Does fast migration imply well-mixing of the population dynamics?



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Well-mixed population dynamics

Population size:

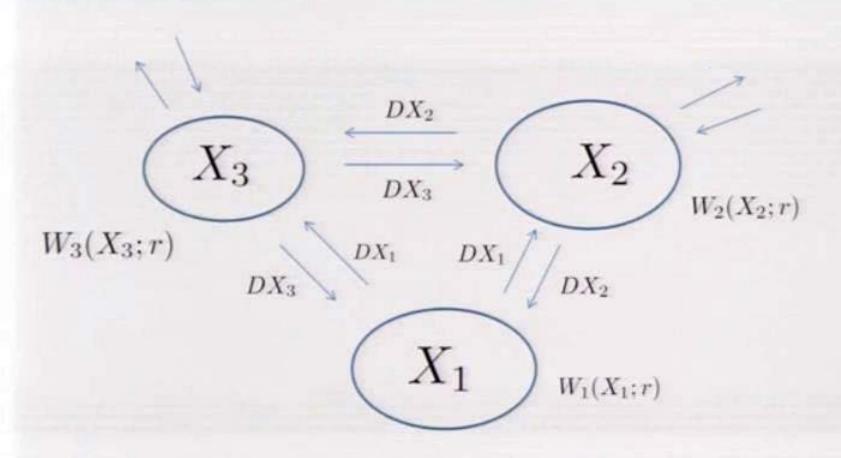
X

Birth-death processes:

$$X \stackrel{W(X;r)}{\to} X + r$$

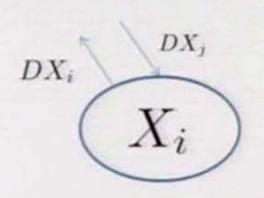
$$\dot{P}(X,t) = \sum W(X-r;r)P(X-r,t) - W(X;r)P(X,t)$$

Qualitative statement of the problem



Does fast migration lead to well-mixing of the total population?

Strong well-mixing condition



$$W_i(X_i; r) = K_i w(x_i; r)$$
$$x_i = K_i^{-1} X_i.$$

(Local dynamics are identical up to carrying capacity)

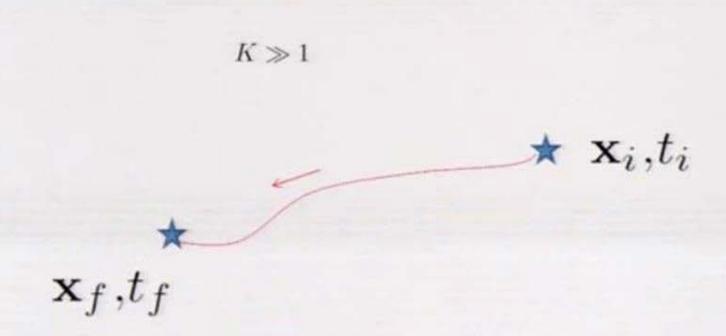
Strong well-mixing condition for the total population $X = \sum_i X_i$

$$D \to \infty$$

$$\dot{P}(X,t) = \sum W(X-r;r)P(X-r,t) - W(X;r)P(X,t)$$

$$W(X;r) = \tilde{K}w(x;r) \quad x = \tilde{K}^{-1}X$$

Mean-field evolution vs. rare events



Mean-field evolution

$$\dot{X}_{i} = \sum_{r} rW_{i}(X_{i}; r) + D \sum_{j \in I_{i}} (X_{j} - X_{i})$$

$$= \sum_{r} rK_{i}w(K_{i}^{-1}X_{i}; r) + D \sum_{j \in I_{i}} (X_{j} - X_{i})$$

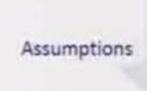
$$\dot{X} = \sum_{r} r \tilde{K} w(\tilde{K}^{-1} X; r) \quad D \to \infty$$

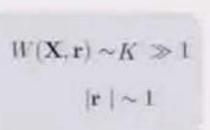
$$\sum_{r,i} r K_i w((NK_i)^{-1}X; r) = \sum_r r \tilde{K} w(\tilde{K}^{-1}X; r)$$

Dynamics of rare events: WKB solution of master equation.

Master equation:

$$\dot{P}(\mathbf{X}, t) = \sum_{\mathbf{r}} [W(\mathbf{X} - \mathbf{r}, \mathbf{r})P(\mathbf{X} - \mathbf{r}, t) - W(\mathbf{X}, \mathbf{r})P(\mathbf{X}, t)]$$







$$P(\mathbf{X}, t) = \exp[-\kappa \cdot (\mathbf{x}, t)]$$

 $\mathbf{x} = \mathbf{X}/K$

WKB Ansatz

Hamilton-Jacobi equation:

$$\partial_t s = -H(\mathbf{x}, \partial_{\mathbf{x}} s)$$

Semiclassical Hamiltonian:

$$H(\mathbf{x}, \mathbf{p}) = \sum_{\mathbf{r}} w(\mathbf{x}, \mathbf{r})(e^{\mathbf{pr}} - 1)$$

$$w(\mathbf{x}, \mathbf{r}) = W(\mathbf{X}, \mathbf{r})/K$$

Kubo, Matsua, & Kitahara (1973); Wentzell (1975), Hu Gang (1987), Dykman, Mori, Ross, & Hunt (1994);

Rare events dynamics of the total population

$$K_i = \kappa_i K, \quad K \gg 1$$

$$H_{total}\left(Q,P\right) = \sum_{r} \sum_{i=1}^{N} \kappa_{i} w\left(\frac{Q}{N\kappa_{i}};r\right) \left(e^{Pr}-1\right) \qquad Q = K^{-1} \sum_{i=1}^{N} X_{i}$$

$$\sum_{i=1}^{N} \kappa_{i} w \left(\frac{Q}{N \kappa_{i}}; r \right) = \bar{\kappa} w \left(\bar{\kappa}^{-1} Q; r \right)$$

Weak well-mixing condition

$$\sum_{i=1}^{N} \kappa_{i} w \left(\frac{Q}{N \kappa_{i}}; r \right) = \overline{\kappa} w \left(\overline{\kappa}^{-1} Q; r \right)$$

$$w\left(x;r\right) = \sum_{n=0}^{\infty} a_n^r x^n$$

$$a_n^r \left[\bar{\kappa}^{1-n} - N^{-n} \sum_{i=1}^N \kappa_i^{1-n} \right] = 0, \quad \forall r, n.$$

$$\kappa_i = \kappa_j \to \bar{\kappa} = N$$

$$\kappa_i \neq \kappa_j \to w(x; r) = a_1^r x + a_{n^*}^r x^{n^*} \quad \forall r$$

Examples. Logistic growth

$$\dot{X}_i = X_i(1 - X_i/K_i)$$

$$W(X_i;r) = aX_i + bX_i^2/K_i$$



$$\bar{K} = N \left(\frac{1}{N} \sum_{i=1}^{N} \frac{1}{K_i} \right)^{-1}$$

Examples. Allee effect

$$A \to 0$$
 $2A \to 3A$ $3A \to 2A$

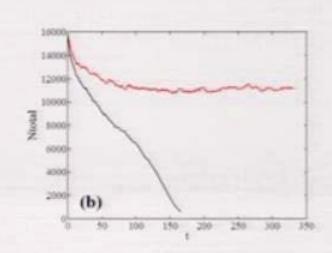
$$\downarrow \qquad \qquad \downarrow$$

$$\mu X_i \qquad (\lambda/2K_i)X_i^2 \qquad (\sigma/6K_i)X_i^3$$

$$\lambda^2 = \mu \sigma$$

$$\lambda^2 > \sigma \mu$$

$$\lambda^2 < \sigma \mu$$



Examples. Allee effect

Local birth-death processes:

$$A \rightarrow 0$$

$$A \rightarrow 0$$
 $2A \rightarrow 3A$

$$3A \rightarrow 2A$$

Local transition rates:

$$\mu X_i$$

$$\mu X_i \quad (\lambda/2K_i)X_i^2 \quad (\sigma/6K_i)X_i^3$$

$$(\sigma/6K_i)X_i^3$$

No well-mixing!

Saddle-node bifurcation:

$$\lambda^2 = \mu \sigma$$

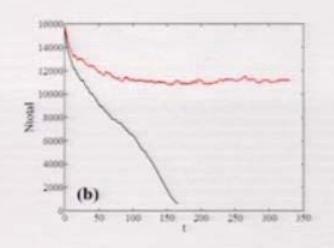
Bistability:

$$\lambda^2 > \sigma \mu$$

Monostability

(population extinction):

$$\lambda^2 < \sigma \mu$$



Mean-field evolution vs. rare events again

$$\kappa_i \approx \kappa_j \quad \forall i, j$$

$$K_i = K \kappa_i, K \gg 1$$

$$|\kappa_i - 1| \sim \epsilon \ll 1$$

$$\epsilon \ll 1/K$$

Summary

- Formulated strong/weak well-mixing condition
- Derived equations of motion for large fluctuations (rare events) of the total population for fast migration case
- Derived necessary & sufficient condition for weak well-mixing by fast migration
- Considered common examples where the condition is met" logistic growth", etc., and is not met: Allee effect.
- Mean-field dynamics is much more robust with respect to the well-mixing assumption than rare events

Fast Migration and Emergent Population Dynamics, M. Khasin, E. Khain, and L. M. Sander Phys. Rev. Lett. 109, 248102 (2012)