CIMPA

Epi-SCIENCE
The Science Behind Population Health
https://revistas.ucr.ac.cr/index.php/episcience

Revista
Interdisciplinaria
Epi-SCIENCE

# CONSEQUENCES OF TRACEABLE MOBILITY IN POPULATIONS EXHIBITING STRONG ALLEE EFFECT

Baltazar Espinoza[1], Yun Kang[2], Oyita Udiani[3]

[1] *Biocomplexity Institute and Initiative, Network Systems Science and Advanced Computing Division, University of Virginia, Virginia, USA.*
[2] *Sciences and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, USA.*
[3] *Department of Mathematics and Applied Mathematics, Virginia Commonwealth University, Richmond, USA.*

✉ be8dq@virginia.edu

Submitted: 06/27/2022; Accepted: 11/16/2022
DOI: https://doi.org/10.15517/es.2023.55393

## Abstract

In this research, we study the impacts of the traceable mobility in a two-patch environment when the population in each patch exhibits strong Allee effects. Traveling individuals are traced across patches by budgeting the average time spent in each patch while keeping their place of residency. Particularly, we focus on the impact that the effective population (residents and visitors) produces on regional dynamics. Our results show that low mobility across regions produces simple dynamics, where orbits converge to single or double extinction or to a coexistence steady state. We derive mobility conditions under which an endangered population may benefit of the presence of a visitant one and avoid extinction – the rescue effect. Nonetheless, increments in the visiting population would also lead the resident population to extinction – the induced extinction effect.

**Keywords:** Mobility; Residency times; Allee effect; Metapopulation; Behavior

CIMPA

Epi-SCIENCE
The Science Behind Population Health
https://revistas.ucr.ac.cr/index.php/episcience

Revista
Interdisciplinaria
Epi-SCIENCE

# CONSECUENCIAS DE LA MOVILIDAD TRAZABLE EN POBLACIONES QUE EXHIBEN FUERTE EFECTO ALLEE

Baltazar Espinoza[1], Yun Kang[2], Oyita Udiani[3]

[1] *Biocomplexity Institute and Initiative, Network Systems Science and Advanced Computing Division, University of Virginia, Virginia, USA.*
[2] *Sciences and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, USA.*
[3] *Department of Mathematics and Applied Mathematics, Virginia Commonwealth University, Richmond, USA.*

✉ be8dq@virginia.edu

Enviado: 27/06/2022; Aceptado: 16/11/2022
DOI: https://doi.org/10.15517/es.2023.55393

---

## Resumen

En esta investigación, estudiamos los impactos de la movilidad rastreable en un entorno de dos parches cuando la población en cada parche exhibe fuertes efectos Allee. Las personas que viajan se rastrean a través de los parches al presupuestar el tiempo promedio que pasan en cada parche, mientras mantienen su lugar de residencia. En particular, nos enfocamos en el impacto que la población efectiva (residentes y visitantes) produce en la dinámica regional. Nuestros resultados muestran que la baja movilidad entre regiones produce una dinámica simple, donde las órbitas convergen en extinción simple o doble, o en un estado estacionario de coexistencia. Derivamos las condiciones de movilidad bajo las cuales una población en peligro puede beneficiarse de la presencia de una visitante y evitar la extinción: el efecto de rescate. No obstante, los incrementos de la población visitante también llevarían a la población residente a la extinción: el efecto de extinción inducida.

**Palabras clave:** Mobilidad; Tiempos de residencia; Efecto Allee; Metapoblación; Comportamiento

---

# 1. Introduction

The Allee effect was first introduced in 1931 by Warder C. Allee as the idea of "inverse density dependence in an isolated population" [1, 5], has played an important role in conservation ecology. By mirroring the concept of carrying capacity, the Allee effect predicts a non-zero threshold, for which species extinction is guaranteed if the population crosses it down.

Reproductive and survival phenomena such as the reduction of mates encounters and environment improvement have been proposed as component Allee effect mechanisms. However, it is not clear whether these may or may not have consequences on the population scale, producing a demographic Allee effect [6, 5]. Nonetheless, mathematical models often incorporate the demographic Allee effect from a phenomenological perspective; explicitly incorporating a term producing positive density dependence.

The Allee theory has been widely used to study population dynamics in complex settings. In [12], extinction, exclusion, and coexistence conditions are derived in a model of two species in competition, where both populations show Allee effects. Recent studies have addressed the effects of migration in a two-patch environment for deterministic and stochastic models where populations exhibit strong Allee effects [11]. For the deterministic model, they found that the global extinction or expansion is robust to migration states. The recent development of a framework that tracks individuals' patch-specific residence times during epidemics [2, 3], opens new horizons to study population dynamics in fragmented environments. This novel modeling approach allows explicitly incorporating individuals' exposure to heterogeneous environments by tracking the average time that a typical individual spend in each patch.

In this research, we use the concept of *residency times* to study how the local and the regional diversity in a fragmented habitat is affected by the interactions of local populations. Specifically, we assume a two-patch environment where patch size allows individuals to travel back and forth from their patch of residency. By assuming homogeneous mobility rates within individuals of the same patch, density-independent, and constant mobility over time, we derive conditions under which populations exhibiting a strong Allee effect in isolation can coexist in the presence of short-term mobility. The proposed deterministic two-patch model has coupled via individuals' movement across patches. We derive existence and stability conditions for the set of equilibrium points, and we show that mobility can alter the regional dynamics by: (*i*) a population expected to be endangered in isolation (below its Allee threshold), can be benefited and avoid extinction by the presence of conspecifics as a consequence of mobility – the "rescue effect" [9, 7, 15], and (*ii*) a population expected to be non-endangered in isolation (over its Allee threshold), might be lead to extinction by hosting a visiting population – the "extinction effect" [13]. Our results are illustrated through theoretical work and a series of numerical simulations showing the expected population dynamics at different levels of mobility.

## 2. Methods

Following [11], we use a mean-field approach to capture single species dynamics with a strong Allee effect as follows

$$\dot{N} = rN(N-\theta)(K-N) \tag{1}$$

where $r$ represents the per-capita intrinsic growth rate, $K$ stands for the carrying capacity threshold that avoids unbounded population growth, and $\theta$ between zero and $K$ is the so-called Allee threshold below which the population is endangered and destined to extinction. We extend the single population framework to model population dynamics in an environment composed of two patches, and let $N_i$ denote the population resident of patch $i$, $i \in \{1,2\}$. The Lagrangian type mobility framework [3] allows us to track individuals' daily movement by using a residence times matrix $\mathbb{P} = (p_{ij})_{1\leq i,j\leq n}$, where $p_{ij}$ accounts for the average time that patch $i$ residents spend in patch $j$. By using this formulation, the expected population (also referred to as *effective population*) in patch $i$ accounts for residents and visitant population, and it is described by $\sum_{j=1}^{2} p_{ji}N_j$. For simplicity, we use $p_i$ to denote the time individuals spend in their own patch, and $1-p_i$ the time individuals spend mingling outside its patch of residency. In addition, we assume the intrinsic population growth rate only depends on the resident population density, not on the effective population sojourning in each patch. Consequently, the effective population is reflected in the terms corresponding to the Allee effect and the carrying capacity. The model describing the patch-specific population dynamics accounting for the effective population in a two-patch setting is given by

$$\begin{aligned} \dot{N}_1 &= r_1N_1(p_1N_1 + (1-p_2)N_2 - \theta_1)(K_1 - (p_1N_1 + (1-p_2)N_2)), \\ \dot{N}_2 &= r_2N_2(p_2N_2 + (1-p_1)N_1 - \theta_2)(K_2 - (p_2N_2 + (1-p_1)N_1)) \end{aligned} \tag{2}$$

where $K_i$ and $\theta_i$ stand for the patch-$i$ carrying capacity and Allee extinction threshold in the absence of mobility ($p_i = 1$ and $p_j = 1$). These parameters do not depend on the population sojourning in patch-$i$, instead, these are intrinsic to the environment in relation to a particular species. In the further section, we show that the Lagrangian mobility assumption (letting the population spend a fraction of daily time outside its patch of residency) modulates both: ($i$) the patch-specific minimal resident population expected to undergo extinction, which we call, *the effective Allee threshold*, $\left(\theta_i^{eff} = \frac{\theta_i}{p_i}\right)$; and, ($ii$) the patch-specific maximum resident population size sustainable, which we call, *the effective carrying capacity*, $\left(K_i^{eff} = \frac{K_i}{p_i}\right)$.

**Lemma 1.** *Let $r_i, K_i, \theta_i$, $i \in \{1,2\}$ be strictly positive. The model (2) is positively invariant and bounded in $\mathbb{R}^2$.*

The proof of (1) is provided in the SI appendix.

## 3. Results

We found that simple dynamics are exhibited for low mobility levels. In these scenarios, all orbits converge to stable nodes. The following theorem states the existence and stability conditions of the equilibrium points exhibited by the model (2) in the presence of Lagrangian-type mobility.

**Theorem 1.** *Model (2) exhibits at most nine equilibrium points: five boundary equilibria and four interior equilibria. Moreover, double extinction is always a possible outcome, i.e., the equilibrium $E_{0,0}$ is locally stable for all mobility regimes. At the same time, coexistence at the effective Allee thresholds levels is not possible, i.e., the equilibrium $E_{\theta_1,\theta_2}$ is unstable under all traveling regimes.*

The proof of theorem (1) is provided in the SI appendix.

Table 1 shows the model's (2) equilibria, existence, and stability conditions. The set of interior equilibria is given by

$$\Lambda = \{E_{K_1,K_2}, E_{\theta_1,K_2}, E_{K_1,\theta_2}, E_{\theta_1,\theta_2}\},$$

where the equilibrium $E_{K_1,K_2}$ is the only one interior attractor corresponding to the coexistence scenario; $E_{\theta_1,K_2}$ and, $E_{K_1,\theta_2}$ are semi-stable equilibria, and $E_{\theta_1,\theta_2}$ is an unstable equilibrium. Moreover, the set of boundary equilibria is given by

$$\Omega = \{E_{K_1,0}, E_{\theta_1,0}, E_{0,K_2}, E_{0,\theta_2}, E_{0,0}\},$$

where the equilibrium $E_{0,0}$ corresponds to the global extinction scenario, while the equilibria $E_{K_1,0}$ and $E_{0,K_2}$ stand for the single species survival scenarios. The boundary equilibria are of particular interest since these define effective thresholds in the presence of Lagrangian mobility: the *effective Allee threshold* $\left(\theta_i^{eff} = \frac{\theta_i}{p_i}\right)$, which is the population size of patch-$i$ residents below which the population undergoes extinction in isolation, i.e., under one-way mobility ($p_1 < 1$ and $p_j = 1$); and, the *effective carrying capacities* $\left(K_i^{eff} = \frac{K_i}{p_i}\right)$, which is the maximum population size sustainable of patch-$i$ residents. Thus, in the proposed Lagrangian perspective, the effective Allee and carrying capacity thresholds depend on both: the resident's population size and the population's mobility.

**Table 1:** Equilibria existence and stability.

| **Equilibrium** | **Existence** | **Stability** |
|---|---|---|
| $E_{0,0} = (0,0)$ | Always | Always stable |
| $E_{K_1,0} = \left(\frac{K_1}{p_1}, 0\right)$ | $p_1 \neq 0$ | $p_1 > \frac{K_1}{K_1+\theta_2}$ or $p_1 < \frac{K_1}{K_1+K_2}$ |
| $E_{\theta_1,0} = \left(\frac{\theta_1}{p_1}, 0\right)$ | $p_1 \neq 0$ | Always unstable |
| $E_{0,K_2} = \left(0, \frac{K_2}{p_2}\right)$ | $p_2 \neq 0$ | $p_2 > \frac{K_2}{\theta_1+K_2}$ or $p_2 < \frac{K_2}{K_1+K_2}$ |
| $E_{0,\theta_2} = \left(0, \frac{\theta_2}{p_2}\right)$ | $p_2 \neq 0$ | Always unstable |
| $E_{K_1,K_2} = \left(\frac{K_2 - p_2(K_1+K_2)}{1-p_1-p_2}, \frac{K_1 - p_1(K_1+K_2)}{1-p_1-p_2}\right)$ | $p_1 > \frac{K_1}{K_1+K_2}$ and $p_2 > \frac{K_2}{K_1+K_2}$<br>or<br>$p_1 < \frac{K_1}{K_1+K_2}$ and $p_2 < \frac{K_2}{K_1+K_2}$ | $p_1 > \frac{K_1}{K_1+K_2}$ and $p_2 > \frac{K_2}{K_1+K_2}$ |
| $E_{\theta_1,K_2} = \left(\frac{K_2 - p_2(K_2+\theta_1)}{1-p_1-p_2}, \frac{\theta_1 - p_1(\theta_1+K_2)}{1-p_1-p_2}\right)$ | $p_1 > \frac{\theta_1}{\theta_1+K_2}$ and $p_2 > \frac{K_2}{\theta_1+K_2}$<br>or<br>$p_1 < \frac{\theta_1}{\theta_1+K_2}$ and $p_2 < \frac{K_2}{\theta_1+K_2}$ | $p_1 < \frac{K_1}{K_1+K_2}$, $p_2 < \frac{K_2}{K_1+K_2}$<br>and<br>$\frac{p_1 r_1(K_1-\theta_1)}{p_2 r_2(K_2-\theta_2)} > \frac{p_1(\theta_1+K_2)-\theta_1}{p_2(\theta_1+K_2)-K_2}$ |
| $E_{K_1,\theta_2} = \left(\frac{\theta_2 - p_2(K_1+\theta_2)}{1-p_1-p_2}, \frac{K_1 - p_1(K_1+\theta_2)}{1-p_1-p_2}\right)$ | $p_1 > \frac{K_1}{K_1+\theta_2}$ and $p_2 > \frac{\theta_2}{K_1+\theta_2}$<br>or<br>$p_1 < \frac{K_1}{K_1+\theta_2}$ and $p_2 < \frac{\theta_2}{K_1+\theta_2}$ | $p_1 < \frac{K_1}{K_1+\theta_2}$, $p_2 < \frac{\theta_2}{K_1+\theta_2}$<br>and<br>$\frac{p_2 r_2(K_2-\theta_2)}{p_1 r_1(K_1-\theta_1)} > \frac{p_1(K_1+\theta_2)-K_1}{p_2(K_1+\theta_2)-\theta_2}$ |
| $E_{\theta_1,\theta_2} = \left(\frac{\theta_2 - p_2(\theta_1+\theta_2)}{1-p_1-p_2}, \frac{\theta_1 - p_1(\theta_1+\theta_2)}{1-p_1-p_2}\right)$ | $p_1 > \frac{\theta_1}{\theta_1+\theta_2}$ and $p_2 > \frac{\theta_2}{\theta_1+\theta_2}$<br>or<br>$p_1 < \frac{\theta_1}{\theta_1+\theta_2}$ and $p_2 < \frac{\theta_2}{\theta_1+\theta_2}$ | Always unstable |

It follows from Theorem 1 that for certain initial conditions, Lagrangian-type mobility produces global extinction. We also study how mobility impacts the critical size needed for a population to get established. Varying traveling regimes produce changes in the patch-specific abundance distribution, as a consequence, we found that coexistence can be characterized in two scenarios: (*i*) when only one population travels, the traveling population increases its size to its effective carrying capacity, while the host population decreases its size below its carrying capacity–in this scenario, the carrying capacity equals the effective carrying capacity of the host population, for instance, see Figure 2; (*ii*) when both populations travel, both population sizes are strictly lower than the corresponding effective carrying capacities, for instance, see Figure 3.

Notice that the populations' abundance ratio ($K_1/K_2$) plays a critical role in the traveling regimes supporting coexistence. For instance, big differences in the patch-carrying capacities asymmetrically weigh the effects of populations traveling regimes. A direct implication of the previous observation is that the equilibrium $E_{K_1,K_2}$ is more sensitive to changes in traveling regimes of the dominant (more abundant) population.

In order to facilitate results interpretation, we use the following color key to denote equilibria stability: attractor equilibria are colored red, semi-stable equilibria are colored blue, while unstable equilibria are colored green. The regional dynamics of the proposed system in terms of the number of attractors are summarized as follows:

- Nine equilibrium points - in the absence of mobility.
  Under this scenario, the system exhibits 4 attractors, corresponding to a double extinction equilibrium ($E_{0,0}$), 2 single extinction equilibrium ($E_{K_1,0}$, and $E_{0,K_2}$), and a coexistence equilibrium ($E_{K_1,K_2}$). Moreover, the system exhibits four interior saddle-nodes ($E_{\theta_1,K_2}$, $E_{K_1,\theta_2}$, $E_{0,\theta_2}$, $E_{\theta_1,0}$); and a single interior source ($E_{\theta_1,\theta_2}$), see Figure 1.
- Eight equilibrium points - one-way mobility.
  The system exhibits 3 attractors: a double extinction, a single extinction, and the coexistence equilibrium; three boundaries, an interior saddle-node, and a source. In the scenario of high enough one-way mobility, the system loses one of its interior saddle-nodes, this occurs via a transcritical bifurcation when a saddle-node hits a stable single extinction equilibrium $(0, K_2)$ or $(K_1, 0)$. Figure 2 shows this scenario when only the $N_1$ population increases mobility and drives a transcritical bifurcation. In this scenario, the equilibrium point $E_{K_1,\theta_2}$ equals $E_{K_1,0}$, undergoing a transcritical bifurcation, where the equilibrium point $E_{K_1,\theta_2}$ loses its biological meaning afterward and, where the equilibrium point $E_{K_1,0}$ becomes stable.

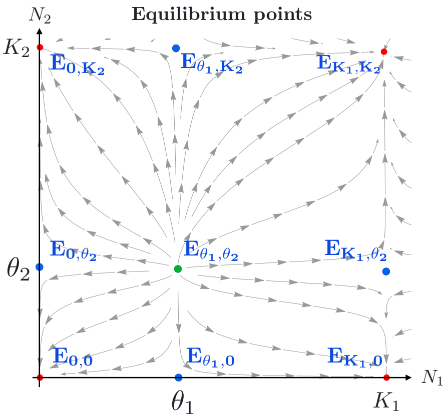

**Figure 1:** In the absence of mobility, the system exhibits up to nine equilibrium points.

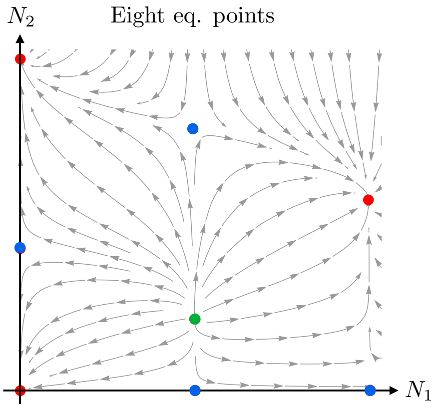

**Figure 2:** Eight equilibrium points. Three attractors: coexistence, single extinction, and double extinction, four saddle-nodes, and a source.

- Seven equilibrium points.
  After a saddle-node vanished, mobility and the ratio of the populations' vulnerabilities $\left(\eta = \frac{\frac{K_1}{\theta_1}}{\frac{K_2}{\theta_2}}\right)$ define three ways to reach this scenario:
  (a) saddle-node and coexistence equilibrium vanished in the case $\eta < 1$.
  The less vulnerable population increases its traveling regime enough to drive the host population to extinction. In this case, the system exhibits three boundary attractors: two single extinction and the double extinction equilibrium; two boundaries and an interior saddle point; and the interior source point. Figure 3 shows the $N_2$ population traveling regime that leads coexistence equilibrium to vanish.
  (b) saddle-node and source vanished, when $\eta > 1$.
  In this case, the more vulnerable population increases traveling, and as a consequence, the source node vanishes before the coexistence equilibrium does it. In this case, the system exhibits three attractors: double extinction, single extinction, and coexistence equilibrium; three boundary saddle-nodes and the interior source equilibrium. In Figure 4, the $N_2$ population is assumed more vulnerable than $N_1$, and as $p_2$ goes to zero, the source node vanishes.
  (c) Both interior saddle-node equilibria vanish, given that both populations travel. In a two-way mobility regime, both interior saddle-nodes vanish. In this case, the system exhibits two attractors: double extinction and coexistence equilibrium points; four saddle-nodes, and a source node. Figure 5 shows the phase

plane where orbits converge either to coexistence or double extinction. Note: the coexistence equilibrium basin of attraction increases significantly. In the following section, the coexistence equilibrium basin of attraction is analyzed as mobility varies.

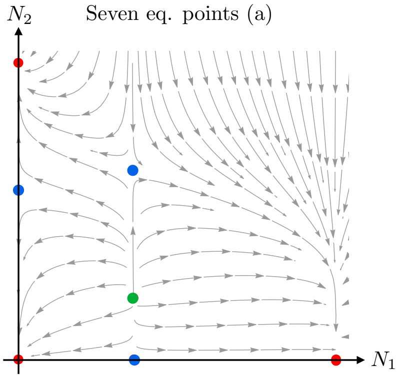

**Figure 3:** Case (a): Interior saddle-node and coexistence equilibria vanished. Three attractors: two single extinction and global extinction, three saddle-nodes, and a source.

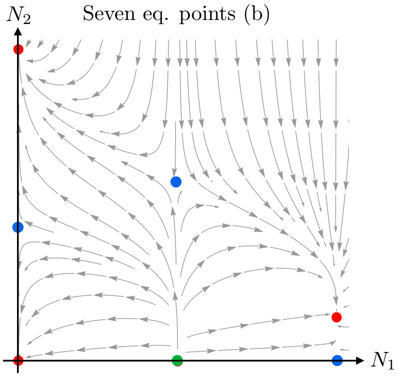

**Figure 4:** Case (b): Interior saddle-node and source equilibria vanished. Three attractors: coexistence, single extinction, and global extinction, three saddle-nodes, and a source.

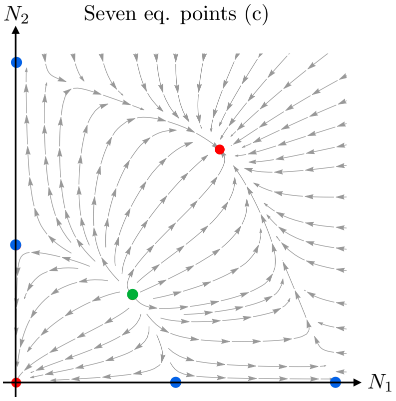

**Figure 5:** Case (c): Both interior saddle-nodes vanished. Two attractors, coexistence and global extinction.

- Six equilibrium points.
  Since the interior equilibria account for two saddle-nodes, a source, and an attractor;

in terms of the last interior point surviving, there are three possible scenarios for the system to exhibit six equilibrium points: saddle-node, source, and coexistence equilibrium. In the scenario where both populations travel, Figure 6 shows the coexistence equilibrium would survive, while Figure 7 shows the source would survive. Moreover, if one of the populations travels, Figure 8 shows that only a single interior saddle-node equilibrium survives.

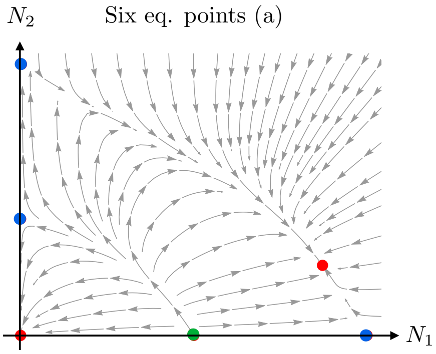

**Figure 6:** Only coexistence equilibrium survives.

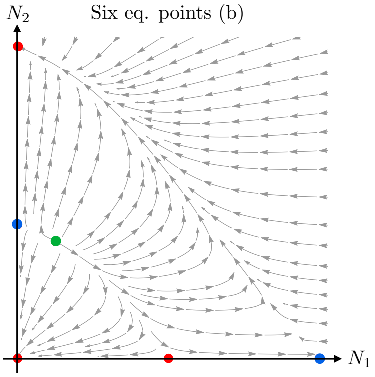

**Figure 7:** Only interior source equilibrium survives.

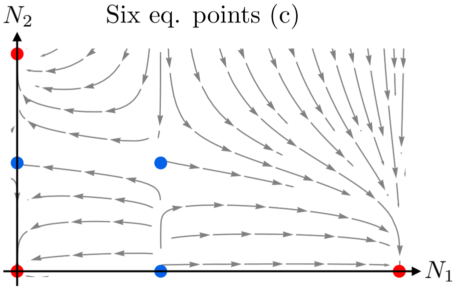

**Figure 8:** Only interior saddle-node equilibrium survives.

Note that, in the case when both populations are equally vulnerable $\left(\frac{\theta_1}{K_1} = \frac{\theta_2}{K_2}\right)$, the system goes directly from having eight equilibrium points to six, by losing the coexistence and source equilibrium at the same mobility level.

- Five equilibrium points.
  This case corresponds to the scenario where one of the populations leads the second to extinction. The only possible scenario (in the weakly connected system) to show five equilibrium points is when only boundary equilibria remain. In this case, the

system exhibits two attractors: double extinction and single extinction, and three saddle-nodes. Figure 9 shows this scenario when $N_2$ population leads $N_1$ population to extinction.

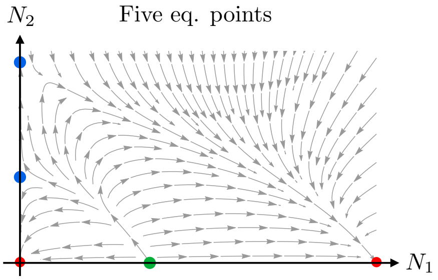

**Figure 9:** In this scenario, only the $N_1$ population travels, driving the $N_2$ population to extinction. Consequently, all interior equilibria vanish, and global extinction or extinction of the host population is possible.

Then, $p_1^* = \frac{K_1}{K_1+\theta_2}$ and $p_2^* = \frac{K_2}{K_2+\theta_1}$, are the minimum mobility levels capable of perturbing the system enough to produce a qualitative change. Although these do not affect coexistence equilibrium stability, mobility at those levels is able to unstabilize the single extinction attractors, leaving coextinction or coexistence as the only steady states. In the SI appendix section A, we explore the system's (2) bifurcations as the population $N_1$ increases its mobility level.

### 3.1. Mobility may induce endangered populations rescue or extinction of established populations

It is well known that an endangered population can benefit from the presence of conspecifics as a consequence of mobility, this is called "the rescue effect". However, a detrimental impact can also occur when the patch's maximum carrying capacity is exceeded by the effective population size sojourning. The following results establish mobility conditions under which the rescue and the induced extinction effects are produced.

**Theorem 2** (The rescue effect)**.** *Assume the population $N_j$ is expected to be endangered in isolation (below its Allee threshold, $N_j < \theta_j$), and let the population $N_i$ be well established in isolation (over its Allee threshold, $N_i > \theta_i$). The following traveling conditions lead to populations coexistence*

$$\frac{\theta_j}{K_i + \theta_j} < 1 - p_i < \frac{K_j}{K_i + K_j}, \tag{3}$$

*where $\{i, j\} \in \{1, 2\}$ and $i \neq j$. In other words, the $N_i$ population produces the rescue effect on the population $N_j$ under the mobility conditions in (3).*

The proof of the theorem (2) is included in the SI appendix. Inequality (3) shows that the rescue effect is reached whenever the equilibrium $E_{K_1,0}$ (or $E_{0,K_2}$, by the symmetry of the system) switches from being stable to unstable by undergoing a transcritical bifurcation along with the equilibrium points $E_{K_1,\theta_2}$ ($E_{0\theta_1,K_2}$), as mobility increases. In other words, an already established population ($N_i > \theta_i$) can prevent an endangered population from going to extinction ($N_j < \theta_j$) whenever its traveling time $(1 - p_i)$ is greater than $\frac{\theta_j}{K_i+\theta_j}$. In this scenario, the presence of conspecifics helps an endangered population avoid extinction induced by a strong Allee effect exhibited in isolation. Notice that the rescue threshold $\frac{\theta_j}{K_i+\theta_j}$ can be expressed as $\frac{1}{1+K_i/\theta_j}$, meaning that environmental heterogeneity expressed by the ratio between the visitant population's carrying capacity to the resident's population Allee threshold $\left(\frac{K_i}{\theta_j}\right)$ measures the effort required for the visitant population to produce a rescue effect:

- $K_i \ll \theta_j$ implies that $\frac{\theta_j}{K_i+\theta_j} \approx 1$, and the rescue effect is difficult to achieve since it requires "high" mobility levels.
- $K_i \gg \theta_j$ implies that $\frac{\theta_j}{K_i+\theta_j} \approx 0$, and the rescue effect requires "low" mobility levels of the visiting population.

Figure 10 shows the scenario when both populations are able to produce the rescue effect by traveling enough to destabilize both equilibria: $E_{K_1,0}$ and $E_{0,K_2}$.

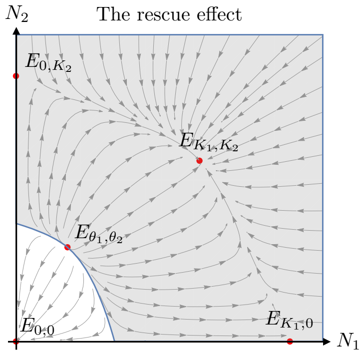

**Figure 10:** The rescue effect occurs when one of the populations is not at risk of extinction ($N_i > \theta_i$). The shaded region represents the basin of attraction of the coexistence equilibrium $E_{K_1,K_2}$, while the white region shows the basin of attraction of the double extinction equilibrium $E_{0,0}$.

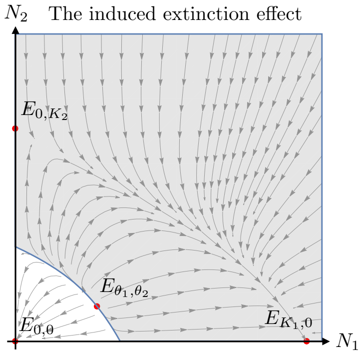

**Figure 11:** Induced extinction of the $N_2$ population caused by high mobility of the $N_1$ population. The shaded region represents the basin of attraction of the single extinction equilibrium $E_{K_1 0}$, while the white region shows the basin of attraction of the double extinction equilibrium $E_{0,0}$.

**Theorem 3** (The induced extinction effect)**.** *Assume populations* $N_i$ *and* $N_j$ *with mobility conditions* $\frac{\theta_j}{K_i+\theta_j} < 1 - p_i < \frac{K_j}{K_i+K_j}$ *where* $\{i, j\} \in \{1, 2\}$ *and* $i \neq j$*. The* $N_i$ *population induces the* $N_j$ *population extinction by increasing its mobility according to the following conditions,*

$$1 - p_i > \frac{K_j}{K_i + K_j} \tag{4}$$

*where* $i, j \in \{1, 2\}$ *and* $i \neq j$*.*

The proof of the theorem (3) is included in the SI appendix. The induced extinction result shows that if a visitant population $N_i$ travels more than the hosting population in relative abundance $\left(1 - p_i > \frac{K_j}{K_i+K_j}\right)$, the presence of a visitant population equal or greater than the host's patch-specific carrying capacity leads the host population to extinction. Figure 11 shows the phase plane in the scenario when the $N_1$ population induces the $N_2$ population extinction by traveling above its relative abundance $1 - p_1 \geq \frac{K_2}{K_1+K_2}$. Notice that mobility-induced extinction can occur only in the scenario where the population induced to extinction travels enough to destabilize the boundary equilibrium corresponding to the single survival scenario ($\frac{\theta_j}{K_i+\theta_j} < 1 - p_i < \frac{K_j}{K_i+K_j}$). If this mobility condition is not attained, single-population survival or double extinction are possible outcomes, depending on the initial conditions.

Our previous results highlight the impact of the population abundance heterogeneity, which can be expressed in terms of heterogeneity among the patches in a fragmented environment. This plays a critical role in shaping the stability region of the species coexistence equilibrium ($E_{K_1,K_2}$) by weighting the effects of the populations' mobility. On the other hand, our results show the role of the populations' relative vulnerability ($K_1/\theta_1, K_2/\theta_2$) in shaping the stability regions of the single species equilibrium points ($E_{\theta_1,K_2}$ and $E_{K_1,\theta_2}$).

## 4. Conclusions

We investigated the population dynamics exhibited in a two-patch Lagrangian mobility model, where the patch-specific population dynamics are intertwined. In the Lagrangian mobility framework, the effective carrying capacities, the effective Allee thresholds, and the populations' mobility determine the persistence of a population. Mobility alters the patch-specific expected population, which in turn impacts population persistence or extinction conditions. We found that mobility leads the regional species abundance to converge towards stable nodes of double extinction, single species persistence, or species coexistence. Individuals daily traveling across regions modulate the regional species abundance by modulating the patch-specific *effective populations*. Depending on the mobility regime, the expected population abundance differs from those expected in populations exhibiting the Allee effect in isolation.

Our results suggest that in the presence of Lagrangian-type mobility: (*i*) the patch-specific population size is smaller or equal to the patch-effective carrying capacity, (*ii*) a population expected to be endangered in the absence of mobility, may survive in the presence of mobility even if the resident population size is below the Allee extinction threshold, and, (*iii*) an established population may lead to extinction if it travels and hosts a “big enough” visitant population. The intuition behind the first result is that the patch resources are shared among the resident and the visitant population. Therefore, limiting the resident population growth to a lower or equal level than the patch’s carrying capacity. Our second and third results are direct implications of the increment of the *expected population* size due to mobility. While a population may be endangered in isolation, the presence of conspecifics would prevent the population from undergoing extinction. On the other hand, an established population may suffer a critical reduction of the resources available in its own patch of residency by hosting a visiting population. Consequently, producing that the effective population size surpasses the patch carrying capacity.

Individual-level movement processes on short timescales can affect community processes and patterns on longer, ecological timescales [14]. While previous work has been done using a migration mobility perspective, that is, without labeling individuals residency across patches, [11], we find Lagrangian mobility to be a suitable framework to study the regional impact of individuals’ moving across heterogeneous environments, while at the same time being consistent with concepts from the niche theory [10, 4, 8].

## References

[1] WC Allee and Edith S Bowen. “Studies in animal aggregations: mass protection against colloidal silver among goldfishes”. In: *Journal of Experimental Zoology* 61.2 (1932), pp. 185–207. DOI: 10.1002/jez.1400610202.

[2] Derdei Bichara et al. “SIS and SIR epidemic models under virtual dispersal”. In: *Bulletin of mathematical biology* 77.11 (2015), pp. 2004–2034. DOI: 10.1007/s11538-015-0113-5.

[3] Carlos Castillo-Chavez, Derdei Bichara, and Benjamin R Morin. “Perspectives on the role of mobility, behavior, and time scales in the spread of diseases”. In: *Proceedings of the National Academy of Sciences* 113.51 (2016), pp. 14582–14588. DOI: 10.1073/pnas.1604994113.

[4] Jonathan M Chase and Mathew A Leibold. *Ecological niches: linking classical and contemporary approaches.* University of Chicago Press, 2009.

[5] Franck Courchamp, Ludek Berec, and Joanna Gascoigne. *Allee effects in ecology and conservation.* OUP Oxford, 2008.

[6] Franck Courchamp, Tim Clutton-Brock, and Bryan Grenfell. "Inverse density dependence and the Allee effect". In: *Trends in ecology &amp; evolution* 14.10 (1999), pp. 405–410. DOI: 10.1016/S0169-5347(99)01683-3.

[7] Anders Eriksson et al. "The emergence of the rescue effect from explicit within-and between-patch dynamics in a metapopulation". In: *Proceedings of the royal society B: biological sciences* 281.1780 (2014), pp. 2013–3127. DOI: 10.1098/rspb.2013.3127.

[8] Oscar Godoy et al. "Towards the integration of niche and network theories". In: *Trends in Ecology & Evolution* 33.4 (2018), pp. 287–300. DOI: 10.1016/j.tree.2018.01.007.

[9] Nicholas J Gotelli. "Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis". In: *The American Naturalist* 138.3 (1991), pp. 768–776. DOI: 10.1086/285249.

[10] Alexandre H Hirzel and Gwenaëlle Le Lay. "Habitat suitability modelling and niche theory". In: *Journal of applied ecology* 45.5 (2008), pp. 1372–1381. DOI: 10.1111/j.1365-2664.2008.01524.x.

[11] Yun Kang and Nicolas Lanchier. "Expansion or extinction: deterministic and stochastic two-patch models with Allee effects". In: *Journal of Mathematical Biology* 62.6 (2011), pp. 925–973. DOI: 10.1007/s00285-010-0359-3.

[12] G Livadiotis et al. "Competition models with Allee effects". In: *Journal of Difference Equations and Applications* 20.8 (2014), pp. 1127–1151. DOI: 10.1080/10236198.2014.897341.

[13] Tobias Reichenbach and Erwin Frey. "Instability of spatial patterns and its ambiguous impact on species diversity". In: *Physical review letters* 101.5 (2008), pp. 58–102. DOI: 10.1103/PhysRevLett.101.058102.

[14] Ulrike E. Schlägel et al. "Movement-mediated community assembly and coexistence". In: *Biological Reviews* 95.4 (2020), pp. 1073–1096. DOI: 10.1111/brv.12600.

[15] Nathan D Van Schmidt and Steven R Beissinger. "The rescue effect and inference from isolation–Extinction relationships". In: *Ecology Letters* 23.4 (2020), pp. 598–606. DOI: 10.1111/ele.13460.