A Multi-Class Extension of the Mean Field Bolker-Pacala Population Model*

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Abstract

We extend our earlier mean field approximation of the Bolker-Pacala model of population dynamics by dividing the population into N classes, using a mean field approximation for each class but also allowing migration between classes as well as possibly suppressive influence of the population of one class over another class. For $N \geq 2$, we obtain one symmetric non-trivial equilibrium for the system and give global limit theorems. For $N = 2$, we calculate all equilibrium solutions, which, under additional conditions, include multiple non-trivial equilibria. Lastly, we prove geometric ergodicity regardless of the number of classes when there is no population suppression across the classes.

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1 Introduction

The Bolker-Pacala (BP) model of population dynamics, from biology, involves processes of birth, death, and migration, as well as competition or suppression. In a previous paper [1], we analyzed a mean-field approximation of the BP model, obtaining results such as local and global central limit theorems for population size. While that model treated basic population questions, in this paper we extend the mean-field approach to address additional topics.

Specifically, we consider a population now divided into N classes or "boxes," and analyze a mean-field approximation for each box. We allow the possibility of migration between boxes and of competitive effects or the suppression of the population in one box by the population in other boxes. While it is possible to think of the boxes as geographical areas, it is perhaps most intriguing to view them as segments of a population such as

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social classes. In this case, the N-box BP model becomes a model of social stratification. Migration between boxes corresponds, then, to social mobility with the parameters for migration giving the rates of social mobiliy. The parameters for competition *within* boxes may correspond to constraints, such as economic constraints, on the size of classes. It is questionable whether suppression *across* classes would exist or whether these parameters would be 0.

For $N = 2$ and 3 we obtain two new results:

- first, allowing suppression of population across boxes creates the possibility of more than one non-trivial equilibrium population level;

- second, when there is only one non-trivial equilibrium, such as in the absence of such cross-box suppression, the equilibrium level is not affected by migration from one box to another.

The paper is laid out as follows. In Section 2, we describe the N-box mean field Bolker-Pacala model. In the following Sections 3 and 4, we give a global analysis, showing the existence of one symmetric, non-trivial equilibrium point, and presenting global limit theorems for $N \geq 2$. Exact results for $N = 2$ are given there. In Section 5, we establish the geometric ergodicity of the process regardless of the number of boxes when population suppression from other boxes is 0, and gives the equilibrium point when internal competition is identical for all boxes.

2 Preliminaries: description of the process

We begin with an introduction of the general Bolker-Pacala model, which can be formulated as follows. There is some initial homogeneous population on $\mathbb{R}^d$, that is, a locally finite point process

$$n_0(\Gamma) = \#(\text{particles in } \Gamma \text{ at time } t = 0),$$

where Γ denotes a bounded and connected region in $\mathbb{R}^d$. We refer to individual members of the population as particles and the location of a particle on $\mathbb{R}^d$ as the site of that particle. For instance, one can consider $n_0(\Gamma)$ to be a Poissonian point field with intensity $\rho > 0$, i.e.,

$$P\{n_0(S) = k\} = \exp(-\rho|S|)\frac{(\rho|S|)^k}{k!}, \ k = 0, 1, 2, \dots$$

where $S \subset \Gamma$ and $|S|$ represents the (finite) Lebesgue measure of S, and the number of points in each set of any disjoint collection of subsets of Γ is independent. The following rules dictate the evolution of the field:

i) Each particle, independent of the others, during time interval $(t, t+dt)$ can produce a new particle (offspring or seed) with probability $\beta\, dt + o(dt^2) = A^+ dt + o(dt^2)$, $A^+ > 0$. The initial particle remains at its initial position x but the offspring jumps to $x + z + dz$ with probability

$$a^+(z)dz, \quad A^+ = \int_{\mathbb{R}^d} a^+(x)dx.$$

Note that this can be seen equivalently as two random events, the birth of a particle and its dispersal, as in Bolker and Pacala's presentation [2, 3], or as a single random event, as in our model. (We stress that this differs from the classical branching process, in which the "parental" particle and its offspring commence independent motion from the same point.) We will assume that all offspring evolve independently according to the same rules.

ii) Each particle at point x during the time interval $(t, t+dt)$ dies with probability $\mu dt + o(dt^2)$, where μ is the mortality rate.

iii) The competition factor leads to many interesting properties in this model. If two particles are located at the points $x, y \in \mathbb{R}^d$, then each of them dies with probability $a^-(x-y)dt + o(dt^2)$ during the time interval $(t, t+dt)$ (due to independence, the probability that both die is $o(dt^2)$). This requires, of course, that $a^-(\cdot)$ be integrable; set

$$A^- = \int_{\mathbb{R}^d} a^-(z)dz.$$

The total effect of competition on a particle is the sum of the effects of competition with all individual particles.

Here we have interacting particles, in contrast to the usual branching process. One can expect physically that for arbitrary non-trivial competition ($a^- \in C(\mathbb{R}^d)$, $A^- > 0$), there will exist a limiting distribution of the particles. At each site $x \in \mathbb{R}^d$, with population at time t given by $n(t, x)$, three rates are relevant, the birth rate β and mortality rate μ, each proportional to $n(t, x)$ and the death rate due to competition, proportional to $n(t, x)^2$. Heuristically, when $n(t, x)$ is small the linear effects will dominate. Thus, if $\beta > \mu$ the population is expected to increase. As the population grows and $n(t, x)$ becomes large enough, however, the quadratic effect due to competition will become increasingly dominant, which will prevent unlimited population growth. At present, this fact has been proven only under strong restrictions on a^+ and a^- [5].

3 The N-box model

In the first part of Section 3.1, we recall the mean-field approximation to the Bolker Pacala model from [1], in which we considered the 1-box model. In Section 3.2, we generalize our mean-field approximation to the N-box model.

3.1 The 1-box model

The mean field approximation, "1-box model" of the BP process from [1] led to the special Markov chain: the logistic random walk on the half-axis $\mathbb{Z}_+ = \{0, 1, 2, \ldots\}$. In this model, we considered a system of particles (thinking of particles as individual members of some population). All particles live on the lattice, $\mathbb{Z}^d$. Each lattice point $\mathbf{x}$ has an associated square $\mathbf{x} + [0, 1)^d$, and the number of particles at $\mathbf{x}$ represents the number of inhabitants in the continuous model of that square in $\mathbb{R}^d$ that is associated with $\mathbf{x} \in \mathbb{Z}^d$.

We let $Q_L \subset \mathbb{Z}^d$ be a box with $|Q_L| = L$, L a large parameter, and suppose that no particles exist outside of Q_L.

We modify the notation from [1] slightly to match the notation in this paper. We recall the migration rate between sites on the lattice and competition rate, at which a particle at $\mathbf{x}$ outcompetes another particle at $\mathbf{y}$, in the 1-box model:

$$a^+(\mathbf{x},\mathbf{y}) \equiv \frac{a^+}{L} \quad \text{for } \mathbf{x},\mathbf{y} \in Q_L \cap \mathbb{Z}^d,$$
$$a^-(\mathbf{x},\mathbf{y}) \equiv \frac{a^-}{L^2} \quad \text{for } \mathbf{x},\mathbf{y} \in Q_L \cap \mathbb{Z}^d$$

for constants $a^+, a^- \geq 0$. With such rates, the distribution of a particle after a jump due to migration is uniform on Q_L. Let β and μ be the birth and mortality rates, respectively. We assume that $\beta > \mu$.

If $n(t,\mathbf{x})$ represents the number of particles at site $\mathbf{x} \in Q_L \cap \mathbb{Z}^d$ (we do not restrict the number of particles per site), then

$$N_L(t) = \sum_{\mathbf{x} \in Q_L \cap \mathbb{Z}^d} n(t,\mathbf{x})$$

is the total number of particles in Q_L at time t. $N_L(t)$ is a Markov process, which we call the "logistic" Markov chain.

The transition rates for $N_L(t)$ are

$$P\big(N_L(t+dt) = j \mid N_L(t) = n\big) = \begin{cases} n\beta\, dt + o(dt^2) & \text{if } j = n+1 \\ n\mu\, dt + a^- \cdot n^2/L\, dt + o(dt^2) & \text{if } j = n-1 \\ o(dt^2) & \text{otherwise} \end{cases}$$

We observe that if $N_L(t)$ is large, the random walk has a left drift, whereas if $N_L(t)$ is small, the random walk has a drift to the right. An important point is the equilibrium point, n_L^*, where the rates to the left and to the right are equal, that is,

$$\beta n_L^* = \mu n_L^* + \frac{a^- \cdot n_L^{*2}}{L},$$

Thus,

$$n_L^* = \left\lfloor \frac{L(\beta - \mu)}{a^-} \right\rfloor.$$

We showed in [1] that as $L \to \infty$, $N_L(t)$ tends quickly to a neighborhood of n_L^* and afterward fluctuates randomly around n_L^*. See [1] for further results including a local Central Limit Theorem and large deviations.

3.2 The N-box model

The more general N-box model gives rise to a random walk on

$$(\mathbb{Z}_+)^N = \{(n_1, n_2, \ldots, n_N) \mid n_i \in \mathbb{Z}_+, 1 \leq i \leq N\}.$$

Consider a system of N disjoint rectangles $Q_{i,L} \subset \mathbb{R}^2$, $i = 1,2,\ldots,N$, with

$$\left|Q_{i,L} \cap \mathbb{Z}^2\right| = L.$$

As in the usual BP model, introduce the migration potential a^+ and the competition potential a^- that are constant on each $Q_{i,L}$. For $\mathbf{x} \in Q_{i,L}, \mathbf{y} \in Q_{j,L}$,

$$a_L^-(\mathbf{x},\mathbf{y}) = a_{ij}^-/L^2, \qquad i,j = 1,2,\ldots,N, \tag{3.1}$$

and

$$a_L^+(\mathbf{x},\mathbf{y}) = a_{ij}^+/L, \qquad i,j = 1,2,\ldots,N. \tag{3.2}$$

Specifically, a_{ij}^- indicates the depressive effect on the population in box i due to the population in box j (i.e., competition between boxes i and j), while $a_L^+(\mathbf{x},\mathbf{y})$ is the rate of migration from $\mathbf{x} \in Q_{i,L}$ to $\mathbf{y} \in Q_{j,L}$.

Let $\bigcup_{i=1}^N Q_{i,L} = Q_L$. Then set

$$A_i^+ := \sum_{\mathbf{y} \in Q_L} a^+(\mathbf{x},\mathbf{y}) = \sum_{j=1}^N a_{ij}^+, \quad A_i^- := \sum_{\mathbf{y} \in Q_L} a^-(\mathbf{x},\mathbf{y}) = \sum_{j=1}^N a_{ij}^-$$

Assume that

$$A_i^+, A_i^- \le A < \infty$$

uniformly in L. In this setup, the number of squares N is fixed. The parameters $\beta_i, \mu_i > 0$ represent the natural (biological) birth and death rates of particles in box i, $i = 1,\ldots,N$, respectively.

The population in each square $Q_{i,L}$, $i = 1,\ldots,N$, at time t will be represented by

$$\boldsymbol{n}(t) = \{n_1(t), n_2(t), \ldots, n_N(t)\}, \tag{3.3}$$

a continuous time random walk on $(\mathbb{Z}_+)^N$ with rates obtained from, for $i,j = 1,2,\ldots,N$,

$$\boldsymbol{n}(t+dt|\boldsymbol{n}(t)) \tag{3.4}$$
$$= \boldsymbol{n}(t) + \begin{cases} e_i & \text{w. pr. } \beta_i n_i(t)dt + o(dt^2) \\ -e_i & \text{w. pr. } \mu_i n_i(t)dt + \dfrac{n_i(t)}{L}\displaystyle\sum_{j=1}^N a_{ij}^- n_j(t)dt + o(dt^2) \\ e_j - e_i & \text{w. pr. } n_i(t)a_{ij}^+ dt + o(dt^2), \quad j \neq i \\ 0 & \text{w. pr. } 1 - \displaystyle\sum_{i=1}^N (\beta_i + \mu_i) n_i(t)dt \\ & \qquad -\dfrac{1}{L}\displaystyle\sum_{i,j} n_i(t)n_j(t)a_{ij}^- dt + \sum_{i,j} n_i(t)a_{ij}^+ + o(dt^2) \\ \text{other} & \text{w. pr. } o(dt^2) \end{cases}$$

where e_i is the vector with 1 in the i^{th} position and 0 everywhere else.

We define the *transition function* $p(\mathbf{n}(t), \mathbf{n}(t)+\mathbf{k})$ from the principal probabilities above, that is,

$$
p(\mathbf{n}(t),\mathbf{n}(t)+\mathbf{k}) \tag{3.5}
$$
$$
= \begin{cases} \beta_i n_i(t) & \mathbf{k}=e_i \\ \mu_i n_i(t) + \dfrac{n_i(t)}{L}\displaystyle\sum_{j=1}^{N} a_{ij}^{-} n_j(t) & \mathbf{k}=-e_i \\ n_i(t) a_{ij}^{+} & \mathbf{k}=e_j-e_i,\ j\neq i \\ -\displaystyle\sum_{i=1}^{N}(\beta_i+\mu_i)n_i(t) - \dfrac{1}{L}\sum_{i,j} n_i(t)n_j(t)a_{ij}^{-} + & \mathbf{k}=0 \\ \qquad +\displaystyle\sum_{i,j} n_i(t)a_{ij}^{+} & \\ 0 & \text{all other } \mathbf{k} \end{cases}
$$

4 Global analysis for N boxes

4.1 Preliminaries

Let us temporarily fix L. We set

$$
\frac{n_i(t)}{L} := z_i(t), \qquad i=1,\ldots,N.
$$

Define

$$
f_L(\mathbf{z}(t),\mathbf{k}) := \frac{1}{L} p(\mathbf{n}(t),\mathbf{n}(t)+\mathbf{k}),
$$

where $\mathbf{z}(t)=(z_1(t),\ldots,z_N(t))$, $\mathbf{n}(t)=(n_1(t),\ldots,n_N(t))$, and $\mathbf{k}=(k_1,\ldots,k_N)$, $k_i=1,0,$ or -1 for $i=1,\ldots,N$, and p is the transition function (3.5). Then

$$
f_L(\mathbf{z}(t),\mathbf{k}) = \begin{cases} \beta_i z_i & \mathbf{k}=e_i, & i=1,\ldots,N \\ \mu_i z_i + a_{i,i}^{-} z_i^2 + \displaystyle\sum_{j\neq i} a_{i,j}^{-} z_i z_j & \mathbf{k}=-e_i, & i=1,\ldots,N \\ a_{i,j}^{+} z_i & \mathbf{k}=e_j-e_i, & i,j=1,\ldots,N; i\neq j \\ -\sum_{i=1}^{N}(\beta_i+\mu_i)z_i(t) & \mathbf{k}=0 & \\ \quad -L\sum_{i,j} z_i(t)z_j(t)a_{ij}^{-} & & \\ \quad +\sum_{i,j} z_i(t)a_{ij}^{+} & & \\ 0 & \text{otherwise} & \end{cases}
$$

Note that $f_L(\mathbf{z}(t),\mathbf{k})$ does not, in fact, depend on L.

Set the migration rate out of box i

$$
M_i^{+} := \sum_{j\neq i} a_{i,j}^{+}.
$$

For the functional limit theorems to follow, define for $i = 1, \dots, N$,

$$F_i(\mathbf{z}(t)) := \sum_{k_i=-1}^{1} k_i f(\mathbf{z}(t), \cdot) \left(\beta_i - \mu_i - M_i^+\right) z_i - a_{i,i}^- z_i^2 - \sum_{j \neq i} a_{i,j}^- z_i z_j + \sum_{j \neq i} a_{j,i}^+ z_j \tag{4.1}$$

and consider the system of differential equations

$$\frac{d\mathbf{z}(t)}{dt} = \mathbf{F}(\mathbf{z}(t)) \tag{4.2}$$

An equilibrium for the system occurs precisely at the points where

$$\mathbf{0} = \mathbf{F}(\mathbf{z}), \tag{4.3}$$

with one solution being $\mathbf{z} \equiv \mathbf{0}$.

Set $p_i := \beta_i - \mu_i - M_i^+$. In matrix form, we have the equation

$$A \begin{bmatrix} z_1 \\ \vdots \\ z_N \end{bmatrix} + B \begin{bmatrix} z_1^2 \\ \vdots \\ z_N^2 \end{bmatrix} = \mathbf{0},$$

where B is a diagonal matrix:

$$A = \begin{bmatrix} p_1 & a_{2,1}^+ & a_{3,1}^+ & \cdots & a_{N,1}^+ \\ a_{1,2}^+ & p_2 & a_{3,2}^+ & \cdots & a_{N,2}^+ \\ \vdots & & \ddots & & \vdots \\ \vdots & & & \ddots & \vdots \\ a_{1,N}^+ & \cdots & & a_{N-1,N}^+ & p_N \end{bmatrix}, \quad B = \begin{bmatrix} a_{1,1}^- & & & \\ & a_{2,2}^- & & \mathbf{0} \\ \mathbf{0} & & \ddots & \\ & & & a_{N,N}^- \end{bmatrix}.$$

When $a_{i,j}^+ = 0$ and $a_{i,j}^- = 0, i \neq j$, that is, there is no migration between boxes and no suppression across boxes, there is a unique non-zero equilibrium

$$z_i = \frac{\beta_i - \mu_i}{a_{i,i}^-}, \quad i = 1, \dots, N.$$

This is, as would be expected, essentially the equilibrium for N distinct, independent "single box" mean field Bolker Pacala models, as found in [1].

4.2 More on equilibrium points

We assume, in this section, symmetric conditions, that is, that conditions are identical for all boxes. Thus, the biological birth and mortality rates are the same in each box:

$$\beta_i \equiv \beta \text{ and } \mu_i \equiv \mu, \ i = 1, 2, \dots.$$

The "inner" competition rates within boxes are equal, satisfying

$$a_I^- := a_{ii}^-, \qquad i = 1, 2, \dots$$

and "outer" competition (from box to box) is the same

$$a_O^- := a_{ij}^-, \qquad i \neq j.$$

We also set the common migration rate

$$a^+ := a_{ij}^+, \qquad i \neq j.$$

So that the system does not inevitably die out, we assume that $\beta > \mu$.

We begin with the case of two boxes ($N = 2$) or classes. The system (4.2) may have up to four distinct non-negative singular points, that is, solutions of (4.3). All four solutions are real and non-negative only if

$$a_O^- > a_I^- \quad \text{and} \quad \beta - \mu > 2a^+ \frac{a_O^- + a_I^-}{a_O^- - a_I^-} \tag{4.4}$$

They are as follows:

1) The trivial singular point, an unstable equilibrium for $\beta > \mu$, at $(0, 0)$.

2) $\left(\frac{\beta-\mu}{a_I^- + a_O^-}, \frac{\beta-\mu}{a_I^- + a_O^-}\right)$, which always exists, even when (4.4) is not satisfied.

3)
$$\begin{pmatrix} \frac{\beta-\mu-2a^+}{2a_I^-} + \frac{\sqrt{(\beta-\mu-2a^+)^2(a_O^- - a_I^-)^2 - 4a_I^- a^+ (a_O^- - a_I^-)(\beta-\mu-2a^+)}}{2a_I^-(a_O^- - a_I^-)}, \\ \frac{\beta-\mu-2a^+}{2a_I^-} - \frac{\sqrt{(\beta-\mu-2a^+)^2(a_O^- - a_I^-)^2 - 4a_I^- a^+ (a_O^- - a_I^-)(\beta-\mu-2a^+)}}{2a_I^-(a_O^- - a_I^-)} \end{pmatrix}$$

4)
$$\begin{pmatrix} \frac{\beta-\mu-2a^+}{2a_I^-} - \frac{\sqrt{(\beta-\mu-2a^+)^2(a_O^- - a_I^-)^2 - 4a_I^- a^+ (a_O^- - a_I^-)(\beta-\mu-2a^+)}}{2a_I^-(a_O^- - a_I^-)}, \\ \frac{\beta-\mu-2a^+}{2a_I^-} + \frac{\sqrt{(\beta-\mu-2a^+)^2(a_O^- - a_I^-)^2 - 4a_I^- a^+ (a_O^- - a_I^-)(\beta-\mu-2a^+)}}{2a_I^-(a_O^- - a_I^-)} \end{pmatrix}$$

Proposition 4.1. *In the event that all four equilibria exist, the third and fourth equilibria are stable while the second one is a saddle point and is not stable.*

Proof. For the stability of the third and fourth, a computation shows that the eigenvalues of the Jacobian matrix of $\mathbf{F}(\mathbf{z}) = (F_1(\mathbf{z}), F_2(\mathbf{z}))$ with F_1 and F_2 as in (4.1) at an equilibrium point $\mathbf{z}^* = (z_1^*, z_2^*)$,

$$J(\mathbf{z}^*) = \begin{pmatrix} \beta - \mu - a^+ - 2a_I^- z_1^* - a_O^- z_2^* & a^+ - a_O^- z_1^* \\ a^+ - a_O^- z_2^* & \beta - \mu - a^+ - 2a_I^- z_2^* - a_O^- z_1^* \end{pmatrix}$$

are of the form

$$\lambda_1 = \frac{A + \sqrt{B}}{2a_I^-(a_O^- - a_I^-)} \quad \text{and} \quad \lambda_2 = \frac{A - \sqrt{B}}{2a_I^-(a_O^- - a_I^-)}$$

for the third and fourth equilibrium points, where

$$\begin{aligned}
A &= (a_O^- - a_I^-)((\mu-\beta)a_O^- + 2a^+(a_O^- + a_I^-)),\\
B &= \left(a_I^- - a_O^-\right)^2\Big[\beta^2\left(-2a_I^- + a_O^-\right)^2 + \left(a_O^-\right)^2(2a^+ + \mu)^2\\
&\qquad + 4\left(a_I^-\right)^2\left(-3\left(a^+\right)^2 + \mu^2\right) - 4a_I^- a_O^-\left(2\left(a^+\right)^2 + 3a^+\mu + \mu^2\right)\\
&\qquad - 2\beta\left(4\mu\left(a_I^-\right)^2 + \left(a_O^-\right)^2(2a^+ + \mu) - 2a_I^- a_O^-(3a^+ + 2\mu)\right)\Big].
\end{aligned}$$

It follows that $A < 0$ since the first factor of A is positive and the second factor of A is negative by (4.4). Since $A < 0$, $B \le 0$ implies that the real part of each eigenvalue, $\Re(\lambda_i) < 0$, $i = 1,2$, and, therefore, the claimed stability. If $B > 0$, then consider

$$A^2 - B = -4a_I^-\left(a_I^- - a_O^-\right)^2\left(\beta - 2a^+ - \mu\right)\left[(\beta-\mu)\left(a_I^- - a_O^-\right) + 2a^+\left(a_O^- + a_I^-\right)\right]$$

By (4.4), $\beta - 2a^+ - \mu > 0$, since

$$\frac{a_O^- + a_I^-}{a_O^- - a_I^-} > 1$$

and also by (4.4),

$$(\beta-\mu)\left(a_I^- - a_O^-\right) + 2a^+\left(a_O^- + a_I^-\right) < 0,$$

we conclude that $\Re(\lambda_i) < 0$, $i = 1,2$, in this case as well.

To see that the second equilibrium point is not stable in this case, one can similarly evaluate the eigenvalues of the Jacobian matrix. A proof for general N is given below, thus we omit the details here. □

However, if (4.4) is not satisfied, then we have only one non-trivial singular point,

$$\left(\frac{\beta-\mu}{a_I^- + a_O^-}, \frac{\beta-\mu}{a_I^- + a_O^-}\right),$$

which is a stable equilibrium in this case. Note that this is the only non-trivial equilibrium if $a_O^- = 0$, i.e., there is no suppression across boxes or classes. This is the same equilibrium point, then, that is found for single boxes in the absence of any migration or mobility.

Note, also, that even if $a_O^- > a_I^-$ the existence of the third and fourth equilibria depends on low rates of migration between boxes (or social mobility between classes); these equilibria vanish if a^+ is too great. This is somewhat contrary to what one might suppose, that low rates of migration or mobility would keep the equilibria inside boxes at or near the original equilibria.

For three boxes or classes, $N = 3$, the results are similar. In particular, two equilibria always exist:

1) The trivial singular point, an unstable equilibrium for $\beta > \mu$, at $(0,0,0)$, and

2) $\left(\frac{\beta-\mu}{a_I^- + 2a_O^-}, \frac{\beta-\mu}{a_I^- + 2a_O^-}, \frac{\beta-\mu}{a_I^- + 2a_O^-}\right)$.

If population suppression across boxes or classes does not occur, $a_O^- = 0$, the second of these is the only non-trivial equilibrium. Otherwise, under additional conditions, including again, sufficiently low migration between boxes, multiple equilibria can exist.

Proposition 4.2. *For $N \geq 2$, the points* $\mathbf{0}$ *and* $\mathbf{z}^* \in \mathbb{R}^N$ *with*

$$z_i^* = \frac{\beta - \mu}{a_I^- + (N-1)a_O^-}$$

are equilibrium points of (4.2), *with* $\mathbf{z}^*$ *being stable only when*

$$(\beta - \mu)\left(a_O^- - a_I^-\right) < Na^+\left(a_I^- + (N-1)a_O^-\right) \tag{4.5}$$

Proof. One can check that $\mathbf{0}$ and $\mathbf{z}^*$ are equilibrium points by plugging them directly into (4.3). To see that $\mathbf{z}^*$ is stable under the condition (4.5), we again consider the Jacobian of $\mathbf{F}(\mathbf{z}) = (F_1(\mathbf{z}), \ldots, F_N(\mathbf{z}))$ with F_i as in (4.1) with entries given by

$$\left(J\left(\mathbf{z}^*\right)\right)_{ij} = \begin{cases} \beta - \mu - (N-1)a^+ - 2a_I^- z_i^* - a_O^-(N-1)z_i^*, & i = j, \\ a^+ - a_O^- z_i^*, & i \neq j \end{cases}$$

Given the special form of this matrix, the distinct eigenvalues are

$$\lambda_1 = \frac{(\beta - \mu)\left(a_O^- - a_I^-\right) - Na^+\left(a_I^- + (N-1)a_O^-\right)}{a_I^- + (N-1)a_O^-} \quad \text{and} \quad \lambda_2 = \mu - \beta.$$

To see this, note that

$$\left(J\left(\mathbf{z}^*\right) - \lambda_1 I_N\right)_{ij} = a^+ - \frac{a_O^-(\beta - \mu)}{a_I^- + (N-1)a_O^-},$$

where I_N is the $N \times N$ identity matrix, for all $i, j = 1, \ldots, N$. This matrix has rank 1, thus the eigenspace of λ_1 is $(N-1)$-dimensional and so the multiplicity of λ_1 is $N-1$. To check that λ_2 is an eigenvalue with multiplicity 1, we note that

$$\left(J\left(\mathbf{z}^*\right) - \lambda_2 I_N\right)_{ij} = \begin{cases} -(N-1)\left[a^+ - \frac{a_O^-(\beta-\mu)}{a_I^- + (N-1)a_O^-}\right], & i = j, \\ a^+ - \frac{a_O^-(\beta-\mu)}{a_I^- + (N-1)a_O^-} & i \neq j \end{cases}$$

If we add each of rows 2 through N to the first row of $J(\mathbf{z}^*) - \lambda_2 I_N$, we obtain a zero row and it follows that

$$J\left(\mathbf{z}^*\right) - \lambda_2 I_N$$

has rank $N-1$. Thus λ_2 is an eigenvalue of $J(\mathbf{z}^*)$ of multiplicity 1.

$\lambda_1 < 0$ precisely when condition (4.5) is satisfied and $\lambda_2 < 0$ from our assumption that $\beta > \mu$. □

4.3 Global limit theorems for N boxes

Here, we state a functional law of large numbers and functional central limit theorem, following [7, 8]. We now allow L to vary, so we relabel slightly, setting

$$z_{Li}(t) := \frac{n_i(t)}{L}, \qquad i = 1, \ldots, N$$

and $Z_L(t) = (z_{L1}(t), \ldots, z_{LN}(t))$.

Theorem 4.3 (Functional LLN). *Let* $(z_1^*,\ldots,z_N^*)$ *denote a unique stable equilibrium for the system given in* (4.1) *and* (4.2). *As* $L\to\infty$,

$$Z_L(t)\to Z(t)=(z_1(t),\ldots,z_N(t))$$

uniformly in probability, where $Z(t)$ *is a deterministic process, the solution of*

$$\begin{aligned}\frac{dz_j(t)}{dt}&=F_j(z_1(t),\ldots,z_N(t)),\quad j=1,\ldots,N,\\ z_1(0)&=z_1^*,\ldots,z_N(0)=z_N^*.\end{aligned}\tag{4.6}$$

with $F_1,\ldots,F_N$ *given in* (4.1).

Next, define $g_{ij}(z_1,...,z_N)$:

$$\begin{aligned}g_{ii}(z_1,...,z_N):&=\sum_{k_i=-1}^{1}k_i^2 f(z_1,...,z_N,\cdot,k_i,\cdot)\\ &=\beta z_i+\mu z_i+a_{ii}^-z_i^2+\sum_{j\neq i}(a_{ij}^-z_iz_j+a_{ij}^+z_i+a_{ji}^+z_j)\end{aligned}\tag{4.7}$$

$$\begin{aligned}g_{ij}(z_1,...,z_N)=g_{ji}(z_1,...,z_N):&=\sum_{k_i,k_j=-1}^{1}k_ik_jf(z_1,...,z_N,\cdot,k_i,\cdot,k_j,\cdot)\\ &=-a_{ij}^+z_i-a_{ji}^+z_j\quad\text{for } i\neq j\end{aligned}$$

Theorem 4.4 (Functional CLT). *Let* $z^*=(z_1^*,...,z_N^*)$ *denote a unique stable equilibrium for the system given in* (4.1) *and* (4.2). *If* $\sqrt{L}(Z_L(0)-z^*)=\zeta_0$, *the processes*

$$\zeta_L(t):=\sqrt{L}(Z_L(t)-z^*)$$

converge weakly in the space of cadlag functions on any finite time interval $[0,T]$ *to an Ornstein-Uhlenbeck process (OUP)* $\zeta(t)$ *with initial value* ζ_0, *infinitesimal drift given by*

$$q_1:=\frac{\partial F_1\left(z_1^*,...,z_N^*\right)}{\partial z_1},\ \ldots,\ q_N:=\frac{\partial F_N\left(z_1^*,...,z_N^*\right)}{\partial z_N}$$

and the infinitesimal covariance matrix with entries given by

$$a_{ij}:=g_{ij}\left(z_1^*,...,z_N^*\right).$$

Thus, for the single, symmetric positive equilibrium for $N=2$, with a single inner competition rate a_I^-, a single outer competition rate a_O^-, and a single migration rate a^+, the infinitesimal drift is:

$$q_1=q_2=\frac{-a_I^-(\beta-\mu)}{a_I^-+a_O^-}-a^+,$$

and the infinitesimal covariance matrix entries are:

$$a_{11}=a_{22}=\frac{2(\beta-\mu)(\beta+a^+)}{a_I^-+a_O^-},\quad a_{12}=a_{21}=\frac{-2a^+(\beta-\mu)}{a_I^-+a_O^-}.$$

5 Ergodicity for N boxes

Assume there is no suppression of population across boxes, i.e., $a^-_{ij} = 0$ for $i \neq j$. We also assume that $a^-_{ii} > 0$ for some $i = 1, \ldots, N$. For N boxes, let $\{X_n\}_{n=0}^{\infty}$ on $(\mathbb{Z}_+)^N$ be the embedded discrete time random walk associated with the continuous random walk (3.3). For $\mathbf{x} = (x_1, \ldots, x_N) \in {\mathbb{Z}_+}^N$, set

$$c(\mathbf{x}) = \sum_{i=1}^{N} \left(\beta_i + \mu_i + \frac{a^-_{ii}}{L} x_i \right) x_i + \sum_{i,j=1, i \neq j}^{N} a^+_{ij} x_i.$$

$\{X_n\}$ has transition probabilities, for $\mathbf{x}, \mathbf{y} \in (\mathbb{Z}_+)^N$, $\mathbf{x} \neq \mathbf{0}$

$$P(\mathbf{x}, \mathbf{y}) = \frac{1}{c(\mathbf{x})} \cdot \begin{cases} \beta_i x_i & \text{if } \mathbf{y} = \mathbf{x} + e_i, i = 1, \ldots, N \\ \mu_i x_i + \dfrac{a^-_{ii}}{L} x_i^2 & \text{if } \mathbf{y} = \mathbf{x} - e_i, i = 1, \ldots, N \\ a^+_{ij} x_i & \text{if } \mathbf{y} = \mathbf{x} - e_i + e_j, i \neq j \\ 0 & \text{otherwise} \end{cases} \tag{5.1}$$

and for $\mathbf{x} = \mathbf{0}$,

$$P(\mathbf{x}, \mathbf{y}) = \begin{cases} \dfrac{1}{N} & \text{if } \mathbf{y} = \mathbf{0} + e_i, i = 1, \ldots, N \\ 0 & \text{otherwise} \end{cases} \tag{5.2}$$

Recall that we use $e_i \in \mathbb{Z}^N$ to denote the vector with 1 in the i^{th} position and 0 everywhere else, and $\mathbf{0} = (0, \ldots, 0)$. We impose here a reflective barrier at $\mathbf{0}$ with (5.2).

Theorem 5.1. *A random walk with transition probabilities* (5.1) *and* (5.2) *is geometrically ergodic. That is, it is positive recurrent with exponential convergence to a stable distribution.*

Proof. Using Foster's [6] criterion, [9, Theorem 15.01] (see also similar results in [4]) states that if there is a function $V : (\mathbb{Z}_+)^N \to \mathbb{R}$ with $V(\mathbf{x}) \geq 1$ for all $\mathbf{x} \in (\mathbb{Z}_+)^N$ such that, for a bounded set $B \subset (\mathbb{Z}^+)^N$, constant $\lambda < 1$, and constant $b < \infty$,

$$\sum_{\mathbf{y} \in (\mathbb{Z}_+)^N} P(\mathbf{x}, \mathbf{y}) V(\mathbf{y}) \leq \lambda V(\mathbf{x}) + b \mathbb{1}_B(\mathbf{x}), \tag{5.3}$$

then the Markov chain with probability transition matrix P is geometrically ergodic. Here, $\mathbb{1}_B(\mathbf{x})$ is the indicator function of B. Let

$$V(\mathbf{x}) = \alpha^{||\mathbf{x}||_1},$$

where we will choose appropriate $\alpha > 1$, and $||\mathbf{x}||_1$ is the L^1 norm of $\mathbf{x}$. Note that, for $\mathbf{x} \in (\mathbb{Z}_+)^N$,

$$||\mathbf{x}||_1 = \sum_{i=1}^{N} |x_i| = \sum_{i=1}^{N} x_i.$$

Then, for $\mathbf{x} \notin B$ and if $\lambda\alpha > 1$, criterion (5.3) is equivalent to

$$(\alpha - \lambda)\sum_{i=1}^{N} \beta_i x_i + (1-\lambda)\sum_{i=1}^{N} A_i^+ x_i \le \left(\lambda - \frac{1}{\alpha}\right)\sum_{i=1}^{N}\left(\mu_i + \frac{a_{ii}^-}{L} x_i\right) x_i \tag{5.4}$$

for some $\lambda < 1$, where

$$A_i^+ := \sum_{j=1}^{N} a_{ij}^+$$

is the total migration rate out of box i. Let

$$C_1 = \max_i \beta_i, \quad C_2 = \max_i A_i^+, \quad C_3 = \min_i \left\{ \frac{a_{ii}^-}{L} : a_{ii}^- > 0 \right\}.$$

Then, for $\mathbf{x} \in (\mathbb{Z}_+)^N$ with

$$||\mathbf{x}||_2 \ge \frac{\sqrt{N}\,(\alpha C_1 + C_2)}{C_3\,(\lambda - 1/\alpha)}, \tag{5.5}$$

where

$$||\mathbf{x}||_2 = \left(\sum_{i=1}^{N} x_i^2\right)^{1/2},$$

$$\begin{aligned}
(\alpha - \lambda)\sum_{i=1}^{N} \beta_i x_i + (1-\lambda)\sum_{i=1}^{N} A_i^+ x_i &\le (\alpha-\lambda)\, C_1 ||\mathbf{x}||_1 + (1-\lambda)\, C_2 ||\mathbf{x}||_1 \\
&\le \sqrt{N}\,((\alpha-\lambda)\, C_1 + (1-\lambda)\, C_2)\, ||\mathbf{x}||_2 \\
&\le \sqrt{N}\,(\alpha C_1 + C_2)\, ||\mathbf{x}||_2 \\
&\le C_3\left(\lambda - \frac{1}{\alpha}\right) ||\mathbf{x}||_2^2 \\
&\le \left(\lambda - \frac{1}{\alpha}\right)\sum_{i=1}^{N}\left(\mu_i + \frac{a_{ii}^-}{L} x_i\right) x_i,
\end{aligned}$$

where the second inequaity is due to the Cauchy-Schwarz inequality, and the fourth inequality is due to our assumption (5.5). The other inequalities follow from the definitions of C_1, C_2, and C_3.

Thus, choose

$$M = \frac{\sqrt{N}\,(\alpha C_1 + C_2)}{C_3\,(\lambda - 1/\alpha)},$$

and let

$$B = \left\{ \mathbf{x} \in (\mathbb{Z}_+)^N \;\middle|\; ||\mathbf{x}||_2 \le M \right\}.$$

Then B is a bounded set, $V(\mathbf{x}) \ge 1$ on $(\mathbb{Z}_+)^N$. Let

$$b = \max\left\{ \left| \sum_{\mathbf{y} \in (\mathbb{Z}_+)^N} P(\mathbf{x}, \mathbf{y}) V(\mathbf{y}) - \lambda V(\mathbf{x}) \right| : \mathbf{x} \in (\mathbb{Z}_+)^N, ||\mathbf{x}||_2 \le M \right\}.$$

Then (5.3) is satisfied for all $\mathbf{x} \in (\mathbb{Z}_+)^N$. □

Suppose, finally, that we impose symmetric conditions on all of the boxes:

1) $\beta_i \equiv \beta$ and $\mu_i \equiv \mu$ for all i, with $\beta > \mu$,

2) migration rates between all boxes are equal to a^+, that is, $a^+_{ij} \equiv a^+$ for all i, j,

3) suppression of population within its own box occurs at the same rate for all boxes, i.e., $a^-_{ii} \equiv a^-_I$ for all i.

Then, as is directly checked, the random walk has at least one non-trivial equilibrium point, that is, the drift vector

$$\triangle \mathbf{x} := \sum_{\mathbf{y}} P(\mathbf{x}, \mathbf{y})\mathbf{y} - \mathbf{x} = 0$$

(cf. [9]) at two points, the trivial point 0, and $\mathbf{x}$, where

$$\frac{x_i}{L} = \frac{\beta - \mu}{a^-_I}$$

for all components i. This follows from a computation for each component i that

$$(\triangle \mathbf{x})_i = \frac{1}{c(\mathbf{x})}\left[(\beta - \mu)x_i - \frac{a^-_I}{L}x_i^2 + a^+\Big(\sum_{j \neq i} x_j - (N-1)x_i\Big)\right].$$

The equilibrium result agrees with our earlier results in Proposition 4.2.

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