} = 0.$$ 

Let $\epsilon = 0$ in (30). Then we have

$$\frac{dx_1}{de}(0) = c - r x_1 H_1 \frac{dZ}{de}(0), \quad \frac{dx_2}{de}(0) = -r x_1 H_1 \frac{dZ}{de}(0), \quad \frac{d(2Z)}{de}(0) = \frac{d\eta_1}{de}(0) (31)$$

which implies that $\frac{df}{de}(0) = 0$.

We show $\frac{df}{de}(0+) > 0$ as follows. By differentiating each side of (28) on $\epsilon$ and letting $\epsilon = 0$, we obtain $\eta_1(0) = 0$ and

$$- \frac{d^2 \xi_1}{de^2} - 2 \xi_1 h_1 \frac{d\eta_1}{de} = 2 r H_1^2 \xi_1 \frac{d\eta_1}{de}$$

$$2 H_1^2 \frac{d^2 \xi_1}{de^2} - 2 r h_1^2 (\frac{d\xi_1}{de})^2 = 0$$

so that

$$\frac{d^2 \xi_1}{de^2} = -2 \xi_1 h_1 \frac{d\eta_1}{de} - 2 r h_1^2 (\frac{d\xi_1}{de})^2 - r \xi_1 h_1 \frac{d^2 \eta_1}{de^2}$$

$$\frac{d^2 \eta_1}{de^2} = \frac{1}{C}[2 h_1 \frac{d\xi_1}{de} - 2 r h_1^2 (\frac{d\xi_1}{de})^2 - 2 r h_1^3 (\xi_1 + r h_1 \frac{d\xi_1}{de}) \frac{d\eta_1}{de}]$$

where $C = r^2 \xi_1 h_1^3$.

By differentiating each side of (30) on $\epsilon$ and letting $\epsilon = 0$, we obtain

$$- \frac{d^2 x_1}{de^2} - 2 x_1 H_1 \frac{dZ}{de} = 2 r H_1^2 \frac{dx_1}{de} - r x_1 H_1 \frac{d^2 Z}{de^2} = 0$$

$$- \frac{d^2 x_2}{de^2} - 2 r H_2^2 \frac{dx_2}{de} = -r x_2 H_2 \frac{d^2 Z}{de^2} = 0$$

$$(32)$$

$$2 H_1^2 \frac{d^2 x_1}{de^2} - 2 r H_1^3 \sum_{i=1}^{2} (\frac{dx_i}{de})^2 + r H_1^2 \sum_{i=1}^{2} \frac{d^2 x_i}{de^2} = 0$$

so that

$$\frac{d^2 x_1}{de^2} + \frac{d^2 x_2}{de^2} = -2 r x_1 H_1 \frac{d^2 Z}{de^2} - 2 x_1 H_1 \frac{dZ}{de} - 2 r H_1^2 \frac{dZ}{de}$$

$$= -2 r x_1 H_1 \frac{d^2 Z}{de^2} - 2 x_1 H_1 \frac{dZ}{de} - 2 r H_1^2 \frac{dZ}{de} - 2 r H_1^3 (x_1 + r H_1 \sum_{i=1}^{2} \frac{dx_i}{de}) \frac{dZ}{de}$$

$$(33)$$

From (31) we have

$$\frac{dx_1}{de} + \frac{dx_2}{de} = c - 2 r x_1 H_1 \frac{dZ}{de} = c - r \xi_1 h_1 \frac{d\eta_1}{de}$$

A direct computation shows

$$\frac{d^2 f}{de^2}(0+) = \frac{d^2 (2Z)}{de^2}(0+) - \frac{d^2 \eta_1}{de^2}(0+) = 2 r^2 x_1 H_1^3 (\sigma_0 - c) \frac{dZ}{de} |_{\epsilon=0} > 0. (34)$$
Since $f(0) = 0$, \( \frac{df}{d\epsilon}(0) = 0 \) and \( \frac{d^2 f}{d\epsilon^2}(0+) > 0 \), the function \( f = f(\epsilon) \) is convex downward if \( \epsilon \geq 0 \). Thus there exists \( \epsilon_0 > 0 \) such that \( f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) > 0 \) if \( 0 < \epsilon < \epsilon_0 \). Similarly, there exists \( \epsilon_0 > 0 \) such that \( f(\epsilon) = T_1(\epsilon) - T_0(\epsilon) < 0 \) if \( 0 < \epsilon < \epsilon_0, c > c_0 \), which implies \( T_1 < T_0 \).

Second, we exhibit \( T_1 > T_0 \) under conditions (e.g., \( x_{02} < \frac{m}{r-m} \)). Let

\[
x_{01} = x_0 + \epsilon c, x_{02} = x_0 - \epsilon, r_1 = r + \epsilon, r_2 = r - \epsilon, m_i = m, i = 1, 2 \tag{35}
\]

where \( r > m, x_0 = \frac{m}{r-m}, c \geq 0 \).

By a proof similar to that of Theorem 4.2, we obtain the following result.

**Theorem 4.5.** Let (35) hold. Let \( c < \bar{\epsilon}_0 = \frac{x_0}{rH_1}, H_1 = \frac{1}{1+x_0} \). Then there exists \( \epsilon_0 > 0 \) such that if \( 0 < |\epsilon| < \epsilon_0 \), then \( T_1(\epsilon) > T_0(\epsilon) \), and \( T_1(\epsilon) - T_0(\epsilon) \) is a monotonically increasing function of \( |\epsilon| \).

5. **Discussion and application.** This paper considers dynamics of a consumer-resource system with diffusion, which demonstrate that populations diffusing in heterogeneous environments can reach higher total size (\( T_1 \)) than that (\( T_0 \)) if non-diffusing, and homogeneously distributed resources support higher total population abundance (\( T_3 \) and \( T_2 \)) than \( T_1 \), which coincide with experimental observations by Zhang et al. (2017). The biological reason is as follows.

The inequality \( T_1 > T_0 \) in Theorem 4.2 holds if

\[
x_{01} > x_{02}, \quad \frac{r_1 - r_2}{x_{01} - x_{02}} > c_0 \tag{36}
\]

which means that for one increased unit of nutrient input in patch 1 (i.e., \( x_{01} - x_{02} = 1 \)), the increased growth rate in the patch should be larger than a certain value (i.e., \( r_1 - r_2 > c_0 \)). If \( r_1 - r_2 < c_0 \), then \( T_1 < T_0 \) by Theorem 4.2. On the other hand, the condition (1) given by Freedman and Waltman (1977) can be written as

\[
K_1 > K_2, \quad \frac{r_1 - r_2}{K_1 - K_2} > \bar{\epsilon}_0 \tag{37}
\]

where \( \bar{\epsilon}_0 = \frac{r_2}{K_2} \). Thus, while conditions in (36) and (37) are different, both of them imply that the larger the nutrient input (resp. the carrying capacity) in a patch, the higher the growth rate. That is, there is a positive relationship between resource input and growth rate since carrying capacity in a homogeneous environment is determined by resource. The biological reason for \( T_1 > T_0 \) in Theorem 4.2 is explained as follows. Assume \( x_{01} = x_0 + \epsilon, x_{02} = x_0 - \epsilon, r_1 = r + \epsilon, r_2 = r - \epsilon \) with \( \epsilon > 0, c > 0 \) and both patches approach their carrying capacities \( y_{i1}^+ \) without diffusion. From (4) we have \( y_{21}^+ < y_{11}^+ \). Then assume there is diffusion \( D: Dy_{21}^+ \) (resp. \( Dy_{11}^+ \)) individuals are transferred to patch 1 (resp. patch 2) with \( Dy_{21}^+ < Dy_{11}^+ \). Since \( r_1 \) is high, subpopulation 1 rebounds quickly to diffusion losses and subpopulation 2 remains “overfilled”, such that \( T_1 > T_0 \). This is confirmed by experimental observations that the “extra individuals” reside in the low nutrient patches. However, when \( r_1 \) is not high, the increase of \( Dy_{21}^+ \) (< \( Dy_{11}^+ \)) in patch 1 cannot compensate the loss of \( Dy_{11}^+ \) in patch 2 \( r_2 \) is low, such that \( T_1 < T_0 \). Similar discussions can be given for \( T_1 > T_0 \) (resp. \( T_1 < T_0 \)) in source-sink populations in Theorem 4.4 and the extinction of consumer because of diffusion in Theorem 3.1(iii).

The reason for \( T_3 = T_2 > T_1 \) is as follows. Assume \( x_{01} = x_0 + \epsilon, x_{02} = x_0 - \epsilon, r_1 = r_2 \) with \( \epsilon > 0 \) and both patches approach their carrying capacities without diffusion. From (4) we have \( y_{22}^+ < y_{12}^+ \). Then assume there is diffusion \( D: Dy_{22}^+ \) (resp. \( Dy_{12}^+ \)) individuals are transferred to patch 1 (resp. patch 2) with \( Dy_{22}^+ < Dy_{12}^+ \). Since
$r_1 = r_2$, the larger resource $x_{01}$ in patch 1 is wasted because $Dy_2^+ < Dy_1^+$, such that $T_1 < T_2$. The reason for $T_3 = T_2$ is that in homogeneously distributed resources, there is no difference between patches, which means there is no difference between diffusion and non-diffusion, that is, $T_3 = T_2$.

An interesting finding in Theorem 3.1 is that varying the diffusion rate can result in survival/extinction of the consumer. As shown in Theorem 3.1(i)(iii), consumer cannot persist in patch 2 without diffusion. When the growth rates are intermediate such that $r_i > m_i$ and $\sum_{i=1}^2 (r_i x_{0i} / (1 + x_{0i}) - m_i) < 0$, the consumer persists in both patches if the diffusion rate is small (i.e., $0 < D < D_0$), while it goes to extinction if the diffusion is large (i.e., $D > D_0$). The reason is that if the diffusion rate is small, subpopulation 1 has sufficient time to rebound to diffusion losses, which leads to its survival. Otherwise, the consumer goes to extinction because of the sink patch 2.

We showed $T_1 > T_0$ under condition (36), which is different from that of Zhang et al. (2017) by adding the second inequality in (36). The biological reason may be that in a well with a fixed volume in the experiments, a large nutrient input may imply a high (maximal) growth rate: the larger the input, the higher the density of the nutrient in the fixed-volume well, then the more convenient for the consumer to get the nutrient by saving time and energy, which means higher growth rate. That is, $r_i = r_i(x_{0i})$ may be an increasing function in the experiments, as required by (36). Since this assumption has not been confirmed by experiments, we’ll check it in a future work.

![Figure 1](image-url)  
**Figure 1.** Phase-plane diagram of subsystem (3). Stable and unstable equilibria are identified by solid and open circles, respectively. Vector fields are shown by gray arrows. Isoclines of the nutrient and consumer are represented by red and blue lines, respectively. Let $N_{01} = 0.02, r_1 = k = 0.1, \gamma = m_1 = 0.01$. All positive solutions of (3) converge to equilibrium $E^+(0.111, 8.85)$.

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