

Analytical classification of dispersal effects on total biomass in the presence of a weak Allee effect

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Abstract: We investigate the impact of the weak Allee effect on the total biomass of a single species inhabiting a two-patch environment connected by asymmetric dispersal. In the proposed model, the first patch exhibits logistic growth, while the second patch follows a weak Allee threshold. We establish the global existence, nonnegativity, and boundedness of solutions, and prove that the system admits a unique positive equilibrium that is globally asymptotically stable. Analytical results are derived for the asymptotic regime of high dispersal rates using singular perturbation theory, revealing an emergent weak Allee effect at the metapopulation scale. We conduct a complete classification of the parameter space to determine when dispersal increases, decreases, or has a unimodal effect on total equilibrium biomass, and provide geometric and monotonicity analyses of the equilibrium. Numerical simulations illustrate the theoretical trichotomy and highlight the ecological implications of dispersal management in fragmented landscapes. Our results generalize previous studies on logistic models to include the weak Allee effect, offering new insights into the interplay between dispersal intensity, asymmetry, and population persistence.

Keywords: population dynamics, weak Allee effect, two-patch model, asymmetric dispersal, total biomass, monotonicity analysis, singular perturbation theory, Tikhonov's theorem

MSC2020: 37N25, 92D25, 34D23, 34D15

I. INTRODUCTION

Population dynamics is a broad and active area of applied mathematics, addressing a variety of problems ranging from the persistence of species to the effects of environmental heterogeneity and migration. One classical question concerns the role of dispersal in shaping the long-term behaviour of populations in fragmented habitats. Comprehensive overviews of the mathematical and ecological aspects of such problems can be found in the works of Levin [1,2] and Holt [3].

In many ecological situations, the spatial domain is best represented as a finite set of discrete habitat patches connected by migration pathways. Examples include archipelagos inhabited by bird populations and their predators, or networks of lakes connected by streams. Such discrete-space formulations fall within the framework of *insular biogeography*. From the mathematical side, the monograph of Levin, Powell, and Steele [4] provides a thorough account of patch-dynamics models, while Hanski and Gilpin [5] present a more ecological perspective. In this setting, the central mathematical question is to determine how dispersal influences global population abundance and persistence, and to understand the consequences of habitat fragmentation.

A seminal contribution in this direction is due to Freedman and Waltman [6], who in 1977 analysed the following two-patch logistic growth model with symmetric dispersal:

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \varepsilon(x_2 - x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \varepsilon(x_1 - x_2),\end{aligned}\quad (1)$$

where $x_i(t)$ denotes the population density in patch i , $r_i > 0$ is the intrinsic growth rate, $K_i > 0$ is the carrying capacity, and $\varepsilon \geq 0$ is the symmetric dispersal rate. They showed that, under certain conditions, the total equilibrium abundance may exceed the sum of the carrying capacities, $K_1 + K_2$. Holt [3] extended these ideas to source–sink systems. More recently, Arditi et al. [7] provided a complete mathematical analysis of (1) for symmetric dispersal.

In a subsequent work, Arditi et al. [8] generalised (1) to account for asymmetric dispersal rates, leading to the model

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \varepsilon(\gamma_{12}x_2 - \gamma_{21}x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \varepsilon(\gamma_{21}x_1 - \gamma_{12}x_2),\end{aligned}\quad (2)$$

where $\gamma_{ij} > 0$ ($i \neq j$) are directional migration coefficients, and $\varepsilon\gamma_{12}$ (resp. $\varepsilon\gamma_{21}$) denotes the migration rate from patch 2 to patch 1 (resp. from patch 1 to patch 2). They observed that the positive equilibrium $(x_1^*(\varepsilon), x_2^*(\varepsilon))$ is the intersection of an ellipse and a parabola, and used a graphical method to characterise the regions of parameter space where dispersal is either beneficial or detrimental to total biomass.

Other variations of the two-patch logistic framework have been considered. Wu et al. [9] studied the asymmetric source–sink model

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \varepsilon(x_2 - s x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \varepsilon(s x_1 - x_2),\end{aligned}$$

where $s > 0$ controls the dispersal asymmetry. They showed that depending on the magnitude of s , dispersal can increase, decrease, or even drive to extinction the total population, with clear thresholds separating these behaviours.

Dispersal effects have also been investigated in the presence of *Allee effects*, where the per-capita growth rate is reduced at low population densities. For example,

Kang et al. [10] considered

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 (x_1 - \theta) (1 - x_1) + \varepsilon(x_2 - x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 (x_2 - \theta) (1 - x_2) + \varepsilon(x_1 - x_2),\end{aligned}\quad (3)$$

where θ is the Allee threshold. They showed that ε and θ strongly influence the global dynamics. System (3) corresponds to the special case of symmetric migration, namely when the dispersal rates are identical in both directions between the two patches. This simplification allows a more transparent analytical formulation and highlights the role of balanced exchanges in the population dynamics.

Another model with an *additive* Allee effect was proposed by Chen et al. [11]:

$$\begin{aligned}\frac{dx_1}{dt} &= -x_1 + \varepsilon(\gamma_{12}x_2 - \gamma_{21}x_1), \\ \frac{dx_2}{dt} &= x_2 \left(1 - x_2 - \frac{\sigma}{x_2 + a}\right) + \varepsilon(\gamma_{21}x_1 - \gamma_{12}x_2),\end{aligned}$$

where $\sigma, a > 0$ are Allee-effect parameters. They distinguished between weak ($0 < \sigma < a$) and strong ($\sigma > a$) Allee effects, and demonstrated how changes in σ , a , and dispersal rates γ_{12}, γ_{21} can alter persistence and total biomass.

A substantial literature now exists on the interaction between dispersal and Allee effects in discrete-space models; see, for instance, [10, 12–16] for studies in discrete habitats, and [17–20] for work on maximising total biomass in multi-patch environments. The present paper contributes to this line of research by incorporating a *weak* Allee effect in a two-patch logistic model with asymmetric dispersal, and by providing a complete analytical classification of how dispersal intensity influences total equilibrium biomass.

The paper is organized as follows. Section I introduces the ecological background and reviews related work. Section II presents the single-species dynamics with Allee effects. Section III formulates the two-patch model and establishes its basic properties, while Section IV analyzes its equilibria and geometric structure.

Section V studies the high-dispersal limit, and Section VI classifies the effects of dispersal on total biomass. Section VII provides a geometric interpretation, Section VIII illustrates the results with numerical simulations, and Section IX concludes the paper.

II. SINGLE-SPECIES DYNAMICS WITH ALLEE EFFECTS

We begin by considering a classical model that incorporates the Allee effect:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) (x - M), \quad (4)$$

where $x(t)$ denotes the population density at time $t \geq 0$, and $r > 0$, $K > 0$, and $M \in \mathbb{R}$ are given parameters. The parameter r is the intrinsic growth rate, K is the environmental carrying capacity, and M represents the Allee threshold. We assume throughout that $M < K$.

The Allee effect describes a phenomenon where the per-capita growth rate is reduced at low population densities. Model (4) exhibits two qualitatively distinct types of Allee effects:

- A *weak Allee effect* occurs when $M \leq 0 < K$. In this case, the per-capita growth rate remains positive for all $x > 0$, and the population can grow from arbitrarily small densities.
- A *strong Allee effect* occurs when $0 < M < K$. In this setting, the population must exceed the critical threshold M to survive, otherwise it goes extinct.

These two cases are illustrated in Figure 1.

To understand the qualitative behavior of the system, we study the equilibria of (4). The right-hand side vanishes when $x = 0$, $x = M$, or $x = K$. Hence, the model admits:

- One or two positive equilibria depending on the value of M ;
- Always the trivial equilibrium $x = 0$, representing extinction.

A. Case 1: Weak Allee Effect $M \leq 0$

In this case, all three equilibria $0 < M < K$ are ordered such that $x = 0$ is an equilibrium with *unstable* dynamics (since the growth rate is positive near the origin). The unique stable equilibrium on $\mathbb{R}_+$ is $x = K$, which is locally asymptotically stable (LAS). The population density always converges to K for any initial condition $x(0) > 0$, regardless of the magnitude of the Allee term.

B. Case 2: Strong Allee Effect $0 < M < K$

The dynamics are substantially different. In this case:

- $x = 0$ is a *locally stable* equilibrium (extinction state),
- $x = M$ is an *unstable* equilibrium (the Allee threshold),
- $x = K$ is a *locally asymptotically stable* equilibrium (saturation state).

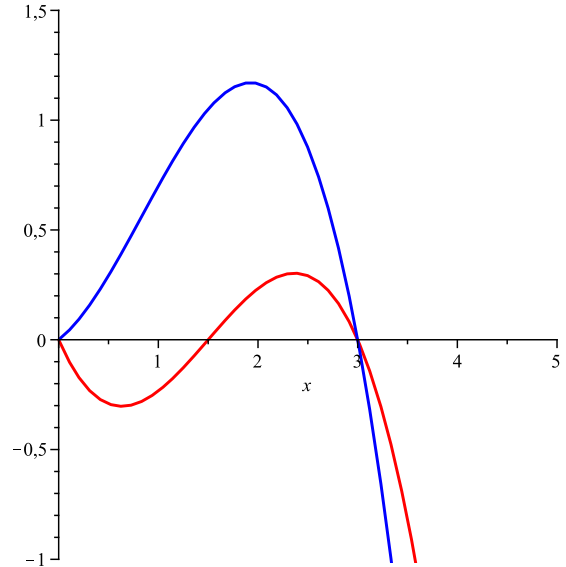


Fig. 1: Population growth rate in model (4). The blue curve corresponds to a weak Allee effect with parameters $r = 0.7$, $K = 7$, and $M = -0.5$. The red curve corresponds to a strong Allee effect with $r = 0.7$, $K = 7$, and $M = 1.5$.

The population converges to extinction if the initial population satisfies $x(0) < M$, and it converges to the carrying capacity K if $x(0) > M$. Therefore, the threshold M delineates the long-term survival of the species: it must be exceeded to escape extinction.

The qualitative behavior of system (4) can thus be summarized as follows:

- If $M < 0$, the Allee effect is weak, and every positive initial condition leads to persistence: $\lim_{t \rightarrow \infty} x(t) = K$.
- If $M > 0$, the Allee effect is strong, and extinction or survival depends on the initial condition:

$$\lim_{t \rightarrow \infty} x(t) = \begin{cases} 0, & \text{if } x(0) < M, \\ K, & \text{if } x(0) > M. \end{cases}$$

This threshold phenomenon under strong Allee effects has significant implications in conservation biology and population management, as small populations may face extinction purely due to insufficient initial density.

III. MATHEMATICAL MODEL AND PRELIMINARY RESULTS

We consider a two-patch population model where the two patches are connected via asymmetric dispersal. The first patch exhibits logistic growth, while the second patch is subject to Allee effects as described in

Equation (4). The resulting system of ordinary differential equations is given by:

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \varepsilon (\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) (x_2 - M) \\ &\quad + \varepsilon (\gamma_{21} x_1 - \gamma_{12} x_2),\end{aligned}\quad (5)$$

where $x_i(t)$ denotes the population density in patch $i \in \{1, 2\}$ at time $t \geq 0$. The parameters $r_i > 0$ and $K_i > 0$ represent the intrinsic growth rate and the carrying capacity in patch i , respectively. The constant $M \in \mathbb{R}$ is the Allee threshold in patch 2, and we assume $M \leq 0 < K_2$, which corresponds to a weak Allee effect.

From an ecological perspective, the weak Allee effect describes situations in which the per capita growth rate decreases at low population density due to mechanisms such as difficulties in mate finding, reduced cooperative interactions, or increased vulnerability to predation. Nevertheless, unlike the strong Allee effect, population persistence remains possible even at low densities, provided that the population stays positive.

In this work, the growth function adopted in Patch 2 captures these ecological features through a non-linear term of Nagumo type, which combines logistic saturation at high densities with reduced reproductive efficiency at low densities. Such formulations are commonly used in population dynamics to model species living in fragmented or heterogeneous environments where local demographic conditions may induce Allee-type responses.

The parameter $\varepsilon > 0$ denotes the global dispersal rate, while the constants $\gamma_{12} > 0$ and $\gamma_{21} > 0$ quantify the directional migration rates from patch 2 to patch 1 and from patch 1 to patch 2, respectively. The migration is said to be symmetric when $\gamma_{12} = \gamma_{21}$.

We now address the basic properties of system (5), in particular the nonnegativity and boundedness of solutions. We show that the system is well-posed in the positive quadrant and that all trajectories remain uniformly bounded over time.

Proposition 1. *Let the initial conditions be $(x_1(0), x_2(0)) \in \mathbb{R}_+^2$. Then, the solution $(x_1(t), x_2(t))$ of system (5) remains nonnegative and uniformly bounded for all $t \geq 0$. Moreover, the set Σ is positively invariant and globally attracting,*

$$\Sigma = \left\{ (x_1, x_2) \in \mathbb{R}_+^2 \mid x_1 + x_2 \leq \frac{\xi_2^*}{\xi_1^*} \right\},$$

where

$$\begin{aligned}\xi_1^* &= \min\{r_1, r_2(K_2 - M)\}, \\ \xi_2^* &= r_1 K_1 + r_2 K_2 (K_2 - M).\end{aligned}$$

Proof: We first prove the non-negativity of solutions. Let $(x_1(0), x_2(0)) \in \mathbb{R}_+^2$. Since system (5) is locally Lipschitz, it admits a unique local solution. Moreover, the non-negative quadrant $\mathbb{R}_+^2$ is positively invariant. Indeed, if $x_1(t) = 0$, then

$$\frac{dx_1}{dt}(t) = \varepsilon \gamma_{12} x_2(t) \geq 0,$$

and if $x_2(t) = 0$, then

$$\frac{dx_2}{dt}(t) = \varepsilon \gamma_{21} x_1(t) \geq 0.$$

Therefore, the vector field points inward on the boundary of $\mathbb{R}_+^2$, implying that any solution starting in $\mathbb{R}_+^2$ remains non-negative for all times for which it exists. Next, let us define the total population size

$$T(t) = x_1(t) + x_2(t).$$

Summing the two equations in (5), the migration terms cancel, and we obtain

$$\begin{aligned}\frac{dT}{dt}(t) &= r_1 x_1(t) \left(1 - \frac{x_1(t)}{K_1}\right) \\ &\quad + r_2 x_2(t) \left(1 - \frac{x_2(t)}{K_2}\right) (x_2(t) - M).\end{aligned}$$

Since $x_1(t), x_2(t) \geq 0$, we can estimate the growth terms from above. More precisely,

$$r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) \leq r_1 (K_1 - x_1),$$

and

$$r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) (x_2 - M) \leq r_2 (K_2 - M) (K_2 - x_2).$$

Consequently,

$$\frac{dT}{dt}(t) \leq -\xi_1^* T(t) + \xi_2^*,$$

where

$$\xi_1^* := \min\{r_1, r_2(K_2 - M)\},$$

and

$$\xi_2^* := r_1 K_1 + r_2 K_2 (K_2 - M).$$

Using Gronwall's inequality, we deduce that

$$T(t) \leq \left(T(0) - \frac{\xi_2^*}{\xi_1^*}\right) e^{-\xi_1^* t} + \frac{\xi_2^*}{\xi_1^*}, \quad \forall t \geq 0. \quad (6)$$

In particular,

$$T(t) \leq \max \left\{ T(0), \frac{\xi_2^*}{\xi_1^*} \right\}, \quad \forall t \geq 0.$$

Hence, both components $x_1(t)$ and $x_2(t)$ remain uniformly bounded for all time, which excludes finite-time blow-up and guarantees the global existence of solutions.

Finally, estimate (6) shows that the set

$$\Sigma = \left\{ (x_1, x_2) \in \mathbb{R}_+^2 : x_1 + x_2 \leq \frac{\xi_2^*}{\xi_1^*} \right\}$$

is positively invariant and attracts all trajectories of system (5). Therefore, Σ is a global attractor for the dynamics. ■

IV. EQUILIBRIUM ANALYSIS AND GEOMETRIC PROPERTIES OF THE TWO-PATCH MODEL WITH DISPERSAL AND WEAK ALLEE EFFECT

In the absence of migration ($\varepsilon = 0$), system (5) admits (K_1, K_2) as a nontrivial equilibrium, which is locally asymptotically stable (LAS) in $\mathbb{R}_+^2$. The origin $(0, 0)$ and the boundary equilibria $(K_1, 0)$ and $(0, K_2)$ are always unstable. For $\varepsilon > 0$, under the condition $M \leq 0$, Theorem 6 in [18] guarantees the existence of a unique positive equilibrium, denoted $E^*(\varepsilon) := (x_1^*(\varepsilon), x_2^*(\varepsilon))$, which is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{0\}$.

In the uncoupled case (no dispersal), boundary equilibria can arise from the independent local dynamics in each patch. However, once dispersal couples the patches, most boundary equilibria disappear; only the trivial equilibrium $(0, 0)$ remains on the boundary. Under our assumptions, $(0, 0)$ is unstable. Since the biological objective of this paper is to study persistence and biomass distribution between the two connected patches, our analysis focuses mainly on positive interior equilibria.

Geometrically, the equilibria of system (5) are characterized as the solutions of the algebraic system

$$\begin{aligned} 0 &= r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \varepsilon (\gamma_{12} x_2 - \gamma_{21} x_1), \\ 0 &= r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) (x_2 - M) \\ &\quad + \varepsilon (\gamma_{21} x_1 - \gamma_{12} x_2). \end{aligned} \quad (7)$$

By summing the two equations in (7), the migration terms cancel each other, showing that every equilibrium

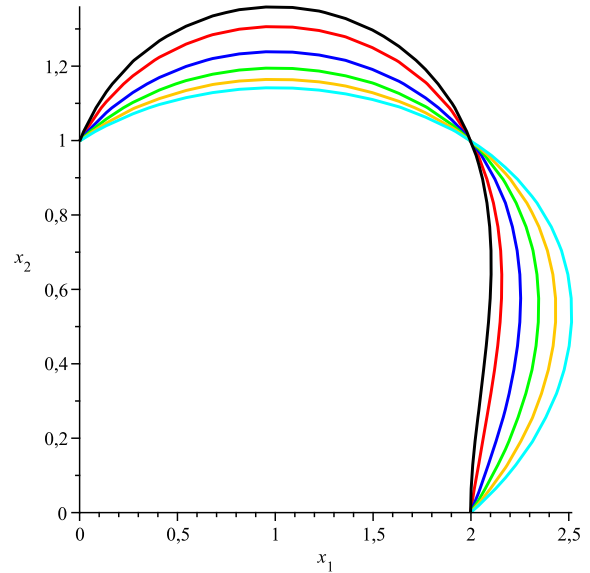


Fig. 2: The curves $\wp$ for $r_1 = 4$, $r_2 = 3$, $K_1 = 2$, $K_2 = 1$, and $M = 0$ (black curve), $M = -0.35$ (red curve), $M = -1$ (blue curve), $M = -1.65$ (green curve), $M = -2.3$ (orange curve), and $M = -2.95$ (cyan curve).

point necessarily belongs to the curve $\wp$ defined by

$$\begin{aligned} \wp : \Phi(x_1, x_2) &:= r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) \\ &\quad + r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) (x_2 - M) = 0. \end{aligned} \quad (8)$$

Hence, the curve $\wp$ represents the set of points where the total local growth of the metapopulation vanishes. In particular, $\wp$ is entirely independent of the dispersal intensity ε and of the migration coefficients γ_{ij} , meaning that dispersal only determines how the trajectories intersect this equilibrium manifold.

When $M \leq 0$, the curve $\wp$ passes through the four points

$$(0, 0), \quad (K_1, 0), \quad (0, K_2), \quad \text{and} \quad A := (K_1, K_2),$$

as illustrated in Figure 3. Moreover, the function Φ can be decomposed as

$$\Phi(x_1, x_2) = \Phi_1(x_1) + \Phi_2(x_2),$$

where

$$\Phi_1(x_1) = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right),$$

and

$$\Phi_2(x_2) = r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) (x_2 - M).$$

Since both Φ_1 and Φ_2 are concave on the biologically relevant domain, the function Φ inherits the same concavity property, which strongly constrains the geometry of $\wp$. In particular, if $(x_1, x_2) \in \wp$ satisfies $x_1 < K_1$, then necessarily $x_2 > K_2$, and conversely, if $x_2 < K_2$, then one must have $x_1 > K_1$. This property reflects the compensatory balance between the two local growth contributions along the equilibrium manifold.

Finally, Figure 2 illustrates the deformation of the curve $\wp$ for several values of the Allee threshold parameter M , highlighting the influence of the weak Allee effect on the geometry of the equilibrium set.

Solving the first equation of (7) for x_2 yields a parabola $\mathcal{P}_\varepsilon$, defined by the equation $x_2 = \varphi_\varepsilon(x_1)$, where φ_ε is given by:

$$\mathcal{P}_\varepsilon : \varphi_\varepsilon(x_1) := \frac{1}{\gamma_{12}} \left(\gamma_{21}x_1 - \frac{r_1}{\varepsilon}x_1 \left(1 - \frac{x_1}{K_1} \right) \right). \quad (9)$$

The parabola $\mathcal{P}_\varepsilon$ (shown in blue in Figure 3 for various parameter values) depends on the migration rate ε . It always passes through the origin and the point $\mathcal{B} := \left(K_1, \frac{\gamma_{21}}{\gamma_{12}}K_2 \right)$. Thus, the equilibrium points correspond to the non-negative intersections between $\wp$ and $\mathcal{P}_\varepsilon$. Consequently, $E^*(\varepsilon)$ is determined by the intersection of $\wp$ and $\mathcal{P}_\varepsilon$ (see Fig. 3) and satisfies:

$$\wp \cap \mathcal{P}_\varepsilon : \begin{cases} 0 = r_1x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) \\ \quad + r_2x_2^*(\varepsilon) \left(1 - \frac{x_2^*(\varepsilon)}{K_2} \right) (x_2^*(\varepsilon) - M), \\ x_2^*(\varepsilon) = \frac{1}{\gamma_{12}} \left(\gamma_{21}x_1^*(\varepsilon) - \frac{r_1}{\varepsilon}x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) \right). \end{cases}$$

We define the *total equilibrium population* at the positive equilibrium under dispersal rate ε as:

$$T^*(\varepsilon) = x_1^*(\varepsilon) + x_2^*(\varepsilon), \quad (10)$$

representing the total asymptotic population abundance. For $\varepsilon = 0$, the total equilibrium population is:

$$T^*(0) = K_1 + K_2. \quad (11)$$

The primary objective of this paper is to investigate the influence of the weak Allee effect and dispersal on the total population size, and to conduct a comprehensive mathematical analysis of the two-patch model (5) across the full parameter space for $M \leq 0$.

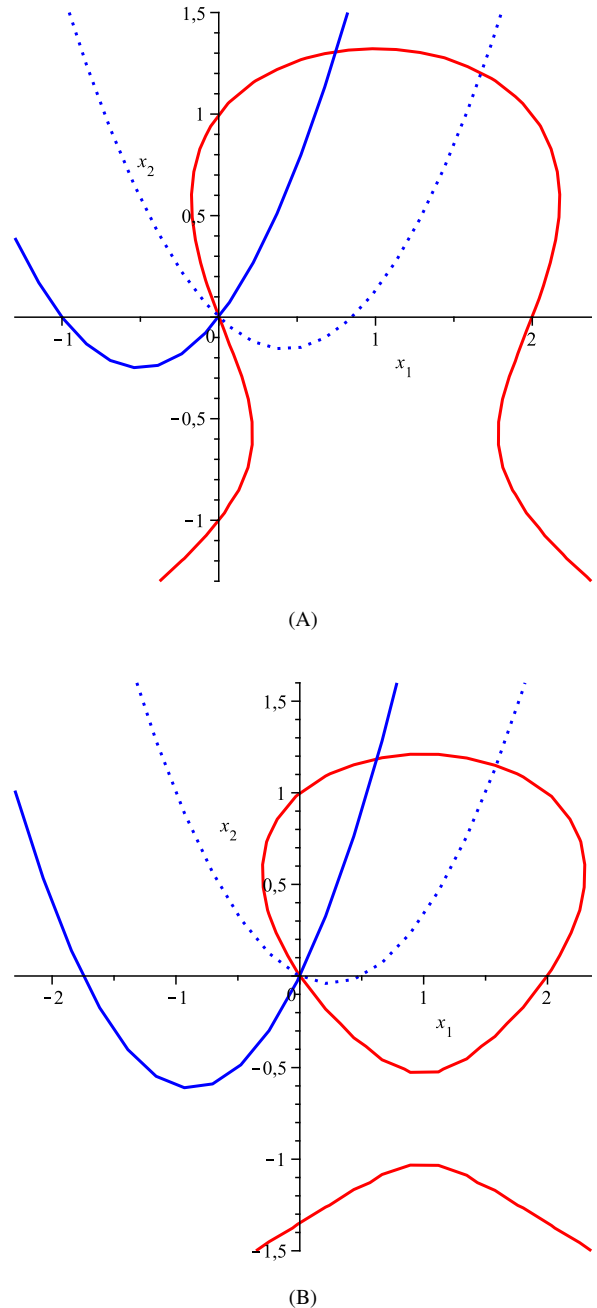


Fig. 3: Possible configurations of the curves $\wp$ (red) and $\mathcal{P}_\varepsilon$ (blue, solid and dashed lines), where $r_1 = 5$, $r_2 = 3$, $K_1 = 2$, $K_2 = 1$, $\varepsilon = 1$, $\gamma_{12} = \gamma_{21} = 2$, and the Allee threshold parameter M is -1 for case (A) and -1.35 for case (B).

V. ASYMPTOTIC BEHAVIOR OF THE MODEL UNDER HIGH DISPERSAL RATES

This section analyzes the asymptotic properties of System (5) as the migration rate becomes unbounded ($\varepsilon \rightarrow \infty$). From a biological viewpoint, the asymptotic regime $\varepsilon \rightarrow \infty$ corresponds to extremely rapid dispersal between the two patches. In this case, migration occurs on a much faster timescale than local population growth, leading to an effective homogenization of the metapopulation. Consequently, the populations in both patches rapidly approach a fixed proportional distribution determined by the dispersal coefficients. The global dynamics can then be described by a reduced aggregated equation, in which the original local parameters contribute through weighted averages reflecting the long-term spatial redistribution of the population. We have the result:

Theorem 1. Let $E^*(\varepsilon)$ denote the positive equilibrium of System (5). Then:

$$\lim_{\varepsilon \rightarrow \infty} E^*(\varepsilon) = T^*(\infty)(u_1, u_2),$$

where $u_1 = \gamma_{12}/(\gamma_{12} + \gamma_{21})$, $u_2 = \gamma_{21}/(\gamma_{12} + \gamma_{21})$, and $T^*(\infty) = \lim_{\varepsilon \rightarrow \infty} T^*(\varepsilon)$ with

$$\begin{aligned} T^*(\infty) &= K_1 + K_2 \\ &+ (-r_1 u_1^2 K_2 + r_2 u_2^2 K_1 K_2 + r_2 u_2^2 K_1 M \\ &- 2r_2 u_2^3 K_1 (K_1 + K_2) + \sqrt{\Delta}) / (2r_2 u_2^3 K_1), \end{aligned} \quad (12)$$

where

$$\begin{aligned} \Delta &= \left(-\frac{r_1 u_1^2}{K_1} + r_2 u_2^2 + \frac{r_2 u_2^2 M}{K_2} \right)^2 \\ &+ \frac{r_2 u_2^3 (r_1 u_1 - r_2 u_2 M)}{K_2}. \end{aligned}$$

Moreover, under symmetric movement ($\gamma_{12} = \gamma_{21}$)

$$\begin{aligned} T^*(\infty) &= K_1 + K_2 + (-r_1 K_2 + r_2 K_1 K_2 + r_2 M K_1 \\ &- r_2 K_1 (K_1 + K_2) + \sqrt{\Delta}) / (r_2 K_1). \end{aligned} \quad (13)$$

Proof: The equilibrium $E^*(\varepsilon)$ satisfies:

$$\begin{aligned} r_1 x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) \\ + r_2 x_2^*(\varepsilon) \left(1 - \frac{x_2^*(\varepsilon)}{K_2} \right) (x_2^*(\varepsilon) - M) &= 0, \\ x_2^*(\varepsilon) &= \frac{1}{\gamma_{12}} \left(\gamma_{21} x_1^*(\varepsilon) \right. \\ &\left. - \frac{r_1}{\varepsilon} x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) \right). \end{aligned} \quad (14)$$

As $\varepsilon \rightarrow \infty$, System (14) reduces to:

$$\begin{aligned} r_1 x_1^*(\infty) \left(1 - \frac{x_1^*(\infty)}{K_1} \right) \\ + r_2 x_2^*(\infty) \left(1 - \frac{x_2^*(\infty)}{K_2} \right) (x_2^*(\infty) - M) &= 0, \\ x_2^*(\infty) &= \frac{\gamma_{21}}{\gamma_{12}} x_1^*(\infty). \end{aligned} \quad (15)$$

Solutions to (15) include 0 and

$$E^*(\infty) = (x_1^*(\infty), x_2^*(\infty)) = T^*(\infty)(u_1, u_2).$$

Convergence of $E^*(\varepsilon)$ to $E^*(\infty)$ follows by excluding the origin as a limit point. Specifically, for all $\varepsilon > 0$, there exists $i \in \{1, 2\}$ such that $x_i^*(\varepsilon) > K_i$, ensuring $E^*(\varepsilon)$ is bounded away from 0. If $\gamma_{12} x_2^*(\varepsilon) < \gamma_{21} x_1^*(\varepsilon)$ for all $\varepsilon > 0$, then

$$r_2 x_2^*(\varepsilon) (1 - x_2^*(\varepsilon)/K_2) (x_2^*(\varepsilon) - M) < 0.$$

Since $x_2^*(\varepsilon) > 0$ and $M \leq 0$, we deduce $x_2^*(\varepsilon) > K_2$. Thus $E^*(\varepsilon) \rightarrow E^*(\infty)$ as $\varepsilon \rightarrow \infty$. The symmetric case (13) follows directly from (12) when $\gamma_{12} = \gamma_{21}$. ■

Remark 1. The quantities

$$u_1 = \frac{\gamma_{12}}{\gamma_{12} + \gamma_{21}}, \quad u_2 = \frac{\gamma_{21}}{\gamma_{12} + \gamma_{21}},$$

represent the asymptotic equilibrium proportions of the population in Patch 1 and Patch 2, respectively. These proportions are entirely determined by the dispersal coefficients and describe the long-term spatial distribution induced by migration between the two patches.

Singular perturbation theory elucidates the system's behavior under perfect mixing ($\varepsilon \rightarrow \infty$):

Theorem 2. Let $(x_1(t, \varepsilon), x_2(t, \varepsilon))$ solve System (5) with nonnegative initial conditions (x_1^0, x_2^0) . As $\varepsilon \rightarrow \infty$

$$x_1(t, \varepsilon) + x_2(t, \varepsilon) = Z(t) + o_\varepsilon(1), \quad (16)$$

uniformly in $t \in [0, \infty)$, and for any $t_0 > 0$

$$\begin{aligned} x_1(t, \varepsilon) &= u_1 Z(t) + o_\varepsilon(1) \\ x_2(t, \varepsilon) &= u_2 Z(t) + o_\varepsilon(1) \end{aligned} \quad (17)$$

uniformly in $t \in [t_0, \infty)$, where $Z(t)$ satisfies:

$$\begin{aligned} \frac{dZ}{dt} &= -\frac{r_2 u_2^3}{K_2} Z^3 + \left(-\frac{r_1 u_1^2}{K_1} + r_2 u_2^2 + \frac{r_2 u_2^2 M}{K_2} \right) Z^2 \\ &+ (r_1 u_1 - r_2 u_2 M) Z, \\ Z(0) &= x_1^0 + x_2^0. \end{aligned} \quad (18)$$

Proof: Define $X(t, \varepsilon) = x_1(t, \varepsilon) + x_2(t, \varepsilon)$. Rewriting (5) in (X, x_1) coordinates yields:

$$\begin{aligned} \frac{dX}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) \\ &\quad + r_2 (X - x_1) \left(1 - \frac{X - x_1}{K_2}\right) (X - x_1 - M), \\ \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \varepsilon (\gamma_{12} X - (\gamma_{12} + \gamma_{21}) x_1). \end{aligned} \quad (19)$$

As $\varepsilon \rightarrow \infty$, (19) becomes a slow-fast system with slow variable X and fast variable x_1 . Rescaling time via $\tau = \varepsilon t$ gives the fast subsystem:

$$\frac{dx_1}{d\tau} = \frac{1}{\varepsilon} r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \gamma_{12} X - (\gamma_{12} + \gamma_{21}) x_1.$$

Taking $\varepsilon \rightarrow \infty$ yields the fast dynamics:

$$\frac{dx_1}{d\tau} = \gamma_{12} X - (\gamma_{12} + \gamma_{21}) x_1. \quad (20)$$

The slow manifold is the set of equilibria of (20):

$$x_1^* = \frac{\gamma_{12}}{\gamma_{12} + \gamma_{21}} X = u_1 X. \quad (21)$$

As x_1^* is globally asymptotically stable (GAS) for (20), Tikhonov's theorem [21, 22] implies that after rapid attraction to the slow manifold, solutions of (19) are approximated by the reduced system obtained by substituting (21) into the X -dynamics:

$$\begin{aligned} \frac{dX}{dt} &= r_1 u_1 X \left(1 - \frac{u_1 X}{K_1}\right) \\ &\quad + r_2 u_2 X \left(1 - \frac{u_2 X}{K_2}\right) (u_2 X - M) \\ &= -\frac{r_2 u_2^3}{K_2} X^3 + \left(-\frac{r_1 u_1^2}{K_1} + r_2 u_2^2 + \frac{r_2 u_2^2 M}{K_2}\right) X^2 \\ &\quad + (r_1 u_1 - r_2 u_2 M) X. \end{aligned}$$

This recovers (18). Since (18) admits the GAS equilibrium $X^* = T^*(\infty)$ (given by (12)), Tikhonov's theorem guarantees approximations (16) and (17) hold uniformly for $t \in [0, \infty)$ and $t \in [t_0, \infty)$ ($t_0 > 0$), respectively. ■

Under infinite dispersal, approximation (16) reveals that the total population follows a weak Allee effect (18). Consequently, as $t, \varepsilon \rightarrow \infty$, the total population $x_1(t, \varepsilon) + x_2(t, \varepsilon)$ converges to $T^*(\infty)$ (Theorems 1 and 2). Approximation (17) indicates that after a brief initial layer, population densities align with the proportions u_1 and u_2 . Thus as $t, \varepsilon \rightarrow \infty$, $x_i(t, \varepsilon) \rightarrow u_i T^*(\infty)$ for $i = 1, 2$.

Under extreme dispersal rates ($\varepsilon \rightarrow \infty$), the system undergoes fundamental ecological reorganization.

Rapid movement homogenizes the landscape, effectively merging distinct patches into a single well-mixed habitat where individuals lose spatial memory. Population densities stabilize at fixed proportions (u_1 and u_2) determined by the ratio of dispersal rates γ_{ij} , reflecting an equilibrium distribution across the landscape. Crucially, the total population exhibits a weak Allee effect (Eq. 18) - an emergent property arising from coupled local dynamics through dispersal that depresses per capita growth at intermediate densities.

This transition occurs via a rapid redistribution phase where individuals reorganize according to dispersal ratios before settling into slow demographic trends. Ecologically, high connectivity eliminates patch-specific population identities, creates system-wide density dependence governed by parameter averages, and enables rescue effects where productive patches sustain neighboring populations. Ultimately, intense dispersal transforms locally distinct populations into an integrated meta-population with collective dynamics governed by landscape-level processes rather than local conditions.

Let us consider the differential equation (18). We factorize the right-hand side as

$$\begin{aligned} \frac{dZ}{dt} &= Z \left(-\omega_2 Z^2 + \omega_1 Z + \omega_0 \right), \\ \omega_1 &= -\frac{r_1 u_1^2}{K_1} + r_2 u_2^2 + \frac{r_2 u_2^2 M}{K_2}, \\ \omega_2 &= \frac{r_2 u_2^3}{K_2} > 0, \quad \omega_0 = r_1 u_1 - r_2 u_2 M. \end{aligned}$$

Thus, we have that $Z = 0$ is always an equilibrium. Nonzero equilibria satisfy

$$f(Z) := \omega_2 Z^2 - \omega_1 Z - \omega_0 = 0,$$

with discriminant

$$\tilde{\Delta} = \omega_1^2 + 4\omega_2\omega_0.$$

If $\tilde{\Delta} \geq 0$, there are two real equilibria

$$Z_{\pm} = \frac{\omega_1 \pm \sqrt{\omega_1^2 + 4\omega_2\omega_0}}{2\omega_2}.$$

The stability of $Z = 0$ is governed by

$$f'(0) = \omega_0 = r_1 u_1 - r_2 u_2 M.$$

Hence

$$\begin{cases} Z = 0 \text{ is stable if } \omega_0 < 0 \text{ (i.e. } r_1 u_1 < r_2 u_2 M), \\ Z = 0 \text{ is unstable if } \omega_0 > 0. \end{cases}$$

For a nonzero equilibrium $Z^* > 0$, we compute

$$f'(Z^*) = Z^* (-2\omega_2 Z^* + \omega_1).$$

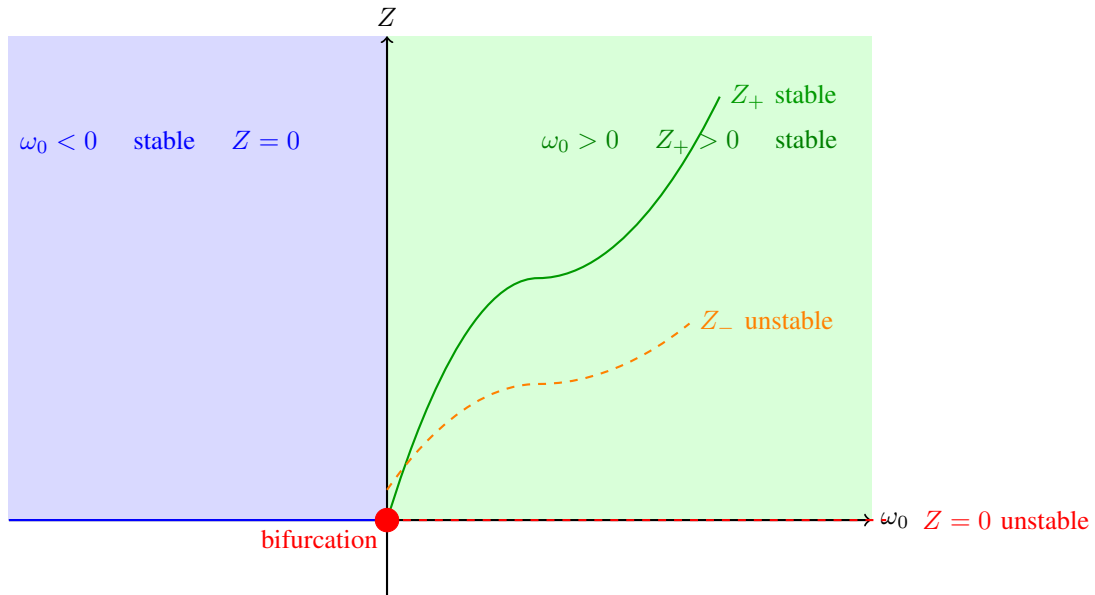


Fig. 4: Enlarged bifurcation diagram with parameter ω_0 . For $\omega_0 < 0$, only the trivial equilibrium $Z = 0$ exists and is stable (blue domain). At $\omega_0 = 0$, a bifurcation occurs. For $\omega_0 > 0$, the trivial state becomes unstable (red dashed line), and two positive equilibria appear: a stable branch Z_+ (green) and an unstable branch Z_- (orange).

Therefore, Z^* is stable if $Z^* > \frac{\omega_1}{2\omega_2}$, and unstable otherwise.

- If $\omega_0 > 0$, then $\tilde{\Delta} > \omega_1^2$ and there exists at least one positive root $Z_+ > 0$ which may be stable depending on the inequality $Z_+ > \omega_1/(2\omega_2)$.
- If $\omega_0 < 0$, $Z = 0$ is stable and positive equilibria may or may not exist depending on $\tilde{\Delta}$ and the sign of $Z_{\pm}$, see figure 4.

VI. TOTAL EQUILIBRIUM POPULATION

In this section, we analyze the effect of dispersal and weak Allee effect on the total equilibrium population for the system (5) and how the total biomass changes with dispersal rate. As in [19], for the two-patch logistic model (2), we present two complete classifications of the model parameter space, in each classification, we prove that exactly three cases can occur.

A. Comparative analysis of equilibrium populations at varying dispersal rates

Arditi et al. [8] established a trichotomy for System (2) regarding the total equilibrium population $T^*(\varepsilon)$ relative to $K_1 + K_2$:

- 1) If $T^*(\infty) > K_1 + K_2$, then $T^*(\varepsilon) > K_1 + K_2$ for all $\varepsilon > 0$.

- 2) If $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T^*(\infty) < K_1 + K_2$, there exists $\varepsilon_0 > 0$ such that:

$$T^*(\varepsilon) > K_1 + K_2 \quad \text{for } 0 < \varepsilon < \varepsilon_0,$$

$$T^*(\varepsilon) < K_1 + K_2 \quad \text{for } \varepsilon > \varepsilon_0,$$

$$T^*(\varepsilon_0) = K_1 + K_2.$$

- 3) If $\frac{dT^*}{d\varepsilon}(0) \leq 0$, then $T^*(\varepsilon) < K_1 + K_2$ for all $\varepsilon > 0$. This implies that $T^*(\varepsilon) = K_1 + K_2$ holds only at $\varepsilon = 0$ and at most one positive value ε_0 , which exists iff $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T^*(\infty) < K_1 + K_2$. Elbetch [17] generalized these results to the two-patch Richards model:

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \left(\frac{x_1}{K_1} \right)^\mu \right) + \varepsilon (\gamma_{12} x_2 - \gamma_{21} x_1),$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^\mu \right) + \varepsilon (\gamma_{21} x_1 - \gamma_{12} x_2),$$

for $\mu \neq 1$. We refer to [17] for detailed analysis of migration effects in Richards models.

Lemma 1. The total equilibrium population satisfies:

$$T^*(\varepsilon) = K_1 + K_2 + \varepsilon \left(\frac{K_1}{r_1 x_1^*(\varepsilon)} - \frac{K_2}{r_2 x_2^*(\varepsilon)(x_2^*(\varepsilon) - M)} \right) (\gamma_{12} x_2^*(\varepsilon) - \gamma_{21} x_1^*(\varepsilon)).$$

Proof: The equilibrium equations are:

$$\begin{aligned} r_1 x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) &= -\varepsilon(\gamma_{12} x_2^*(\varepsilon) - \gamma_{21} x_1^*(\varepsilon)), \\ r_2 x_2^*(\varepsilon) \left(1 - \frac{x_2^*(\varepsilon)}{K_2} \right) (x_2^*(\varepsilon) - M) &= -\varepsilon(\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)). \end{aligned} \quad (22)$$

Dividing the first equation by $r_1 x_1^*(\varepsilon)/K_1$ and the second by $r_2 x_2^*(\varepsilon)(x_2^*(\varepsilon) - M)/K_2$ yields:

$$\begin{aligned} x_1^*(\varepsilon) &= K_1 + \varepsilon K_1 \frac{\gamma_{12} x_2^*(\varepsilon) - \gamma_{21} x_1^*(\varepsilon)}{r_1 x_1^*(\varepsilon)}, \\ x_2^*(\varepsilon) &= K_2 + \varepsilon K_2 \frac{\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)}{r_2 x_2^*(\varepsilon)(x_2^*(\varepsilon) - M)}. \end{aligned}$$

Summing these equations gives (11). ■

When $\gamma_{21} K_1 = \gamma_{12} K_2$, the ideal free distribution (IFD) holds: $(x_1^*(\varepsilon), x_2^*(\varepsilon)) \equiv (K_1, K_2)$ with $T^*(\varepsilon) = K_1 + K_2$ for all $\varepsilon \geq 0$. To exclude this trivial case, we assume throughout:

- (H1) $\gamma_{21} K_1 > \gamma_{12} K_2$ ($K_1/u_1 > K_2/u_2$),
 - (H2) $\gamma_{21} K_1 < \gamma_{12} K_2$ ($K_1/u_1 < K_2/u_2$),
- where $u_1 = \gamma_{12}/(\gamma_{12} + \gamma_{21})$, $u_2 = \gamma_{21}/(\gamma_{12} + \gamma_{21})$.

Proposition 2. *The equilibrium satisfies:*

- Under (H1): $\gamma_{21} x_1^*(\varepsilon) > \gamma_{12} x_2^*(\varepsilon)$ for all $\varepsilon > 0$ and

$$\frac{K_1}{u_1} > \frac{x_1^*(\varepsilon)}{u_1} > \frac{x_2^*(\varepsilon)}{u_2} > \frac{K_2}{u_2},$$

- Under (H2): $\gamma_{21} x_1^*(\varepsilon) < \gamma_{12} x_2^*(\varepsilon)$ for all $\varepsilon > 0$ and

$$\frac{K_1}{u_1} < \frac{x_1^*(\varepsilon)}{u_1} < \frac{x_2^*(\varepsilon)}{u_2} < \frac{K_2}{u_2}.$$

Proof: Continuity and the equilibrium equations imply the sign consistency of $\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)$. Suppose equality holds at some $\tilde{\varepsilon} > 0$, then $(x_1^*(\tilde{\varepsilon}), x_2^*(\tilde{\varepsilon})) = (K_1, K_2)$, contradicting (H1) or (H2). From (22):

$$\begin{aligned} r_1 x_1^*(\varepsilon) \left(1 - \frac{x_1^*(\varepsilon)}{K_1} \right) &= -r_2 x_2^*(\varepsilon) \left(1 - \frac{x_2^*(\varepsilon)}{K_2} \right) (x_2^*(\varepsilon) - M) \\ &= \varepsilon(\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)) \begin{cases} > 0 & \text{under (H1),} \\ < 0 & \text{under (H2).} \end{cases} \end{aligned}$$

Thus $x_1^*(\varepsilon) < K_1$ and $x_2^*(\varepsilon) > K_2$ under (H1), with reverse inequalities under (H2). ■

Consequently, for all $\varepsilon \geq 0$,

$$\text{sgn}(\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)) = \text{sgn}(\gamma_{21} K_1 - \gamma_{12} K_2).$$

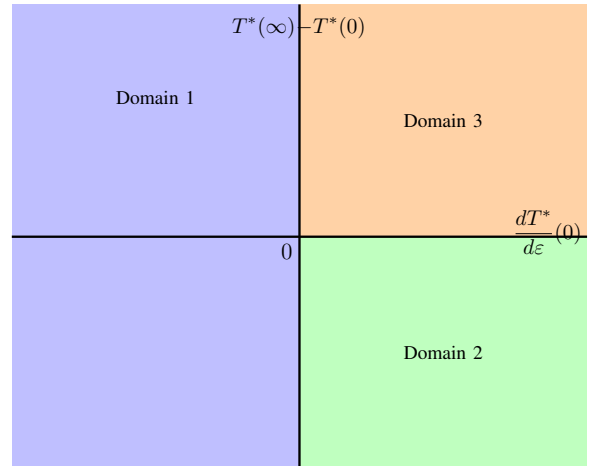


Fig. 5: Illustration of the classification in Theorem 3. The plane is divided into three domains according to the sign of the derivative $\frac{dT^*}{d\varepsilon}(0)$ and the quantity $T^*(\infty) - T^*(0)$. *Blue domain (Domain 1):* if $\frac{dT^*}{d\varepsilon}(0) \leq 0$, then $T^*(\varepsilon) \leq T^*(0)$ for all $\varepsilon \geq 0$. *Green domain (Domain 2):* if $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T^*(\infty) \leq T^*(0)$, then the total biomass initially increases, reaches a maximum, and eventually decreases below $T^*(0)$ for sufficiently large dispersal rates. *Orange domain (Domain 3):* if $T^*(\infty) \geq T^*(0)$, then $T^*(\varepsilon) \geq T^*(0)$ for all $\varepsilon > 0$. The boundaries between the three domains depend on the parameters $\gamma_{12}, \gamma_{21}, K_1, K_2, r_1, r_2$, and M through the expressions of $\frac{dT^*}{d\varepsilon}(0)$ and $T^*(\infty)$.

Proposition 3. *The derivative at $\varepsilon = 0$ is:*

$$\frac{dT^*}{d\varepsilon}(0) = (\gamma_{12} K_2 - \gamma_{21} K_1) \left(\frac{1}{r_1} - \frac{1}{r_2(K_2 - M)} \right). \quad (23)$$

Thus, $\frac{dT^*}{d\varepsilon}(0) = 0$ iff $r_1 = r_2(K_2 - M)$ or $\gamma_{21} K_1 = \gamma_{12} K_2$.

Proof: Differentiating (22) yields:

$$\begin{aligned} \frac{d}{d\varepsilon} \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix} &= \frac{\gamma_{21} x_1^* - \gamma_{12} x_2^*}{\nu(x_1^*, x_2^*)} \\ &\begin{pmatrix} \varepsilon \gamma_{21} \frac{x_1^*}{x_2^*} + \alpha_2 x_2^*(x_2^* - M) & \varepsilon \gamma_{12} \\ \varepsilon \gamma_{21} & \varepsilon \gamma_{12} \frac{x_2^*}{x_1^*} + \alpha_1 x_1^* \end{pmatrix} \begin{pmatrix} -1 \\ 1 \end{pmatrix} \end{aligned}$$

where $\nu > 0$ and $\alpha_i = r_i/K_i$. Summing components gives:

$$\begin{aligned} \frac{dT^*}{d\varepsilon}(\varepsilon) &= \frac{(\gamma_{21} x_1^* - \gamma_{12} x_2^*)}{\nu} \left(\alpha_1 x_1^* \right. \\ &\quad \left. - \alpha_2 x_2^*(x_2^* - M) - \varepsilon \frac{x_1^* + x_2^*}{x_1^* x_2^*} (\gamma_{21} x_1^* - \gamma_{12} x_2^*) \right). \end{aligned} \quad (24)$$

Evaluating at $\varepsilon = 0$ with $x_i^*(0) = K_i$ yields (23). ■

Lemma 2. If $T^*(\varepsilon_0) \leq T^*(0)$ for some $\varepsilon_0 > 0$, then $\frac{dT^*}{d\varepsilon}(\varepsilon) < 0$ for all $\varepsilon \geq \varepsilon_0$. In particular, if $\frac{dT^*}{d\varepsilon}(0) < 0$, then $\frac{dT^*}{d\varepsilon}(\varepsilon) < 0$ for all $\varepsilon > 0$.

Proof: From (11) and Proposition 2:

$$T^*(\varepsilon) - T^*(0) = \frac{\varepsilon}{\alpha_1 \alpha_2 x_1^* x_2^* (x_2^* - M)} \times (\gamma_{21} x_1^* - \gamma_{12} x_2^*) (\alpha_1 x_1^* - \alpha_2 x_2^* (x_2^* - M)). \quad (25)$$

If $T^*(\varepsilon_0) \leq T^*(0)$, (25) implies the product in (24) is negative. Since $\gamma_{21} x_1^* - \gamma_{12} x_2^* \neq 0$ by Proposition 2, we conclude that $\frac{dT^*}{d\varepsilon}(\varepsilon_0) < 0$. ■

Theorem 3. For System (5) with $\gamma_{21} K_1 \neq \gamma_{12} K_2$:

- 1) If $\frac{dT^*}{d\varepsilon}(0) \leq 0$, then $T^*(\varepsilon) \leq T^*(0)$ for all $\varepsilon \geq 0$,
- 2) If $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T^*(\infty) \leq T^*(0)$, there exists $\varepsilon_0 > 0$ such that:

$$T^*(\varepsilon) > K_1 + K_2 \quad \forall \varepsilon < \varepsilon_0,$$

$$T^*(\varepsilon) < K_1 + K_2 \quad \forall \varepsilon > \varepsilon_0,$$

$$T^*(\varepsilon_0) = K_1 + K_2,$$

- 3) If $T^*(\infty) \geq T^*(0)$, then $T^*(\varepsilon) \geq T^*(0)$ for all $\varepsilon > 0$.

Proof: Cases (1)-(3) follow from Lemma 2, continuity of T^* , and its differentiability near $\varepsilon = 0$. When $\frac{dT^*}{d\varepsilon}(0) = 0$ (i.e., $r_1 = r_2(K_2 - M)$ by Proposition 3):

- Under (H1) we have:

$$\alpha_1 x_1^* - \alpha_2 x_2^* (x_2^* - M) < r_1 - r_2(K_2 - M) = 0,$$

- Under (H2) we have:

$$\alpha_1 x_1^* - \alpha_2 x_2^* (x_2^* - M) > r_1 - r_2(K_2 - M) = 0.$$

Thus $T^*(\varepsilon) < T^*(0)$ for all $\varepsilon > 0$ in both cases, see Figure 5. ■

These results align with Theorem 4.2 in Gao [23], Theorem 4.5 in Gao and Lou [24], and Theorem 2.4 in Gao and Lou [19].

B. Monotonicity analysis of the total equilibrium population

Theorem 3 determines the relative position of the asymptotic equilibrium values but does not completely describe the monotonic behavior of $T^*(\varepsilon)$ with respect to the dispersal rate ε . To overcome this difficulty, we establish a complete classification analogous to Theorem 4.12 in Gao and Lou [24] and Theorem 2.5 in Gao and Lou [19]. The analysis relies on two fundamental observations.

First, any critical point of $T^*(\varepsilon)$ on $[0, \infty)$ corresponds necessarily to a local maximum. Consequently,

the function $T^*(\varepsilon)$ cannot exhibit oscillatory behavior and admits at most one change of monotonicity. This structural property plays a crucial role in the classification of the three possible dispersal responses.

Second, the asymptotic behavior of the derivative of T^* with respect to the dispersal rate is governed by the quantity $\mathbb{T}'(\infty)$. To make the distinction between the differentiation variable and the point of evaluation explicit, let η denote the value of the dispersal rate at which the derivative is evaluated. Then, for sufficiently large η ,

$$\operatorname{sgn} \left(\frac{dT^*}{d\varepsilon}(\eta) \right) = \operatorname{sgn} \left((\gamma_{21} K_1 - \gamma_{12} K_2) \mathbb{T}'(\infty) \right),$$

provided $\mathbb{T}'(\infty) \neq 0$. Here, $\frac{dT^*}{d\varepsilon}(\eta)$ is the derivative of T^* with respect to its argument, taken at η .

It is important to note that

$$\lim_{\eta \rightarrow \infty} \frac{dT^*}{d\varepsilon}(\eta) = 0,$$

which reflects the saturation effect induced by extremely fast dispersal. Nevertheless, although the derivative converges to zero, its sign for large η still determines whether the total biomass approaches its limiting value from above or below. Hence, the quantity $\mathbb{T}'(\infty)$ provides essential information about the eventual trend of the total biomass under strong migration.

The function $\mathbb{T}'(\varepsilon)$ (where ε is a dummy variable) is defined by

$$\begin{aligned} \mathbb{T}'(\varepsilon) &:= \alpha_1 x_1^*(\varepsilon) - \alpha_2 x_2^*(\varepsilon) (x_2^*(\varepsilon) - M) \\ &\quad - \varepsilon \frac{x_1^*(\varepsilon) + x_2^*(\varepsilon)}{x_1^*(\varepsilon) x_2^*(\varepsilon)} (\gamma_{21} x_1^*(\varepsilon) - \gamma_{12} x_2^*(\varepsilon)), \end{aligned}$$

with $\alpha_i = r_i/K_i$ and $x_i^*(\varepsilon)$ the equilibrium densities at dispersal rate ε . Substituting the asymptotic equilibrium values

$$x_1^*(\infty) = u_1 T^*(\infty), \quad x_2^*(\infty) = u_2 T^*(\infty),$$

we obtain

$$\begin{aligned} \mathbb{T}'(\infty) &= r_2 (u_2 T^*(\infty) - M) - r_1 \\ &\quad + T^*(\infty) (2\alpha_1 u_1 - \alpha_2 u_2 (1 + M + u_2 T^*(\infty))), \end{aligned}$$

where $T^*(\infty)$ is given by (10). This asymptotic quantity encodes the combined influence of the demographic parameters, carrying capacities, Allee threshold, and dispersal proportions on the long-term sensitivity of the total biomass to migration.

Lemma 3. Under assumption (H1), if $\frac{dT^*}{d\varepsilon}(\tilde{\varepsilon}) = 0$ for some $\tilde{\varepsilon} > 0$, then $\frac{d^2 T^*}{d\varepsilon^2}(\tilde{\varepsilon}) < 0$. Thus any critical point of $T^*(\varepsilon)$ on $\mathbb{R}_+$ is a local maximum.

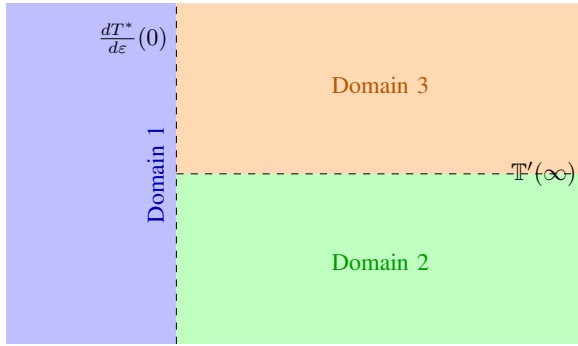


Fig. 6: Classification of the monotonicity result in Theorem 4. Blue domain (Case 1): when $\frac{dT^*}{d\varepsilon}(0) \leq 0$, the total biomass $T^*(\varepsilon)$ is strictly decreasing for all $\varepsilon > 0$. Green domain (Case 2): if $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T'(\infty) < 0$, the function $T^*(\varepsilon)$ first increases, reaches a unique maximum at some $\varepsilon_0 > 0$, and then decreases. Orange domain (Case 3): if $T'(\infty) > 0$, the total biomass $T^*(\varepsilon)$ is strictly increasing for all $\varepsilon > 0$. The dashed lines indicate the boundaries $\frac{dT^*}{d\varepsilon}(0) = 0$ and $T'(\infty) = 0$.

Proof: Differentiate the equilibrium sum equation:

$$r_1 x_1^* \left(1 - \frac{x_1^*}{K_1}\right) + r_2 x_2^* \left(1 - \frac{x_2^*}{K_2}\right) (x_2^* - M) = 0$$

with respect to ε

$$r_1 \left(1 - \frac{2x_1^*}{K_1}\right) \frac{dx_1^*}{d\varepsilon} + r_2 \left(\left(1 - \frac{x_2^*}{K_2}\right) (2x_2^* - M) - \frac{x_2^*}{K_2} (x_2^* - M) \right) \frac{dx_2^*}{d\varepsilon} = 0. \quad (26)$$

At a critical point $\tilde{\varepsilon}$, $\frac{dT^*}{d\varepsilon} = 0$ implies $\frac{dx_1^*}{d\varepsilon} = -\frac{dx_2^*}{d\varepsilon}$. Substituting into (26) gives either $\frac{dx_1^*}{d\varepsilon} = 0$ or

$$\eta := r_1 \left(1 - \frac{2x_1^*}{K_1}\right) = r_2 \left(\left(1 - \frac{x_2^*}{K_2}\right) \times (2x_2^* - M) - \frac{x_2^*}{K_2} (x_2^* - M) \right).$$

Under (H1), $x_1^* < K_1$ implies $\eta < 0$. Differentiate (26) again:

$$\begin{aligned} & r_1 \left(1 - 2\frac{x_1^*(\varepsilon)}{K_1}\right) \frac{d^2x_1^*}{d\varepsilon^2}(\varepsilon) - 2\frac{r_1}{K_1} \left(\frac{dx_1^*}{d\varepsilon}(\varepsilon)\right)^2 \\ & + r_2 \left(1 - \frac{x_2^*(\varepsilon)}{K_2}\right) (2x_2^*(\varepsilon) - M) \frac{d^2x_2^*}{d\varepsilon^2}(\varepsilon) \\ & + (2r_2 + \frac{r_2}{K_2} M - 4\alpha_2 x_2^*(\varepsilon)) \left(\frac{dx_2^*}{d\varepsilon}(\varepsilon)\right)^2 \\ & - \frac{r_2}{K_2} x_2^*(\varepsilon) (x_2^*(\varepsilon) - M) \frac{d^2x_2^*}{d\varepsilon^2}(\varepsilon) \\ & - \frac{r_2}{K_2} (2x_2^*(\varepsilon) - M) \left(\frac{dx_2^*}{d\varepsilon}(\varepsilon)\right)^2 = 0. \end{aligned}$$

At $\varepsilon = \tilde{\varepsilon}$ with $\frac{dx_i^*}{d\varepsilon} = 0$, this simplifies to:

$$\eta \frac{d^2T^*}{d\varepsilon^2} = \frac{2r_1}{K_1} \left(\frac{dx_1^*}{d\varepsilon}\right)^2 + \frac{2r_2}{K_2} (3x_2^* - M - K_2) \left(\frac{dx_2^*}{d\varepsilon}\right)^2.$$

Since $M \leq 0$ and $x_2^* > K_2$ under (H1), the right-hand side is positive. With $\eta < 0$, we conclude $\frac{d^2T^*}{d\varepsilon^2} < 0$. ■

Under (H1), Lemma 3 implies $T^*(\varepsilon)$ is either strictly decreasing, strictly increasing, or unimodal. The monotonicity type is determined by the signs of $\frac{dT^*}{d\varepsilon}(0)$ and $T'(\infty)$.

Theorem 4. Under assumption (H1):

- 1) If $\frac{dT^*}{d\varepsilon}(0) \leq 0$, then $T^*(\varepsilon)$ is strictly decreasing for all $\varepsilon > 0$.
- 2) If $\frac{dT^*}{d\varepsilon}(0) > 0$ and $T'(\infty) < 0$, there exists $\varepsilon_0 > 0$ such that:

$$\frac{dT^*}{d\varepsilon}(\varepsilon) \begin{cases} > 0 & \varepsilon < \varepsilon_0, \\ = 0 & \varepsilon = \varepsilon_0, \\ < 0 & \varepsilon > \varepsilon_0. \end{cases}$$

- 3) If $T'(\infty) > 0$, then $T^*(\varepsilon)$ is strictly increasing for all $\varepsilon > 0$.

These mathematical classifications reveal how dispersal intensity mediates source-sink dynamics in metapopulations. When $\frac{dT^*}{d\varepsilon}(0) > 0$ (Case 2), moderate dispersal enhances total biomass by allowing surplus individuals from productive patches to colonize underutilized areas, creating a net rescue effect. Conversely, when $\frac{dT^*}{d\varepsilon}(0) \leq 0$ (Case 1), dispersal becomes detrimental as it draws individuals away from high-quality habitats faster than they can be replenished, effectively creating ecological traps. The critical threshold ε_0 represents the optimal dispersal rate that maximizes biomass before connectivity-induced homogenization reduces spatial complementarity. These patterns are particularly relevant in fragmented landscapes where dispersal management influences population persistence.

The monotonicity patterns characterize how connectivity regulates ecosystem productivity. Strictly increasing $T^*(\varepsilon)$ (Case 3) occurs when dispersal consistently improves resource exploitation across patches, typical of systems with strong source-sink asymmetry. The unimodal pattern (Case 2) reflects the connectivity paradox: initial dispersal benefits populations by enabling recolonization, but excessive movement suppresses local adaptation and creates synchrony that amplifies extinction risk. The critical threshold ε_0 marks the tipping point where dispersal shifts from beneficial to harmful. Strictly decreasing $T^*(\varepsilon)$ (Case 1) indicates fragile systems where any dispersal reduces biomass,

characteristic of populations near extinction thresholds where emigration exacerbates decline. These dynamics underscore that conservation strategies must balance connectivity to maintain optimal dispersal regimes rather than maximize movement, see figure 6.

C. Linking the initial derivative to the infinite-diffusion regime

We now investigate the relation between the derivative of the total equilibrium biomass at $\varepsilon = 0$ and its limiting value $T^*(\infty)$ as $\varepsilon \rightarrow \infty$.

Recall from (23) that

$$\frac{dT^*}{d\varepsilon}(0) = (\gamma_{12}K_2 - \gamma_{21}K_1) \left(\frac{1}{r_1} - \frac{1}{r_2(K_2 - M)} \right). \quad (27)$$

Since $r_1 > 0$, $r_2 > 0$ and $K_2 - M > 0$, the sign of this derivative is determined by

$$\text{sgn} \left(\frac{dT^*}{d\varepsilon}(0) \right) = \text{sgn} (\gamma_{12}K_2 - \gamma_{21}K_1) \times \text{sgn} (r_2(K_2 - M) - r_1).$$

Hence the sign of the slope at $\varepsilon = 0$ reflects both the asymmetry of the dispersal fluxes (via $\gamma_{12}K_2 - \gamma_{21}K_1$) and the relative growth potentials of the two patches (via $r_2(K_2 - M) - r_1$).

From (12), after substituting

$$u_1 = \frac{\gamma_{12}}{\gamma_{12} + \gamma_{21}}, \quad u_2 = \frac{\gamma_{21}}{\gamma_{12} + \gamma_{21}},$$

we obtain

$$T^*(\infty) = K_1 + K_2 + \frac{N + \sqrt{\Xi}}{2r_2u_2^3K_1}, \quad (28)$$

where

$$N = \left(-r_1\gamma_{12}^2K_2(\gamma_{12} + \gamma_{21}) + r_2\gamma_{21}^2K_1(K_2 + M) \times (\gamma_{12} + \gamma_{21}) - 2r_2\gamma_{21}^3K_1(K_1 + K_2) \right) / (\gamma_{12} + \gamma_{21})^3,$$

and

$$\Xi = \frac{1}{(\gamma_{12} + \gamma_{21})^4} \left(\left(-\frac{r_1\gamma_{12}^2}{K_1} + r_2\gamma_{21}^2 \left(1 + \frac{M}{K_2} \right) \right)^2 + \frac{r_2\gamma_{21}^3(r_1\gamma_{12} - r_2\gamma_{21}M)}{K_2} \right).$$

Since the denominator in (28) is positive, the sign of $T^*(\infty) - (K_1 + K_2)$ is the same as that of $N + \sqrt{\Xi}$.

The expression (27) shows that the derivative at zero depends on the linear form

$$\gamma_{12}K_2 - \gamma_{21}K_1,$$

which measures the imbalance between dispersal fluxes weighted by the patch capacities. On the other hand, the numerator N in (28) contains the higher-order terms

$$-r_1\gamma_{12}^2K_2(\gamma_{12} + \gamma_{21}) + r_2\gamma_{21}^2K_1(K_2 + M) \times (\gamma_{12} + \gamma_{21}) - 2r_2\gamma_{21}^3K_1(K_1 + K_2),$$

that can be viewed as a quadratic and cubic extension of the same combination.

Therefore, although both $\frac{dT^*}{d\varepsilon}(0)$ and $T^*(\infty) - (K_1 + K_2)$ depend on the dispersal asymmetry $\gamma_{12}K_2 - \gamma_{21}K_1$, the relation between their signs is not direct. In particular:

- If $N \geq 0$, then necessarily $T^*(\infty) > K_1 + K_2$, so the total biomass in the infinite-diffusion regime exceeds the purely local carrying capacities. In this case, a positive initial slope in (27) is consistent with the asymptotic increase.
- If $N < 0$, then the contribution of $\sqrt{\Xi}$ may compensate for the negative part of N , and the sign of $T^*(\infty) - (K_1 + K_2)$ depends on the delicate balance between dispersal rates and growth parameters. Consequently, the sign of $\frac{dT^*}{d\varepsilon}(0)$ does not automatically determine the asymptotic sign.

Corollary 1. Assume $K_2 > M$. If

$$-r_1\gamma_{12}^2K_2(\gamma_{12} + \gamma_{21}) + r_2\gamma_{21}^2K_1(K_2 + M) \times (\gamma_{12} + \gamma_{21}) - 2r_2\gamma_{21}^3K_1(K_1 + K_2) \geq 0, \quad (29)$$

then the equilibrium biomass under infinite diffusion satisfies

$$T^*(\infty) > K_1 + K_2.$$

Proof: From (28), we have

$$T^*(\infty) - (K_1 + K_2) = \frac{N + \sqrt{\Xi}}{2r_2u_2^3K_1}.$$

Since $2r_2u_2^3K_1 > 0$, the sign is determined by $N + \sqrt{\Xi}$. If (29) holds, then $N \geq 0$, and because $\sqrt{\Xi} \geq 0$, we obtain $N + \sqrt{\Xi} > 0$, which proves the claim. ■

VII. GEOMETRIC APPROACH TO THE QUALITATIVE BEHAVIOR OF THE EQUILIBRIUM POINT

In this section, we adopt a geometric approach to study the qualitative behavior of the equilibrium point $E^*(\varepsilon)$ of system (5) as the migration rate ε varies. The analysis is based on the relative positions of the curve $\wp$, which contains all possible equilibria, and certain reference lines in the phase plane.

Depending on the parameters, the trajectory of $E^*(\varepsilon)$ along $\wp$ reveals whether the total equilibrium population

is smaller, larger, or equal to the sum of the carrying capacities $K_1 + K_2$ for different values of ε .

We distinguish several cases according to the slope and position of the tangent at A and of the asymptotic line $\mathcal{P}_\infty$.

We first consider the straight line Δ with Cartesian equation

$$x_1 + x_2 = K_1 + K_2,$$

which has slope -1 and passes through the point $A = (K_1, K_2)$.

The equilibrium point $E^*(\varepsilon)$ always lies on the curve $\wp$ (see Appendix A). For $\varepsilon = 0$, we have $E^*(0) = A$. As ε increases, $E^*(\varepsilon)$ moves along an arc of $\wp$ and ends at the point

$$B := E^*(\infty),$$

given by equation (12).

- 1) *Case* $r_1 = r_2(K_2 - M)$. The equation of the tangent line to $\wp$ at A is given by:

$$(x_1 - K_1) \frac{\partial \Phi}{\partial x_1}(A) + (x_2 - K_2) \frac{\partial \Phi}{\partial x_2}(A) = 0, \quad (30)$$

where Φ is defined in (8). Since

$$\frac{\partial \Phi}{\partial x_1}(A) = -r_1, \quad \frac{\partial \Phi}{\partial x_2}(A) = (M - K_2)r_2,$$

equation (30) reduces to:

$$r_1 x_1 + r_2(K_2 - M)x_2 = r_1 K_1 + r_2 K_2(K_2 - M).$$

If $r_1 = r_2(K_2 - M)$, the tangent line to $\wp$ at A coincides with Δ . By concavity of $\wp$, all points of $\wp$ lie below Δ . Therefore, for all $\varepsilon \geq 0$, we have:

$$x_1^*(\varepsilon) + x_2^*(\varepsilon) \leq K_1 + K_2,$$

as illustrated in Figure 7.

- 2) *Case* $r_1 < r_2(K_2 - M)$. The line Δ intersects $\wp$ at a second point C , which lies below the line Σ : $x_2 = \frac{K_2}{K_1}x_1$ (see Figures 8–10). As $\varepsilon \rightarrow \infty$, the curve $\mathcal{P}_\varepsilon$ defined in (9) approaches the oblique line

$$\mathcal{P}_\infty : x_2 = \frac{\gamma_{21}}{\gamma_{12}}x_1.$$

The intersections of $\mathcal{P}_\infty$ with $\wp$ are the origin and $E^*(\infty)$.

- (a) If $\mathcal{P}_\infty$ lies below Σ , i.e. $\gamma_{21}/\gamma_{12} < K_2/K_1$, two situations arise:
- (i) If B lies above Δ (i.e. $X_T^*(\infty) \geq K_1 + K_2$), then $E^*(\varepsilon)$ starts at A when $\varepsilon = 0$ and moves along $\wp$ to B as $\varepsilon \rightarrow \infty$. Consequently,

$$x_1^*(\varepsilon) + x_2^*(\varepsilon) \geq K_1 + K_2, \quad \forall \varepsilon \geq 0,$$

as shown in Figure 8.

- (ii) If B lies below Δ (i.e. $T^*(\infty) < K_1 + K_2$), then $E^*(\varepsilon)$ starts at A , passes through C at some $\varepsilon_0 > 0$, and ends at B . Thus:

$$\begin{cases} x_1^*(\varepsilon) + x_2^*(\varepsilon) > K_1 + K_2, & \varepsilon < \varepsilon_0, \\ x_1^*(\varepsilon) + x_2^*(\varepsilon) < K_1 + K_2, & \varepsilon \geq \varepsilon_0, \end{cases}$$

as illustrated in Figure 9.

- (b) If $\mathcal{P}_\infty$ lies above Σ , i.e. $\gamma_{21}/\gamma_{12} > K_2/K_1$, then:

$$x_1^*(\varepsilon) + x_2^*(\varepsilon) < K_1 + K_2, \quad \forall \varepsilon,$$

as in Figure 10.

- (c) If $\mathcal{P}_\infty$ coincides with Σ (i.e. $A \equiv B$), then $E^*(\varepsilon) = (K_1, K_2)$ for all $\varepsilon \geq 0$ and the total equilibrium population is constant.

VIII. NUMERICAL SIMULATIONS

In this subsection, we illustrate Theorems 3 and 4 by computing the total equilibrium population $T^*(\varepsilon)$ for several parameter sets corresponding to the three monotonicity patterns. To ensure a fair comparison of the total biomass baseline, we keep the sum $K_1 + K_2$ constant across all cases (equal to 8), while varying the individual carrying capacities and the growth rates.

The steady state $(x_1^*(\varepsilon), x_2^*(\varepsilon))$ is obtained by solving the equilibrium system (22) using a Newton–Raphson method for each $\varepsilon > 0$. Table 1 lists the parameter values for the four examples.

The parameter values are purely illustrative and do not correspond to a specific biological system. Their purpose is to confirm and visualize the analytical results. By keeping $K_1 + K_2$ constant, we isolate the effect of dispersal from a baseline total carrying capacity.

Figure 11 displays $T^*(\varepsilon)$ for $\varepsilon \in [0, 5]$ in the four scenarios. In Case 1, T^* decreases monotonically (Theorem 4(1)). In Case 2, T^* is unimodal, reaching a maximum at $\varepsilon = \varepsilon_0$ (Theorem 4(2)). In Cases 3 and 4, T^* increases monotonically (Theorem 4(3)), showing that different combinations of (K_1, K_2, r_1, r_2) can yield the same monotonic pattern.

These simulations clearly confirm the theoretical trichotomy:

- Case 1: Any dispersal reduces total biomass.
- Case 2: Moderate dispersal increases biomass up to ε_0 , then declines.
- Cases 3 and 4: Dispersal consistently increases total biomass, even though the individual carrying capacities differ.

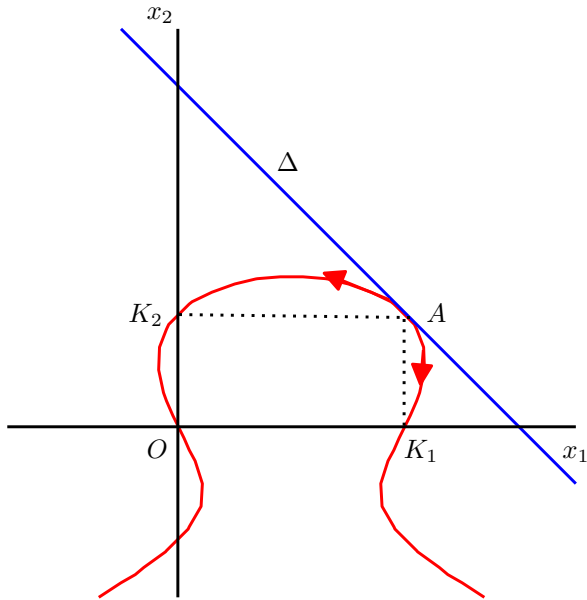


Fig. 7: Illustration of item (1). The curve φ (red) and the line Δ (blue) are shown for certain parameter values. The total equilibrium population is always smaller than $K_1 + K_2$ for all ε , since it belongs to φ . For $\varepsilon = 0$, $E^*(0) = A$; as ε increases, $E^*(\varepsilon)$ moves along φ in one of the two directions indicated by the arrows.

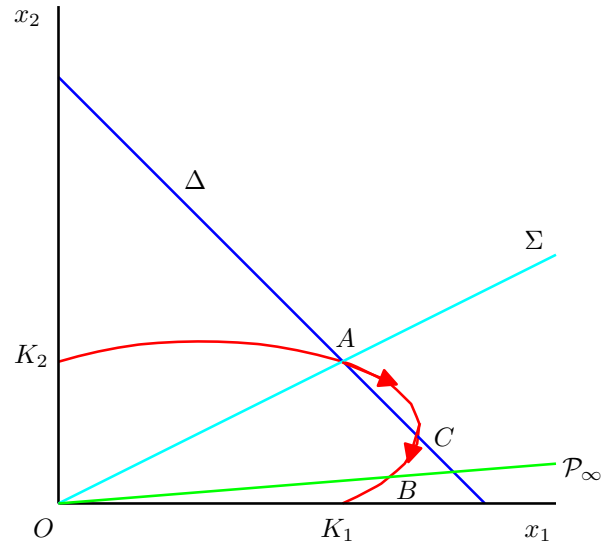


Fig. 9: Illustration of item (2.a.ii). The equilibrium point $E^*(\varepsilon)$ passes through C before ending at B below Δ .

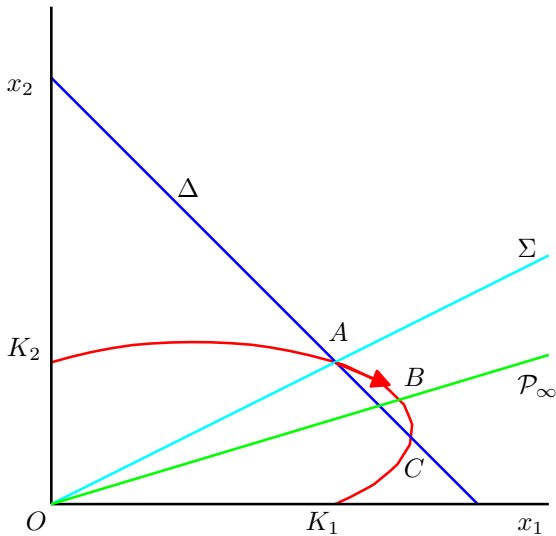


Fig. 8: Illustration of Case 2)(a)(i). The curve φ (red), the lines Δ (blue), Σ (cyan) and $\mathcal{P}_\infty$ (green) are shown. The total equilibrium is always greater than $K_1 + K_2$ for all ε since B lies above Δ .

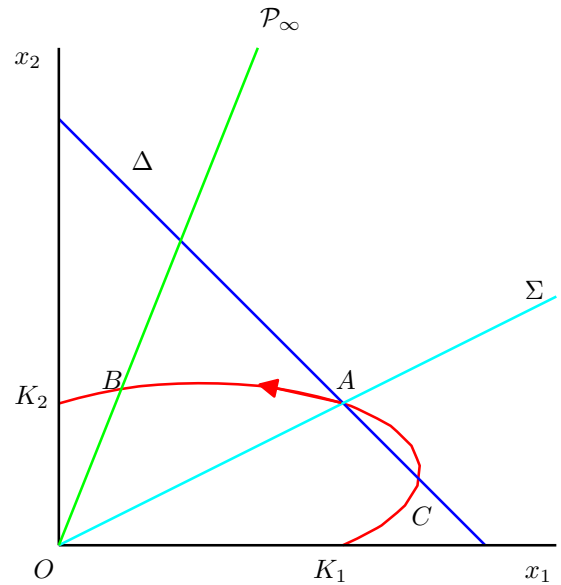


Fig. 10: Illustration of item (2.b). The total equilibrium population remains smaller than $K_1 + K_2$ for all ε .

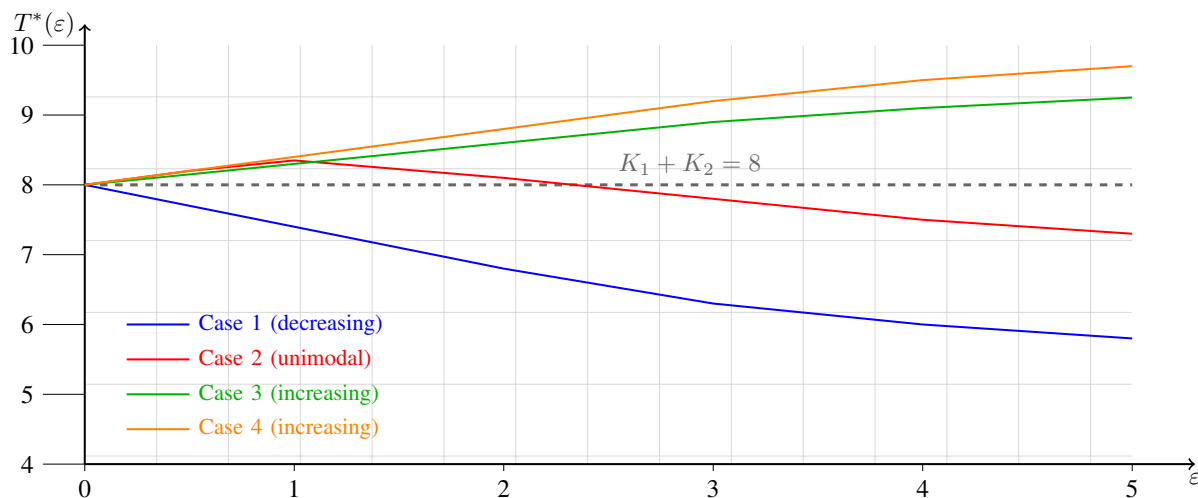


Fig. 11: Numerical variation of $T^*(\varepsilon)$ for the four cases in Table 1. The y -axis starts at 4. The dashed line indicates the common initial total biomass $K_1 + K_2 = 8$ for all cases.

IX. CONCLUSION AND DISCUSSION

In this work, we have investigated the influence of a weak Allee effect on the total biomass of a single-species population distributed over a patchy environment. Using a discrete two-patch population model framework with patch heterogeneity, we established analytical results describing the qualitative behavior of steady states and quantified the changes in total biomass as a function of the dispersal rate. Our study shows that, under a weak Allee effect, the total biomass decreases monotonically with increasing dispersal, and no positive dispersal rate can yield the same biomass as in the absence of dispersal. These results extend previous findings obtained in purely logistic settings, highlighting that the presence of a weak Allee effect does not reverse the biomass–dispersal relationship.

From an ecological perspective, our findings emphasize that promoting movement between patches may not enhance, and may even reduce, the overall population size when a weak Allee effect is present. This has important implications for conservation strategies and habitat management, particularly in fragmented landscapes where both dispersal and Allee effects play significant roles.

Future work could address the extension of these results to multi-species interactions, more general non-linear dispersal mechanisms, and stochastic perturbations, in order to assess the robustness of the observed biomass patterns.

Discussion on the strong Allee effect. When the weak Allee effect is replaced by a *strong* Allee effect,

	r_1	r_2	K_1	K_2	M	γ_{12}	γ_{21}	Monoton.
1	1.2	1.0	5.0	3.0	-1	0.4	0.6	Decreasing
2	1.3	1.2	4.5	3.5	-1	0.4	0.6	Unimodal
3	1.5	1.8	6.0	2.0	-1	0.4	0.6	Increasing
4	1.4	2.0	3.5	4.5	-1	0.4	0.6	Increasing

Table 1: Parameter values used in the simulations. The sum $K_1 + K_2 = 8$ for all cases, so the initial total biomass at $\varepsilon = 0$ is identical. Different growth rates r_i and individual carrying capacities produce the three monotonicity regimes.

the mathematical analysis becomes significantly more challenging. In contrast to the weak case, where the per capita growth rate remains positive at low densities, the strong Allee effect introduces a critical threshold below which the population declines to extinction. This creates multiple equilibria in each patch (extinction, unstable threshold, and carrying capacity) and leads to the possibility of bistability.

From an analytical standpoint, the existence and uniqueness of positive steady states can no longer be guaranteed by straightforward monotonicity arguments, and the total biomass may exhibit discontinuous changes as dispersal varies. Moreover, dispersal can have non-intuitive effects: it may either rescue populations from extinction or, conversely, drive them below the critical threshold in some patches. These phenomena require the use of bifurcation theory, stability switching analysis, and careful treatment of threshold dynamics, making the derivation of general biomass–dispersal relationships far more intricate than in the weak Allee effect scenario.

REFERENCES

- [1] S. A. Levin, Dispersion and Population Interactions, *The American Naturalist*, 108:207–228, 1974.
- [2] S. A. Levin, Spatial Patterning and the Structure of Ecological Communities, In: *Some Mathematical Questions in Biology VII*, American Mathematical Society, 1976.
- [3] R. D. Holt, Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution, *Theoretical Population Biology*, 28:181–208, 1985.
- [4] S. A. Levin, T. M. Powell, J. H. Steele, *Patch Dynamics*, Lecture Notes in Biomathematics, 96, Springer-Verlag, 1993.
- [5] I. Hanski, M. E. Gilpin, *Metapopulation Biology*, Academic Press, 1997.
- [6] H. I. Freedman, P. Waltman, Mathematical Models of Population Interactions with Dispersal. I: Stability of Two Habitats with and without a Predator, *SIAM Journal on Applied Mathematics*, 32:631–648, 1977.
- [7] R. Arditi, C. Lobry, T. Sari, Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation, *Theoretical Population Biology*, 106:45–59, 2015.
- [8] R. Arditi, C. Lobry, T. Sari, Asymmetric dispersal in the multi-patch logistic equation, *Theoretical Population Biology*, 120:11–15, 2018.
- [9] H. Wu, Y. Wang, Y. Li, D. L. DeAngelis, Dispersal asymmetry in a two-patch system with source–sink populations, *Theoretical Population Biology*, 131:54–65, 2020.
- [10] Y. Kang, N. Lanchier, Expansion or extinction: deterministic and stochastic two-patch models with Allee effects, *Journal of Mathematical Biology*, 62:925–973, 2011.
- [11] L. Chen, T. Liu, F. Chen, Stability and bifurcation in a two-patch model with additive Allee effect, *AIMS Mathematics*, 7:536–551, 2022.
- [12] Y. Lv, L. Chen, F. Chen, Stability and bifurcation in a single species logistic model with additive Allee effect and feedback control, *Advances in Difference Equations*, 2020:129, 2020.
- [13] Y. Lv, L. Chen, F. Chen, Z. Li, Stability and Bifurcation in an SI Epidemic Model with Additive Allee Effect and Time Delay, *International Journal of Bifurcation and Chaos*, 31:2150060, 2021.
- [14] D. Pal, G. P. Samanta, Effects of dispersal speed and strong Allee effect on stability of a two-patch predator–prey model, *International Journal of Dynamics and Control*, 6:1484–1495, 2018.
- [15] S. Saha, G. P. Samanta, Influence of dispersal and strong Allee effect on a two-patch predator–prey model, *International Journal of Dynamics and Control*, 7:1321–1349, 2019.
- [16] W. Wang, Population dispersal and Allee effect, *Ricerche di Matematica*, 65:535–548, 2016.
- [17] B. Elbetch, Effect of dispersal in two-patch environment with Richards growth on population dynamics, *Journal of Innovative Applied Mathematics and Computational Sciences*, 2:41–68, 2022.
- [18] B. Elbetch, Generalized logistic equation on Networks, *Comptes Rendus. Mathématique*, 361:911–934, 2023.
- [19] D. Gao, Y. Lou, Total biomass of a single population in two-patch environments, *Theoretical Population Biology*, 146:1–14, 2022.
- [20] C. Grumbach, F. N. Reurik, J. Segura, D. Franco, F. M. Hilker, The effect of dispersal on asymptotic total population size in discrete- and continuous-time two-patch models, *Journal of Mathematical Biology*, 87:60, 2023.
- [21] A. N. Tikhonov, Systems of differential equations containing small parameters in the derivatives, *Matematicheskii sbornik*, 73:575–586, 1952.
- [22] W. Wasow, *Asymptotic Expansions for Ordinary Differential Equations*, Courier Dover Publications, 2018.
- [23] D. Gao, How Does Dispersal Affect the Infection Size?, *SIAM Journal on Applied Mathematics*, 80:2144–2169, 2020.
- [24] D. Gao, Y. Lou, Impact of State-Dependent Dispersal on Disease Prevalence, *Journal of Nonlinear Science*, 31:73, 2021.