# Mean Field Bolker-Pacala Models of Population Dynamics

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# Outline

- Description of mean field model for one population
  - Model and random walk
  - Limit theorems
- Extension of mean field model to multiple, e.g., stratified, populations
  - Multiple equilibria
  - Global limit theorems and ergodicity

# Basic model: Three processes

- Infinite initial population of particles living on the lattice:  $n(0, x), x \in \mathbb{Z}^d$
- 1. Birth and migration
  - Each particle, in time *dt*, produces 1 offspring with probability *b dt*
  - Offspring migrates distance z on lattice with probability a<sup>+</sup>(z)

# Basic model: Three processes

- 2. Mortality
  - Each particle, in time dt, dies with probability  $\mu dt$
- 3. Competition
  - For any two particles, located at x and y, in time dt, probability that each dies is  $a^{-}(x,y) dt$
  - May assume that both do not die
  - Probability that particle dies due to competition is sum due to competition with all other particles

- Consider box  $Q_L \subset \mathbb{Z}^d$  with  $|Q_L| = L$ , L a large parameter.
- Let  $a^+(x) = \frac{\kappa}{L}$  on  $Q_L$ ,  $a^-(x) = \frac{\gamma}{L^2}$  on  $Q_L$   $\gamma > 0$ .
- Total number of particles  $N_L(t) = \sum_{x \in Q_L} n(t, x)$  is the logistic Markov chain
- Transition rates

$$P\left(N_L(t+dt)=j|N_L(t)=n\right) = \begin{cases} nb\,dt+o(dt^2) & \text{if } j=n+1\\ n\mu\,dt+\gamma n^2/L\,dt+o(dt^2) & \text{if } j=n-1\\ o(dt^2) & \text{otherwise} \end{cases}$$

 Modified I.c. to eliminate absorption at 0: Generator

 $\mathcal{L}\psi(n) = \alpha_n \psi(n-1) - (\alpha_n + \beta_n)\psi(n) + \beta_n \psi(n+1), n > 0$  $\mathcal{L}\psi(0) = \beta_0 \psi(1) - \beta_0 \psi(0)$ 

**Transition rates** 

$$\beta_n = b(n+1), n \ge 0$$
  $\alpha_n = \mu n + \frac{\gamma n^2}{L}, n \ge 1$ 

 $\mathbf{O}$ 

As random walk



Equilibrium for appropriately chosen large L

$$\tilde{n}_L^* = \frac{(b-\mu)L}{\gamma}$$
  
– Asymptotics same as for logistic chain

• Local Central Limit Theorem

- Let  $b > \mu$ . If  $k = O(L^{2/3})$  then

for the invariant distribution  $\pi_L$ , where  $\sigma_L^2 = Lb/\gamma$ 

$$\pi_L(n_L^* + k) \sim \frac{e^{-k^2/2\sigma_L^2}}{\sqrt{2\pi\sigma_L^2}}$$

 Proof uses well-known formula for invariant distribution of birth-and-death process

$$\pi(x) = \lim_{t \to \infty} p(t, \cdot, x) = \begin{cases} S^{-1}, & x = 0\\ S^{-1} \frac{\beta_0 \dots \beta_{x-1}}{\alpha_1 \dots \alpha_x}, & x > 0 \end{cases}$$

Where

$$S = 1 + \frac{\beta_0}{\alpha_1} + \frac{\beta_0 \beta_1}{\alpha_1 \alpha_2} + \ldots + \frac{\beta_0 \ldots \beta_n}{\alpha_1 \ldots \alpha_{n+1}} + \ldots$$

And fact that for logistic chain, *S* can be represented in terms of degenerated hypergeometric function.

- Global Central Limit Theorem (Kurtz-type result)
  - If  $b > \mu$ , L > 0,  $\gamma > 0$  then

$$\frac{N_L(t) - \frac{(b-\mu)L}{\gamma}}{\sqrt{L}} \xrightarrow[L \to \infty]{\text{law}} \zeta(t)$$

#### where $\zeta(t)$ is an Ornstein-Uhlenbeck process.

 M. BESSONOV, S. MOLCHANOV. AND J. WHITMEYER, A Mean Field Approximation of the Bolker-Pacala Population Model. Markov Processes and Related Fields, 20, (2014) 329-348.

### Multi-Class Extension: N-Box Model

- Instead of 1-box model, N-box model
- Gives rise to a random walk on

 $(\mathbb{Z}_+)^N = \{(n_1, n_2, \dots, n_N) : n_i \in \mathbb{Z}_+, 1 \le i \le N\}$ 

Migration potential:

$$a_L^+(x,y) = a_{ij}^+/L, \quad i,j = 1, 2, \dots, N$$

- Competition potential:  $a_L^-(x,y) = a_{ij}^-/L^2, \quad i,j=1,2,\ldots,N$
- Population given by

$$n(t) = \{n_1(t), n_2(t), \dots, n_N(t)\}$$

### N-Box Model

• Change in time *dt*:

$$n(t+dt|n(t)) = n(t) + \begin{cases} e_i & \text{w. pr. } bn_i(t)dt + o(dt^2) \\ -e_i & \text{w. pr. } \mu n_i(t)dt + \frac{n_i(t)}{L} \sum_{j=1}^N a_{ij}^- n_j(t)dt + o(dt^2) \\ e_j - e_i & \text{w. pr. } n_i(t)a_{ij}^+ dt + o(dt^2), \quad j \neq i \\ 0 & \text{w. pr. } 1 - \sum_{i=1}^N (b_i + \mu_i)n_i(t)dt \\ & -\frac{1}{L} \sum_{i,j} n_i(t)n_j(t)a_{ij}^- dt + \sum_{i,j} n_i(t)a_{ij}^+ + o(dt^2) \\ \text{other w. pr. } o(dt^2) \end{cases}$$

Where  $e_i$  is vector with 1 in position *i* and 0 everywhere else.

• *Transition function p* from probabilities above:

$$p((\mathbf{n}(t), \mathbf{n}(t)+\mathbf{l}) = \begin{cases} bn_i(t) & 1 = e_i \\ \mu n_i(t) + \frac{n_i(t)}{L} \sum_{j=1}^N a_{ij}^- n_j(t) & 1 = -e_i \\ n_i(t)a_{ij}^+ & 1 = e_j - e_i, \ j \neq i \\ -\sum_{i=1}^N (b_i + \mu_i)n_i(t) - \frac{1}{L} \sum_{i,j} n_i(t)n_j(t)a_{ij}^- + & 1 = 0 \\ +\sum_{i,j} n_i(t)a_{ij}^+ & 0 & \text{all other } 1 \end{cases}$$

• Rescale process. Temporarily fix *L*.

• Set, for all 
$$i, z_i(t) := \frac{n_i(t)}{L}$$

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

• Then

$$f_L(\mathbf{z}(t), \mathbf{l}) = \begin{cases} b_i z_i & 1 = e_i, & i = 1, \dots, N\\ \mu_i z_i + a_{i,i}^- z_i^2 + \sum_{j \neq i} a_{i,j}^- z_i z_j & 1 = -e_i, & i = 1, \dots, N\\ a_{i,j}^+ z_i & 1 = e_j - e_i, & i, j = 1, \dots, N; i \neq j\\ (\text{not needed}) & 1 = 0\\ 0 & \text{otherwise} \end{cases}$$

• Note that  $f_L$  does not depend on L.

• Set 
$$F_i(\mathbf{z}(t)) := \sum_{l_i=-1}^{1} l_i f(\mathbf{z}(t), \cdot)$$
  
• Now letting *L* vary, relabel  $z_{Li}(t) := \frac{n_i(t)}{L}$ ,  
and  $Z_L(t) = (z_{L1}(t), \dots, z_{LN}(t))$ 

For the rescaled system we have a functional Law of Large Numbers, following papers by Kurtz.

**Theorem**. The process  $Z_L(t)$  converges uniformly in probability as  $L \rightarrow \infty$  to a deterministic process, the solution of the system of differential equations

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

with initial point a stable equilibrium  $z^*$  of the system, i.e., solution of  $\mathbf{0} = \mathbf{F}(\mathbf{z}(t))$ 

Functional LLN and CLT for *N*-Box Model Similarly, we have a functional Central Limit Theorem.

In particular,  $\zeta_L(t) := \sqrt{L}(Z_L(t) - z^*)$  converges weakly, as  $L \rightarrow \infty$ , to an Ornstein-Uhlenbeck process

### Results for *N* = 2 and 3 Boxes

- Assume completely symmetric conditions
  - Single birth rate  $\beta$ , single death rate  $\mu$
  - Equal internal competition or "suppression" rates:  $a_i^{-} = a_{ii}^{-}$  for all *i*
  - Equal external competition rates:  $a_0^- = a_{ij}^-$  for all *i*, *j*, *i* \neq *j*
  - Common migration rates:  $a^+ = a_{ij}^+$  for i, j = 1, 2
- Set β > μ so system does not inevitably die out.

#### Results for N = 2 Boxes

 System may have up to 4 distinct nonnegative singular points

All 4 are real and non-negative if  
(\*) 
$$a_{\overline{O}} > a_{\overline{I}}^-$$
 and  $\beta - \mu > 2a^+ \frac{a_{\overline{O}}^- + a_{\overline{I}}^-}{a_{\overline{O}}^- - a_{\overline{I}}^-}$ 

1) Trivial equilibrium at (0,0), unstable if  $\beta > \mu$ . 2)  $\left(\frac{\beta-\mu}{a_{I}^{-}+a_{O}^{-}}, \frac{\beta-\mu}{a_{I}^{-}+a_{O}^{-}}\right)$ , which always exists.

#### Results for N = 2 Boxes

$$\begin{array}{l} 3 \end{pmatrix} \left( \begin{array}{c} \frac{\beta - \mu - 2a^{+}}{2a_{I}^{-}} + \frac{\sqrt{(\beta - \mu - 2a^{+})^{2}(a_{O}^{-} - a_{I}^{-})^{2} - 4a_{I}^{-}a^{+}(a_{O}^{-} - a_{I}^{-})(\beta - \mu - 2a^{+})}{2a_{I}^{-}(a_{O}^{-} - a_{I}^{-})}, \\ \frac{\beta - \mu - 2a^{+}}{2a_{I}^{-}} - \frac{\sqrt{(\beta - \mu - 2a^{+})^{2}(a_{O}^{-} - a_{I}^{-})^{2} - 4a_{I}^{-}a^{+}(a_{O}^{-} - a_{I}^{-})(\beta - \mu - 2a^{+})}{2a_{I}^{-}(a_{O}^{-} - a_{I}^{-})}, \\ 4 \end{pmatrix} \left( \begin{array}{c} \frac{\beta - \mu - 2a^{+}}{2a_{I}^{-}} - \frac{\sqrt{(\beta - \mu - 2a^{+})^{2}(a_{O}^{-} - a_{I}^{-})^{2} - 4a_{I}^{-}a^{+}(a_{O}^{-} - a_{I}^{-})(\beta - \mu - 2a^{+})}{2a_{I}^{-}(a_{O}^{-} - a_{I}^{-})}, \\ \frac{\beta - \mu - 2a^{+}}{2a_{I}^{-}} + \frac{\sqrt{(\beta - \mu - 2a^{+})^{2}(a_{O}^{-} - a_{I}^{-})^{2} - 4a_{I}^{-}a^{+}(a_{O}^{-} - a_{I}^{-})(\beta - \mu - 2a^{+})}{2a_{I}^{-}(a_{O}^{-} - a_{I}^{-})}, \end{array} \right) \end{array}$$

Points 3 and 4 are stable equilibria. Point 2 is a saddle point and not stable.

### Results for N = 2 Boxes

- If condition (\*) is not satisfied, point 2 is the only non-trivial equilibrium and it is stable.
- Point 2 is same equilibrium for each box as for 1-box model.
- Note existence of equilibria 3 and 4 depends on a<sup>+</sup> small enough, i.e., low migration rate.
   Contrary to what one might assume, that low migration would keep the 1-box equilibrium stable.

#### Results for N = 3 Boxes

- Results are similar to N=2
- In particular, 2 equilibria always exist
   1) Trivial equilibrium at (0,0,0), unstable if β > μ.

$$2)\left(\frac{\beta-\mu}{a_{I}^{-}+2a_{O}^{-}},\frac{\beta-\mu}{a_{I}^{-}+2a_{O}^{-}},\frac{\beta-\mu}{a_{I}^{-}+2a_{O}^{-}}\right)$$

- If  $a_0^- = 0$ , then point 2 is only non-trivial nonnegative equilibrium
- Otherwise, under additional conditions, including sufficiently low migration between boxes, multiple non-negative equilibria can occur.

- Finally, we can establish geometric ergodicity
- We create  $\{X_n\}_{n=0}^{\infty}$  on  $(\mathbb{Z}_+)^N$ , the embedded discrete time r.w. associated with our continuous r.w.

Set

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

Transition probabilities: for  $\mathbf{x}, \mathbf{y} \in (\mathbb{Z}_{+})^{N}, \mathbf{x} \neq \mathbf{0}$  $P(\mathbf{x}, \mathbf{y}) = \frac{1}{c(\mathbf{x})} \cdot \begin{cases} \beta_{i} x_{i} & \text{if } \mathbf{y} = \mathbf{x} + e_{i}, i = 1, \dots, N \\ \mu_{i} x_{i} + \frac{a_{ii}^{-}}{L} x_{i}^{2} & \text{if } \mathbf{y} = \mathbf{x} - e_{i}, i = 1, \dots, N \\ a_{ij}^{+} x_{i} & \text{if } \mathbf{y} = \mathbf{x} - e_{i} + e_{j}, i \neq j \\ 0 & \text{otherwise} \end{cases}$ 

for  $\mathbf{x} = \mathbf{0}$  $P(\mathbf{x}, \mathbf{y}) = \begin{cases} \frac{1}{N} & \text{if } \mathbf{y} = \mathbf{0} + e_i, i = 1, \dots, N \\ 0 & \text{otherwise} \end{cases}$ 

**Theorem**. A r.w. with the above transition probabilities is geometrically ergodic. That is, it is positively recurrent with exponential convergence to a stable distribution.

Method of proof: Sufficient condition:  $\sum P(\mathbf{x}, \mathbf{y})V(\mathbf{y}) \le \lambda V(\mathbf{x}) + b\mathbb{1}_B(\mathbf{x})$  $\mathbf{y} \in (\mathbb{Z}_+)^N$ for Lyapunov function  $V(x) \ge 1$ bounded set *B*, constants  $b < \infty$ ,  $\lambda < 1$ Lyapunov function:  $V(\mathbf{x}) = \alpha^{||\mathbf{x}||_1}$ with  $\alpha > 1$ We show  $\alpha$ ,  $\lambda$ , b, and B can be chosen such that the condition is met

Set external competition  $a_{ij}^- = 0$  for  $i \neq j$ Set symmetric conditions: for all *i*,  $\beta_i \equiv \beta$ ,  $\mu_i \equiv \mu_i a_{ij}^+ \equiv a^+, a_{ii}^- \equiv a_I^-, \beta > \mu$ Then, drift vector for this r.w.  $\overrightarrow{\Delta x} := P \overrightarrow{x} - \overrightarrow{x} = 0$ has at least 2 equilibria: 0 and  $\vec{x}$  where for all components *i*:  $\frac{x_i}{L} = \frac{\beta - \mu}{a_i}$ Matches equilibria determined for N = 1, 2, 3.