Fast Migration and Emergent Population Dynamics

Michael Khasin, Evgeniy Khain, and Leonard M. Sander

1Department of Physics, University of Michigan, Ann Arbor, Michigan 48109-1120, USA
2Department of Physics, Oakland University, Rochester, Michigan 48309, USA

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We consider population dynamics on a network of patches, having the same local dynamics, with different population scales (carrying capacities). It is reasonable to assume that if the patches are coupled by very fast migration the whole system will look like an individual patch with a large effective carrying capacity. This is called a “well-mixed” system. We show that, in general, it is not true that the total population has the same dynamics as each local patch when the migration is fast. Different global dynamics can emerge, and usually must be figured out for each individual case. We give a general condition which must be satisfied for the total population to have the same dynamics as the constituent patches.

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Many population models consider patches of habitat, each with a local birth-death dynamics, where the patches are coupled by diffusive migration [1,2]. Here we will consider a special case where all the patches have the same local dynamics except for a parameter that gives the scale of the local population (carrying capacity). That is, we consider a metapopulation that can exchange between patches which are more or less favorable places to be.

Such models are notoriously complex and have rich behavior [2–4]. However, one particular case seems simple: suppose the migration rate is very fast, faster than any other rate in the problem. In this case all the populations will become equal on average. It is tempting to think that the autonomous dynamics of the total population will be the same as that on each patch with some sort of average carrying capacity; i.e., the whole system will act as one patch carrying the total population [5]. In this case the system is “well-mixed.”

In this Letter we will show that this common belief is false in general: there are tight restrictions for the type of dynamics that admits this type of homogenization. If these restrictions are not obeyed the dynamics of the emergent behavior of the total population can be different in nature from that of the individual patches. We will derive the restrictions on the dynamics and give examples of the sort of emergent behavior that we have described, first by using mean-field theory and then including fluctuations.

We first formulate in a more precise form the idea that a total population of a number of local patches evolves like a larger population on a single patch. Let $X$ be the size of a population. The population dynamics is driven by the birth-death processes $X \rightarrow X + r$, each process associated with the rate $W(X; r)$. We assume that the rates can be put into the form

$$W(X; r) = K w(x; r),$$

where $K$ is the carrying capacity. Now consider a connected network of $N$ patches such that the local dynamics of the population $X_i$ is identical on each patch, but the carrying capacities $K_i$ are different. That means the local birth-death processes are of the form $X_i \rightarrow X_i + r_i$, with corresponding rates

$$W_i(X_i; r_i) = K_i w(x; r_i), \quad i = 1, \ldots, N,$$

$$x_i = K_i^{-1} X_i.$$  \hfill (1)

The patches are connected by migration. We define the dynamics of the total population $X = \sum X_i$ to be well mixed if it has transitions $X \rightarrow X + r$, with rates

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

where $w(x; r)$ are local rates. The number $\tilde{K}$ is the effective carrying capacity of the total population. This defines well-mixed population dynamics.

Now assume that the rate of migration between patches is much larger than the local birth-death rates. We first consider the mean-field limit, neglecting fluctuations (which is appropriate for $K_i \sim K \gg 1$). The mean-field equations are

$$\dot{X}_i = \sum_r r W_i(X_i; r) + D \sum_{j \in J_i} (X_j - X_i)$$

$$= \sum_r r K_i w(K_i^{-1} X_i; r) + D \sum_{j \in J_i} (X_j - X_i), \hfill (2)$$

where $D$ is migration rate, taken to be identical for all groups [6], and $J_i$ is the set of indices, associated with the patches, connected by migration to patch $i$. We are interested to see if, for $D \rightarrow \infty$, the total population is driven by the well-mixed dynamics:

$$\dot{X} = \sum_r r \tilde{K} w(\tilde{K}^{-1} X; r),$$

for some effective carrying capacity $\tilde{K}$.

Consider a specific example first where the local dynamics displays the Allee effect [7]; individuals often require the assistance of members of the same species to flourish (e.g., to fend off predators) [7]. The growth rate is
negative for low densities; therefore, in a certain range of parameters the single-patch dynamics is bistable: there is one stable state with finite population and another corresponding to local extinction. The simplest mathematical model of the Allee effect can be written as \( \dot{X} = f(X) \), where \( f \) is a cubic polynomial. The corresponding “particle” system is represented by the following processes:

\[
\begin{align*}
X_i &\to 0; \quad \text{rate } \mu X_i, \\
2X_i &\to 3X_i; \quad \text{rate } (A/2K_i)X_i(X_i - 1), \\
3X_i &\to 2X_i; \quad \text{rate } (\sigma/6K_i^2)X_i(X_i - 1)(X_i - 2),
\end{align*}
\]

on each site, where \( K_i \) is a local carrying capacity. The first two processes are essential for the Allee effect: the parameter \( \mu \) represents the death rate of a low-density population, while the rate \( \lambda \) represents the growth of the population when the density is not too low. The parameter \( \sigma \) represents the usual negative growth when the population becomes overcrowded. The rates have the form of Eq. (1). The mean-field equations are

\[
\dot{X}_i = -\mu X_i + \frac{\lambda}{2K_i}X_i^2 - \frac{\sigma}{6K_i^2}X_i^3 + D \sum_{j \in I_i} (X_i - X_j).
\]

For \( D = 0 \) the local stable stationary states are

\[
X_i^* = \left\{ 0, \frac{3\lambda K_i}{2\sigma} \left[ 1 + \left( 1 - \frac{8\sigma \mu}{3\lambda^2} \right)^{1/2} \right] \right\};
\]

i.e., local bistability (Allee effect) occurs for \( \lambda^2 > (8/3)\sigma \mu \).

For large migration rates the local populations are approximately equal, \( X_i = X/N \), on the long time scale of the local dynamics. The mean-field equation of motion for the total population is obtained by summing up the Eq. (4) and setting \( X_i = X/N \):

\[
\dot{X} = -\mu X + \frac{\lambda}{2K}X^2 - \frac{\sigma}{6K^2}X^3,
\]

\[
\dot{K} = N^2 \left( \sum_i K_i^{-1} \right)^{-1}, \quad \sigma = \frac{\sigma}{N^3} \sum_i \left( \frac{\dot{K}}{K_i} \right)^2.
\]

Comparing Eqs. (5) and (4) we see that the total population \( X \) follows a single-patch dynamics with the rescaled rate \( \dot{\sigma} \) (one could define a different effective carrying capacity \( \frac{\dot{K}}{K} \) through the rate sigma, while the rate lambda would become modified in the emerging global dynamics). Note that for equal local carrying capacities, \( K_i = K_j \) for all \( i, j \), \( \sigma = \sigma. \) On the other hand, for different carrying capacities it can be shown that \( \dot{\sigma} > \sigma; \) i.e., the well-mixing condition is not satisfied.

This can lead to a qualitative difference of the local dynamics and the dynamics of the total population: specifically, the local dynamics is bistable for \( \lambda^2 > \frac{8}{3} \sigma \mu \), while for \( \lambda^2 < \frac{4}{3} \sigma \mu \) the only stable state is extinction of the population. Since \( \dot{\sigma} \geq \sigma \), in a certain range of parameters one can simultaneously have \( \lambda^2 > \frac{8}{3} \sigma \mu \) and \( \lambda^2 < \frac{4}{3} \sigma \mu \). In this case, even though each local population separately can be bistable, the total population in the presence of fast migration is driven to extinction for any initial distribution of local populations.

To illustrate this remarkable dynamics we suppose the local carrying capacity depends on a (discrete) spatial coordinate \( i \): \( K_i = K(1 + \epsilon \sin(2\pi i/L)) \), so that the carrying capacity is a periodic function of \( i \), and \( \epsilon \) determines the relative magnitude of these spatial variations; see Fig. 1(a) (dashed lines). For sufficiently small \( \epsilon \) the nontrivial nonzero state is stable. Since \( \dot{\sigma} \) increases with \( \epsilon \) the system is rapidly driven to extinction when \( \epsilon \) exceeds the threshold determined by \( \lambda^2 = \frac{8}{3} \dot{\sigma} \mu \). Figure 1(a) shows the spatial population profiles \( X_i \) for two values of \( \epsilon \) (above and below the threshold); Fig. 1(b) shows the corresponding time dependence of the total population \( X \).

To gain some intuition we consider the two-site model with \( K_1 = K(1 + \epsilon) \) and \( K_2 = K(1 - \epsilon) \). Figure 2 shows the single-site growth rate [the right-hand side of Eq. (4) for \( D = 0 \)] and the resulting growth rate for the total population [the right-hand side of Eq. (5)], so the solid curve is just a sum of the dashed and dash-dotted curves. The upper panel is for small (subcritical) \( \epsilon \). Here, the stable fixed point of the total population lies between the fixed points of single-site populations with carrying capacities \( K_1 > K_2 \) (circles), \( X_1^* < X_2^* < X_3^* \) for very large migration, the local populations on the two sites are equal \( X_i = X_2 = X_3^* \); the local population is larger than it would be on site 2 with smaller carrying capacity \( (X_1^*) \) in the absence of migration, but it is smaller than it would be on site 1 with larger carrying capacity \( (X_1^*) \). In this case a balance can be achieved. However, this balance is destroyed for sufficiently large \( \epsilon \), as can be seen in the lower panel of Fig. 2. Indeed; as \( \epsilon \) increases, \( 1/\dot{K} = 1/K_1 + 1/K_2 \) approaches \( 1/K_2 \); i.e., both \( \dot{K} \) and \( X^* \) decrease with \( \epsilon \). For sufficiently large \( \epsilon \), \( X^* \) drops far below the unstable fixed point of the larger site \( X^* \) (denoted by the square on the lower panel of Fig. 2). In this case, the balance cannot be achieved: the Allee effect is driven to extinction for any initial distribution of local populations.

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FIG. 2 (color online). The local single-site dynamics [the right-hand side of Eq. (4) for $D = 0$, the dashed and dash-dotted lines] and the corresponding dynamics for the global population $X/N$ [the right-hand side of Eq. (5), the solid line, for large migration] for the two-site model. The upper panel corresponds to subcritical $\epsilon$ ($\epsilon = 0.2$), the bottom panel corresponds to supercritical $\epsilon$ ($\epsilon = 0.4$). The dashed lines correspond to the larger carrying capacity $[K_1 = K(1 + \epsilon)]$, the dash-dotted lines correspond to the smaller carrying capacity $[K_2 = K(1 - \epsilon)]$. Circles correspond to the stable fixed point, the square denotes the unstable fixed point. The parameters are $K = 60$, $\mu = 0.09$, $\lambda = 0.2$, $\sigma = 0.15$.

effect on the larger site will dominate, driving the total population towards extinction.

A general necessary and sufficient condition for the well mixing in the mean-field evolution is obtained from Eqs. (2) and (3) following similar manipulations:

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

is satisfied for some $\tilde{K}$ and all $X$.

We now proceed to the derivation of the necessary and sufficient condition for well mixing beyond mean-field theory. Stochastic population dynamics is driven by the master equation for the probability distribution:

$$
P(X, t) = \sum_{i=1}^{N} W_i(X_i - r; r) P(X - re_i) - \sum_{i=1}^{N} W_i(X_i; r) P(X) + D\tilde{W}_0 P(X),
$$

where $W_i(X_i; r)$ are local transition rates, $(e_i)_j = \delta_{ij}$, and $D\tilde{W}_0(X, r)$ is the migration operator:

$$
W_0(X, r) P(X) = \frac{1}{2} \sum_{j=1}^{N} (X_j + 1) P(X - e_i + e_j) + \frac{1}{2} \sum_{i=1}^{N} (X_i + 1) P(X + e_i - e_j) - \frac{1}{2} \sum_{i=1}^{N} (X_i + X_j) P(X).
$$

We consider on-site dynamics identical on all patches with different local carrying capacities $K_i$. We also assume the carrying capacities are large, $K_i = K K_i$, $K \gg 1$. We seek the dynamics of total population $X = \sum_{i=1}^{N} X_i$ in the limit $D \to \infty$.

For $K \gg 1$ we can use the WKB approximation for the master equation (6) [8–13], looking for the probability distribution in the form

$$
P(X, t) = \exp[-KS(x, t)]; \quad x = K^{-1} X.
$$

For the quasistationary distribution we obtain the Hamilton-Jacobi equation for the action $S(x)$ [14]:

$$
H(x, p) = 0; \quad p_i = \partial_i S(x),
$$

where

$$
H(x, p) = DH_0(x, p) + H_1(x, p),
$$

$$
H_1(x, p) = \sum_{i=1}^{N} \sum_{r} \kappa_i w(\kappa_i^{-1} X; r) (e^{p_i r} - 1),
$$

$$
H_0(x, p) = \frac{1}{2} \sum_{i=1}^{N} \sum_{r} x_i (e^{p_i r} - 1) + \frac{1}{2} \sum_{i=1}^{N} \sum_{r} x_j (e^{p_j r} - 1).
$$

The Hamiltonian (9) generates the fluctuational dynamics of the system, in the sense that the most probable path of the system, leading from $x_i$ at $t = t_i$ to $x_j$ at $t_f$, is determined by (9) [10].

The total population $Q = \sum_j x_j$ is a slow variable, evolving on the time scale unity. The variables $x_i$ are fast, evolving on the time scale of migration $\sim D^{-1} \ll 1$. This time scale separation suggests canonical transformation from $x$ and $p$ to $q_i$, $Q$ and $P_i$, $P_Q$, $i = 2, 3, \ldots, N$:

$$
Q = \sum_j x_j; \quad q_i = x_i; \quad p_i = P_Q; \quad p_i = P_Q + P_i.
$$

We expect that in the new variables the fluctuational dynamics of the system on the time scale $\sim 1$ will display adiabatic slaving of the fast local populations $q_i$ by the slow evolution of the total population $Q$, such that instantaneous sizes of the local populations are all equal, due to the fast migration. We show in Ref. [15] that the evolution of $Q$ and $P_Q$ is driven by the following Hamiltonian:

$$
H_{\text{slow}}(Q, P_Q) = \sum_{i=1}^{N} \sum_{r} \kappa_i w\left(\frac{Q}{N \kappa_i}; r\right)(e^{p_i r} - 1).
$$

In order that the total population follows effective single-site dynamics with a rescaled carrying capacity (well mixing), the Hamiltonian (10) must have the form of a single-site Hamiltonian:

$$
H(Q, P_Q) = \sum_r \tilde{K} w(\tilde{K}^{-1} Q; r)(e^{p r} - 1).
$$

The equivalence of expressions (10) and (11) gives the necessary and sufficient condition for well mixing:
\[
\sum_{i=1}^{N} \kappa_i w(\frac{Q}{N\kappa_i}; r) = \tilde{\kappa} w(\tilde{\kappa}^{-1} Q; r), \quad \forall \ r.
\] (12)
where \( \tilde{\kappa} = \tilde{K}^{-1} \) is the rescaled effective carrying capacity. To make further progress we assume that the on-site birth-death rates can be put into the following form:

\[
w(x; r) = \sum_{n=0}^{\infty} a_n x^n, \quad \forall \ r, x.
\]

Then condition (12) becomes equivalent to

\[
a_n^{\star} \left[ \tilde{\kappa}_i^{1-n} - N^{-n} \sum_{i=1}^{N} \kappa_i^{1-n} \right] = 0, \quad \forall \ r, n.
\] (13)

The general solution of this equation for varying carrying capacities, \( \kappa_i \neq \kappa_j \) for some \( i, j \), is

\[
a_n^{\star} = a_n^{\star} \delta_{n,1} + a_n^{\star} \delta_{n,n}, \quad \forall \ r,
\]

\[
\tilde{\kappa} = N \left( N^{-1} \sum_{i=1}^{N} \kappa_i^{-n^{\star}} \right)^{1/(1-n^{\star})},
\]

where \( n^{\star} \) is an integer. In other words, a rescaled carrying capacity can be found if and only if the on-site birth-death rates \( w(x; r) \) have the form

\[
w(x; r) = a_n^{\star} x + a_n^{\star} x^{n^{\star}}, \quad \forall \ r.
\] (14)

Many population dynamics models have the form (14) for \( n^{\star} = 0, 2 \). For \( n^{\star} = 0 \), as in Poissonian process [16]:

\[
\tilde{\kappa} = N \left( N^{-1} \sum_{i=1}^{N} \kappa_i \right);
\]

i.e., the carrying capacity is \( N \) times the arithmetic mean of the local carrying capacities. For \( n^{\star} = 2 \), as in logistic growth [17],

\[
\tilde{\kappa} = N \left( N^{-1} \sum_{i=1}^{N} \kappa_i^{-1} \right)^{-1};
\]

i.e., the carrying capacity is \( N \) times the harmonic mean of the local carrying capacities.

It is important to note that for identical carrying capacities, \( \kappa_i = 1 \) for all \( i \), the condition (13) is satisfied for arbitrary \( a_n^{\star} \) and \( \tilde{\kappa} = N \); i.e., for identical carrying capacity the total population evolves like a single-site population with a carrying capacity rescaled by the number of sites \( N \). In applications one would like to know if small variations of the carrying capacity can be neglected for the purpose of building a coarse-grained model, i.e., whether the total population behaves approximately as a single site with a rescaled carrying capacity. For the typical evolution of the system, described by the mean-field equations (2), it is sufficient to have \( |\kappa_i - 1| \sim \epsilon \ll 1 \) in order to determine an approximate effective carrying capacity leading to (3). For large fluctuations, the condition is much stricter. From Eq. (13) we see that \( O(\epsilon) \) variations of the local carrying capacities \( \kappa_i \) lead to \( O(\epsilon) \) variation of the effective carrying capacity \( \tilde{\kappa} \) of the total population dynamics. This will lead to \( O(\epsilon) \) variation in the action in Eq. (7). In order that this variation can be neglected, \( \epsilon \ll 1/K \) must hold. We conclude that, in a realistic situation, where \( 1/K \ll \epsilon \ll 1 \), the large fluctuations of the total population cannot be approximated by the single-site dynamics with rescaled carrying capacity, unless Eqs. (13) can be solved exactly. Remarkably, for the same \( \epsilon \) the typical behavior of the total population is well approximated by the single-site dynamics.

In this Letter we have shown that a notion that seems to be completely obvious is false. It is not true, in general, that if we mix very fast, a metapopulation with identical dynamics on patches of habitat (with different carrying capacities) will synchronize to act like a single population with the same dynamics.

We show that this notion is true if local carrying capacities are identical. For varying local carrying capacities such a mixing property holds in very simple special cases, where the local dynamics is characterized by only two types of processes: (i) \( A \rightarrow kA \) and (ii) \( n^*A \rightarrow mA \) for some fixed \( n^* \) (14). Most examples that come to mind are exactly of this sort. But in other cases, such as population dynamics with the Allee effect, the qualitative behavior of the synchronized population can be very different from that of any individual patch.

There is a remarkable difference between the typical behavior of the total population and its large fluctuations for small (\( \epsilon \ll 1 \)) but not too small (\( \epsilon \gg 1/K \)) variations of the local carrying capacities. In this case, while the typical behavior can be well approximated by the single-site dynamics, large fluctuations cannot be approximated except in special cases as described above. Quantitatively, the fluctuation (leading to a state \( Q \)) is large when the WKB approximation is valid, i.e., when the classical action associated with the trajectory of the total population leading to \( Q \) satisfies \( KS(Q) \gg 1 \).

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