



Capacity-based migration model for two populations

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1. Introduction

I present a dynamic, but straightforward, model which describes migratory flux between two populations. I will design a migration function that is dependent on the populations' distance from their respective carrying capacities. This function will be implemented in a coupled system of ODEs which extend the logistic model for single species. By transforming this system into a pair of difference equations, I will exhibit conditions of stability and chaos. I will also exhibit the parallel behavior of r-selected and k-selected groups.

Keywords: Migration function, carrying capacity, migration inertia, logistic model

2. Model Definition

We would like to preserve the logistic model where growth is self-regulated by fixed carrying capacities and growth rates k_P, r_P and k_Q, r_Q in populations P and Q respectively. Migration will be decomposed into two terms: migration from P to Q and migration from Q to P denoted as the functions M_P and M_Q respectively. $M_P, M_Q > 0$ so this defines a positive sign convention for immigration and negative convention for emigration. The continuous system is thus:

$$\begin{aligned} \frac{dP}{dt} &= V(P, k_P, r_P) - M_P(P, Q, k_P, k_Q)P + M_Q(P, Q, k_P, k_Q)Q \\ \frac{dQ}{dt} &= V(Q, k_Q, r_Q) - M_Q(P, Q, k_P, k_Q)Q + M_P(P, Q, k_P, k_Q)P \end{aligned} \quad (1)$$

where $V(N, k_N) = Nr_N \left(\frac{1}{k_N} \right) (k_N - N)$ is simply the Verhulst logistic model for a generic population N . Here the migration functions have been normalized such that $0 \leq M_N \leq 1$ in order to represent per capita rate of migration.

3. Migration function design

We define the critical parameters ψ_P and ψ_Q such that:

$$\psi_P \equiv (k_Q - Q) - (k_P - P) = -\psi_Q \equiv -[(k_P - P) - (k_Q - Q)] \quad (2)$$



These parameters represent the difference of differences between each population and its carrying capacity. Boundary conditions for the migration functions are immediately apparent:

$$\begin{aligned} M_P = 0 &\leftrightarrow \psi_P = 0 & \text{and} & & M_Q = 0 &\leftrightarrow \psi_Q = 0 \\ M_P \approx 1 &\leftrightarrow \psi_P = k_P & & & M_Q \approx 1 &\leftrightarrow \psi_Q = k_Q \end{aligned} \quad (3)$$

Assuming that migrations occur independently we can view migration events as

bijections between the sets $P = \langle P_1, \dots, P_{n-1}, P_n \rangle$ and $Q = \langle Q_1, \dots, Q_{m-1}, Q_m \rangle$. Clearly

$\frac{dM}{d\psi} \propto M - M^2$, analogous to the formulation of the logistic model due to random encounters during resource competition for a single species. Therefore, an approximation for such a function $M(\psi)$ can be obtained from the solution to the differential equation:

$$\frac{dM}{d\psi} = M(\psi)[1 - M(\psi)] \quad (4)$$

which admits the sigmoid solution for $M_0 \approx 0$.

$$M_N(\psi_N) = \frac{M_0}{M_0 + (1 - M_0)e^{-\alpha\psi_N}} - M_0 \quad (5)$$

The constant α arises during integration and can be interpreted as a “migration inertia” which scales the weight of ψ . Note that this is a reasonable approximation for large ψ_P, ψ_Q . This model is preferred over the simpler $M(\psi) = M_0(1 - e^{-\beta\psi})$, where β is another inertial constant, because we honor the sensibilities of a population: acceleration of migration is more pronounced at intermediate ψ since this minimized intra-specific

competition. Differentiating (4) implicitly we see that $\frac{d^2M}{d\psi^2} = \frac{dM}{d\psi}(1 - 2M) = (M - M^2)(1 - 2M)$

and thus the inflection occurs with $M = 1/2$. Such an inflection is absent in the simpler model. The compiled model from (2), is as follows after algebraic simplification, and using the definition that $\psi_P \equiv -\psi_Q$:

$$\begin{aligned} \frac{dP}{dt} &= V(P, k_P, r_P) - M_P(\psi_P)P + M_Q(\psi_Q)Q \\ &= Pr_P \left(\frac{1}{k_P} \right) (k_P - P) - M_0 \left\{ \frac{M_0(Q - P) + e^{-\alpha\psi_P}(Q - M_0Q) + e^{-\alpha\psi_Q}(M_0P - P)}{M_0^2 + M_0(1 - M_0)(e^{-\alpha\psi_Q} + e^{-\alpha\psi_P}) + (1 - M_0)^2} - Q + P \right\} \\ \frac{dQ}{dt} &= V(Q, k_Q, r_Q) - M_Q(\psi_Q)Q + M_P(\psi_P)P \\ &= Qr_Q \left(\frac{1}{k_Q} \right) (k_Q - Q) - M_0 \left\{ \frac{M_0(P - Q) + e^{-\alpha\psi_P}(M_0Q - Q) + e^{-\alpha\psi_Q}(P - M_0P)}{M_0^2 + M_0(1 - M_0)(e^{-\alpha\psi_Q} + e^{-\alpha\psi_P}) + (1 - M_0)^2} - P + Q \right\} \end{aligned} \quad (6)$$



5. Steady-state Analysis

Equilibrium in (6) is achieved when $(P, Q) = (k_p, k_q)$. The migration flux and Verhulst growth disappear. This is the case where ψ becomes very small. When ψ becomes large, some unexpected results arise.

$$\frac{d\psi_p}{dt} \equiv \frac{dP}{dt} - \frac{dQ}{dt} = V(P) - V(Q) - 2[M_p(P) + M_q(Q)]$$

We see that at maximum ψ , migration will contribute at most 1/2 of the character of the logistic growth. To maximize the contribution of migration from Q to P, we must eliminate the logistic growth in P, without loss of generality. Qualitatively, we see that $M_p(P) = M_q(Q) = 0$ is not the only equilibrium condition; more generally, the equilibrium is at $M_p(P) = -M_q(Q)$. With no Verhulst growth, this condition is approximately true at $P \approx k_p$ and $Q \approx k_q$. Due to migration, another steady state exists in which $P > k_p$ and $Q \approx k_q$. See fig 4.

If we isolate either P or Q, the model behaves much like a delay model implemented by Mackey and Glass (1977). This effect is pronounced when we consider the discrete analogue in which migrations occur in time-steps. In this model, the numeric solution passed through periodic, chaotic, and fixed-point solutions. We will find a similar behavior.

4. Discrete transformation

The system in (6) is rather unwieldy. We construct the discrete analog with single time steps. We assume P changes before Q. The parameters k_N and r_N have been omitted in V for convenience:

$$\begin{aligned} P\{t+1\} &= V(P\{t\}) - M_p(\psi_p)P\{t\} + M_q(\psi_q)Q\{t\} + P\{t\} \\ Q\{t+1\} &= V(Q\{t\}) - M_q(\psi_q)Q\{t\} + M_p(\psi_p)P\{t+1\} + Q\{t\} \end{aligned} \quad (7)$$

Equilibrium occurs when $P\{t+1\} = P\{t\}$ and $Q\{t+1\} = Q\{t\}$ which yield the conditions

$$\begin{aligned} V(P\{t\}) - M_p(\psi_p)P\{t\} + M_q(\psi_q)Q\{t\} &= 0 \\ V(Q\{t\}) - M_q(\psi_q)Q\{t\} + M_p(\psi_p)[M_p(\psi_p)P\{t\} + M_q(\psi_q)Q\{t\} + P\{t\}] + Q\{t\} &= 0 \end{aligned} \quad (8)$$

which can be expressed simultaneously in terms of the difference in logistic growths, and in terms of the migration interactions by a linear combination of the conditions in (8) as:

$$V(P) - V(Q) = M_p(2P + M_p P + V(P)) - M_q(2Q - M_p Q) = 0 \quad (9)$$

Immediately we can see one of the stable solutions occurs when both populations return to their carrying capacities. Computing an array of $(P\{t\}, Q\{t\})$ (7) in MATLAB and graphing the solutions results in three important cases shown in figures 1a,b – 3a,b.



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Fig. 1 shows a dynamic where the phase trajectory end at (k_P, k_Q) , so both populations return to their carrying capacities, but this is modulated by oscillations due to migration. $\alpha_0 \in [\alpha_1, \alpha_2]$ was chosen so that the trace and determinant of the Jacobian for (6) were both negative.

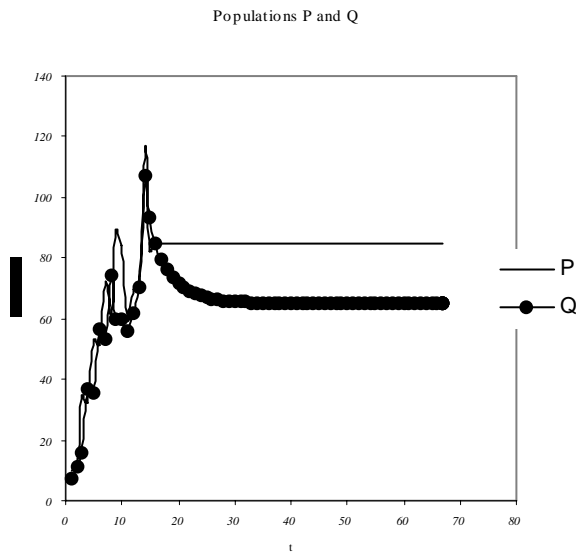


Fig 1a

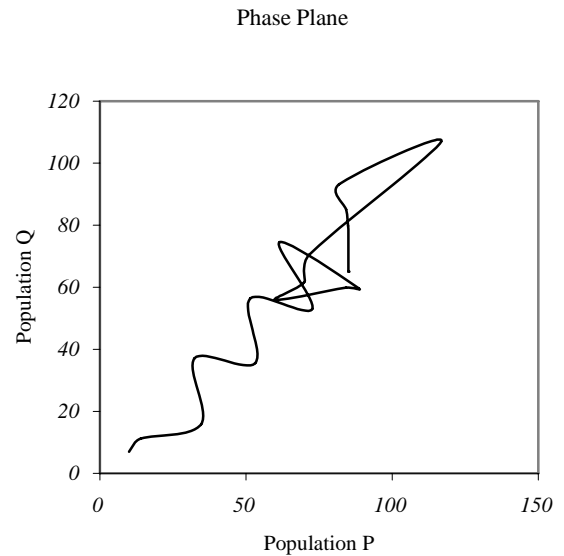


Fig 1b.

Fig. 2 shows an interesting scenario where the migration inertia factor $\alpha = \alpha_3 > \alpha_2$ has been chosen such that there is harmonic oscillation. At each point where $N\{t+1\} = N\{t\}$, the Poincaré-Bendixon box does not exist in cobwebbing.

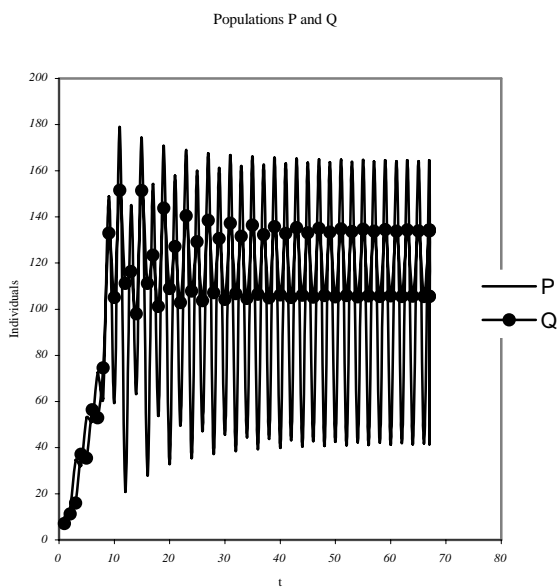


Fig 2a

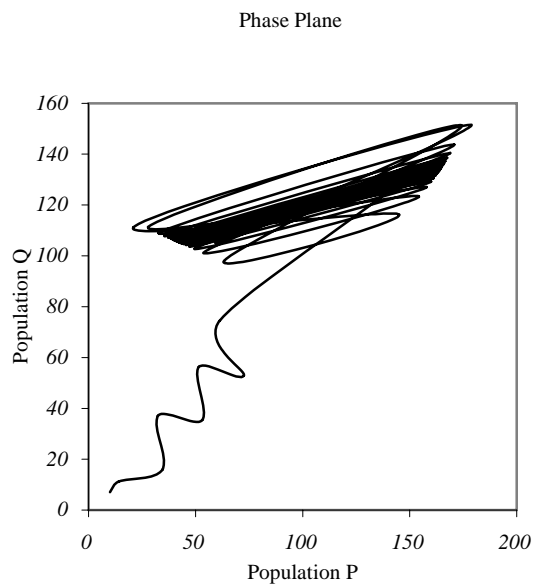


Fig 2b



Fig 3. shows a case where nearly in-phase oscillations come to equilibrium at carrying capacities. Here $\alpha = \alpha_4 \in [\alpha^*, \alpha_1]$ so the eigenvalues $\lambda_1, \lambda_2 \approx 0$. At $\alpha < \alpha^*$, the situation in fig. 2 re-emerges.

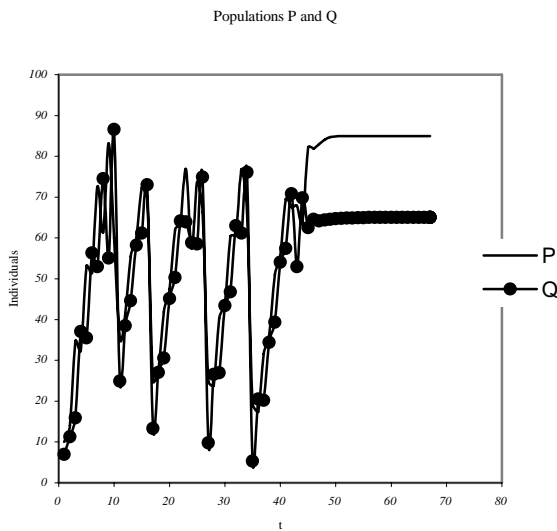


Fig 3a

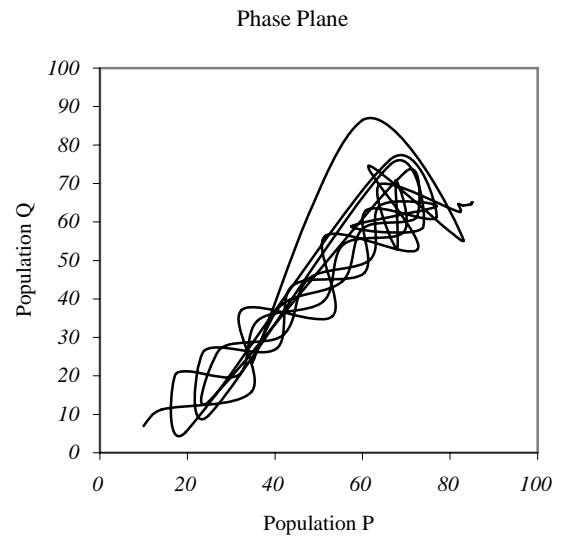


Fig 3b

Fig 4. shows the fixed-point where $P > k_p$. The fixed-point $Q = k_Q$ is maintained by an influx from P. Note the spike in Q before it reaches equilibrium. This is the point in which it passes the inflection in ψ . This spike contributes to the initial influx into P.

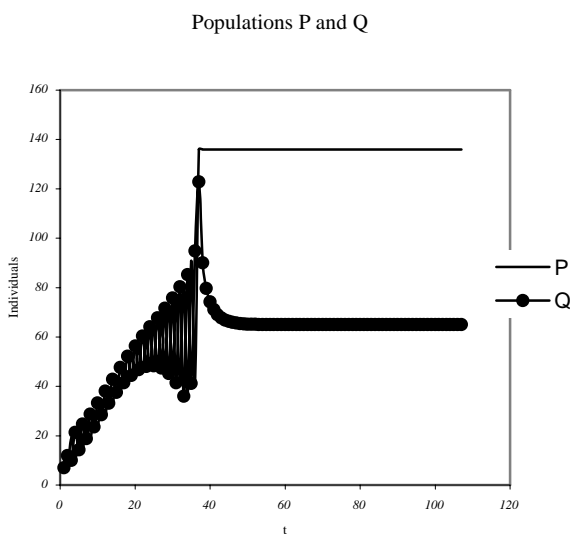


Fig 4a

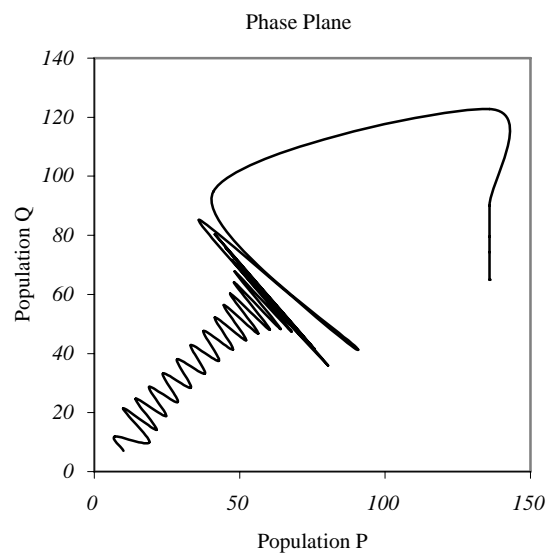


Fig 4b



5. Discussion

It is clear that α is an extremely critical parameter since it determines the equilibria stabilities. Note we have assumed $\alpha_P = \alpha_Q$ so it is impossible to exhibit a stable equilibrium for P and oscillations for Q or vice versa. This parameter really should be interpreted as each individual's perception of the importance of ψ . The models in fig. 1 are most realistic. If α becomes too large, migrations between mass migration events occur, and do not stabilize around k . If α is too small, migrations become too slow to compensate for the growth rate. Thus there exist only two regions of stability in a bifurcation diagram for α .

The $\alpha = \alpha_0$ is characteristic of r-selected populations. It is expected that comparable Verhulst rates will minimize the effects of migration, but since the model is coupled, a fast r in one population will act to make the other population's r congruent. Thus an r-selected population near a k-selected population will tend to crowd the k-selected population.

We recommend for future models that α be decoupled. This would relieve the r dominance. It is also prudent to construct $M: M \left(\frac{d\psi}{dt} \right)$. Again this choice of M reduces competition as a population becomes increasingly k-selected.

6. References

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