

1584

Metapopulation Models with Age Structure

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Abstract

A principal aim of population biologists is to understand the role of intraspecific competition at the metapopulation level (populations of populations). We study the dynamics of a two-patch age-structured metapopulation model where the local (patch) intraspecific competition regimes are of the same type (scramble or contest) or mixed (scramble and contest) types. Metapopulations behave as single patch systems under the same competition regime whenever dispersal is symmetric and all local populations find themselves under contest competition regimes. However, multiple attractors are possible whenever a local patch is under scramble competition regime. The results of this research demonstrate that dispersal between patches, and age-structure provide an evolutionary advantage.

1 Introduction

The importance of spatial structure and the physiological traits of individual species, both in controlling the total population sizes and the local variations in densities, in real-world populations are well known [11-13]. Chronological age of individual species is an example of such physiological traits. The model for this study is a juvenile-adult two-age class discrete-time metapopulation model where local populations are connected by dispersal. Previous studies on the impact of intraspecific competition at the metapopulation level (populations of populations) were initially presented in genetics by Wright[7], ecology by Levins [8,9] and epidemiology by Ross [10]. Our model relates to species that thrive at very low densities with no interference - such species are called pioneer species. For example, pine trees, fish population, and birds.

Similar studies on metapopulation dynamics were carried out by C. Castillo-Chavez and A. Yakubu [16]. However, their studies did not take in account age structure. Hence, in this paper, we extend their work to include a specific simple age-dependent population structure. Specifically, we divide each patch population into non-reproductive juveniles and reproductive adults. Thereafter, our patch system is regulated by discrete-time Ricker's and Verhulst equations.

Scramble and contest competition are two extreme forms of intraspecific competition for resources. A population that is governed by scramble competition support all individuals-even the non-reproductive ones. That is, the resources are distributed equally among individuals. Therefore, beyond a threshold density, none can get enough of a share of the resource to survive or reproduce. This system is modeled by the Ricker's equation where new recruits face scramble competition [4-6]. In contrast, in contest competition the resources are distributed unequally. Some individuals get enough of a share of the resource to survive and reproduce at the expense of the rest. The Verhulst model is an example where new recruits face contest competition [4-6].

The simulations considered for each patch system demonstrates that in single contest intraspecific competition regime the population is either surviving or dying as we vary the growth rate with respect to the growth speed ratio. In contrast, the local dynamics for the single scramble competition regime show

multiple attractors, Hoft bifurcation, and coexisting chaotic attractors. In two-patch systems with dispersal, contest-contest intraspecific competition the dynamics are the same as in single contest with symmetric and asymmetric dispersal, also rescue effect from patch one to patch two occurs.

2 Single Patch System

In this section, we study the single patch model

$$\begin{aligned} J_{(n+1)} &= A_n g(A_n) \\ A_{(n+1)} &= s J_n \end{aligned} \tag{1}$$

where J_n and A_n represent the juvenile and adult population at generation n , and where the per capita growth rate $g : [0, \infty) \rightarrow [0, \infty)$ is a strictly decreasing continuous function and s is the constant proportion of juveniles that survive to adulthood in one generation.

If we let $\bar{J}_n = s J_n$, $\bar{A}_n = A_n$ and $\bar{g} = sg$, then in the new variables (1) becomes

$$\begin{aligned} \bar{J}_{(n+1)} &= \bar{A}_n \bar{g} \bar{A}_n \\ \bar{A}_{(n+1)} &= \bar{J}_n. \end{aligned} \tag{2}$$

Consequently, we study the following system:

$$\begin{aligned} J_{(n+1)} &= A_n g(A_n) \\ A_{(n+1)} &= J_n. \end{aligned} \tag{3}$$

After two generations the population of juveniles are governed by $J_{(n+2)} = J_n g(J_n)$ and that of the adults by $A_{(n+1)} = A_n g(A_n)$. In system (3), the population is under scramble competition if the reproduction function $f(x) = xg(x)$ has a positive fixed point and same initial conditions overshoot it under iteration. For example, if f is the Ricker's model $f(x) = x e^{r-x}$ then the population is under scramble competition.

The population is governed by contest competition if $f(x) = xg(x)$ has a positive fixed point and no initial condition overshoot it under iteration. For example, if f is the Verhulst's model $f(x) = rx/x + b$ then the population is

under contest competition.

Theorem 1: In system (3) if $g < 1$ then the population goes extinct. For example, in Verhulst's model $g < 1$ if $r < b$.

Theorem 2: If $g : [0, \infty) \rightarrow [0, \infty)$ is a strictly decreasing function and $\lim_{x \rightarrow \infty} g(x) < 1$, then there is no population explosion in system (3). For example,

$$\begin{aligned} J_{(n+1)} &= A_n g(A_n) < A_n \\ A_{(n+1)} &= J_n \\ A_{(n+2)} &= J_{(n+2)} < A_n \end{aligned}$$

The model has a compact attractor (trapping region) that contains the omega limit set of every point. Notice that $(0, 0)$ is a fixed point in system (3). Moreover, if $g(0) > 1$ then system (3) has a positive fixed point at $(g^{-1}(1), g^{-1}(1))$. For example, if $g(x) = e^{r-x}$ the positive fixed point is (r, r) and if $g(x) = r/x + b$, the positive fixed point is $(r - b, r - b)$ when $r > b$.

2.1 Contest competition: Verhulst's model

If juveniles and adults are governed by Verhulst's model in every two generations, then system (3) becomes

$$\begin{aligned} J_{(n+1)} &= \frac{A_n r}{A_n + b} \\ A_{(n+1)} &= J_n. \end{aligned} \tag{4}$$

We now analyze the system (4), the fixed points are $(0, 0)$ and $(r - b, r - b)$.

2.1.1 Stability of Fixed Points

To determine the stability of the fixed points we calculate the Jacobian matrix

$$B(J, A) = \begin{pmatrix} 0 & \frac{r}{A+b} - \frac{Ar}{(A+b)^2} \\ 1 & 0 \end{pmatrix}.$$

So,

$$B(0, 0) = \begin{pmatrix} 0 & \frac{r}{b} \\ 1 & 0 \end{pmatrix}$$

we find the $\text{trace} B = 0$ and the $\det B = -r/b$. In accordance to the Jury test [1], determining the stability of a fixed point is as follows: $|\text{trace} B| < 1 + \det B < 2$; $0 < 1 + r/b < 2$, then the point is stable. Here, the fixed point $(0,0)$ is stable only for the case where $r < b$, resulting global population extinction (see Figure 1).

Linearizing about the fixed point $(r - b, r - b)$ we obtain the Jacobian

$$B(r, r) = \begin{pmatrix} 0 & \frac{b}{r} \\ 1 & 0 \end{pmatrix}$$

and we get the $\text{trace} B = 0$ and the $\det B = -b/r$. A

gain we use the Jury test to determine the interval of stability for this fixed point which is $0 < 1 + \frac{b}{r}$. The condition for stability of the fixed point $(r - b, r - b)$ is $r > b$, as a result the population survives but there is no population explosion (see Figure 2).

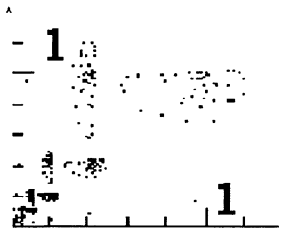


Figure 1: Trajectory graph where $r < b$.

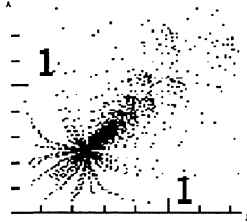


Figure 2: Trajectory graph where $r > b$.

2.2 Scramble competition: Ricker's model

If juveniles and adults are governed by Ricker's model in every two generations, system (3) reduces to

$$\begin{aligned} J_{(n+1)} &= A_n e^{r-A_n} \\ A_{(n+1)} &= J_n \end{aligned} \quad (5)$$

now we analyze system (5), the fixed points are $(0, 0)$ and (r, r) .

2.2.1 Stability of Fixed Points

To determine the stability of the fixed points we calculate the Jacobian matrix

$$B(J, A) = \begin{pmatrix} 0 & e^{r-A} - Ae^{r-A} \\ 1 & 0 \end{pmatrix}$$

Substituting each fixed point into the Jacobian to determine its stability:

$$B(0, 0) = \begin{pmatrix} 0 & e^r \\ 1 & 0 \end{pmatrix}.$$

By evaluating the Jacobian, one gets the trace equal to 0 and the determinant equal to $-e^r$. The eigenvalues of $B(0, 0)$ are $\lambda = \pm\sqrt{e^r} > 1$, thus, the fixed point $(0, 0)$ is unstable. We evaluate the Jacobian at the fixed point (r, r) and obtain

$$B(r, r) = \begin{pmatrix} 0 & e^0 - re^0 \\ 1 & 0 \end{pmatrix}.$$

One gets the trace $B = 0$ and the det $B = r - 1$. The eigenvalues are thus $\lambda = \pm\sqrt{1-r}$.

By the Jury test of stability, if $|\text{trace}B| < 1 + \det B < 2$, that is, if $0 < 2 - r < 2$, the point is stable. Thus if $0 < r < 2$ the fixed point (r,r) is stable (see Figure 3). If $r = 2$ $B(r,r)$ has an eigenvalue equals -1 , a signature for Hopf bifurcation. Figure 2 shows Hopf bifurcation in system (5) as we vary r . System (5) supports multiple attractors with fractal basin border (refer to Figure 4 and 5).

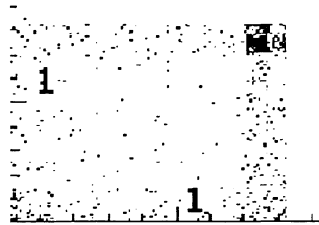


Figure 3: Trajectory graph where $0 < r < 2$.

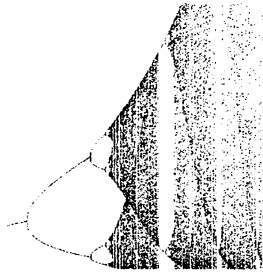


Figure 4: Hopf bifurcation diagram.

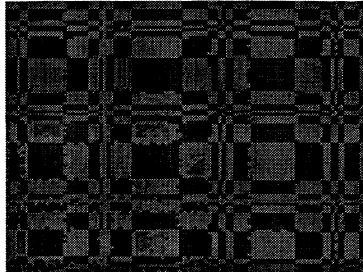


Figure 5: Basin of attraction when $r = 2.7$, with 2 coexisting chaotic attractors.

3 Two Patch Systems

3.1 Contest-Contest competition

Now, we study the impact of dispersal in a two patch model with subpopulation under contest-contest competition.

Let d_1 and d_2 be the dispersal rate of the first species and d_3 and d_4 be the dispersal rate of the second species characterize by (A_1, J_1) and (A_2, J_2) respectively. Where r_1 and r_2 are the carrying capacity of population for the first and second species respectively and b_1 and b_2 are the growth speed ratio's for the first and second species. The equation for the contest-contest competition is given by

$$J_1(n+1) = (1-d_1) \frac{A_1(n)r_1}{A_1(n)+b_1} + d_2 \frac{A_2(n)r_2}{A_2(n)+b_2} \quad (6)$$

$$A_1(n+1) = (1-d_3)J_1(n) + d_4J_2(n)$$

$$J_2(n+1) = (1-d_2) \frac{A_2(n)r_2}{A_2(n)+b_2} + d_1 \frac{A_1(n)r_1}{A_1(n)+b_1} \quad (7)$$

$$A_2(n+1) = (1-d_4)J_2(n) + d_3J_1(n)$$

For the single patch system we were able to determine the fixed points and find there stability mathematically. A graphically analysis is considered for our two-patch system under contest-contest competition.

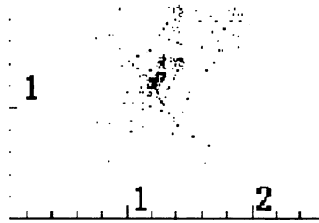


Figure 6: Trajectory graph where $r > b$, symmetric dispersal.



Figure 7: Trajectory graph where $r > b$, asymmetric dispersal.

As shown above in Figure 6 and 7, contest-contest competition is similar to single contest competition. The dynamics is locally stable fixed point, when $r > b$ with symmetric and asymmetric dispersion, the population survives without explosion. Similar to single contest regime for $r < b$ the population goes extinct. The coupling of one dying and one living patch result a rescue effect, that is population in patch decreases while population in patch two increases (look at Figure 8).

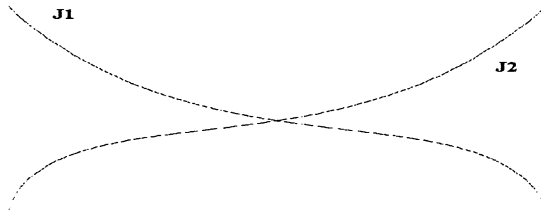


Figure 8: Rescue Effect

3.2 Scramble-Scramble competition

In this section, we study a two-patch population with dispersal that is modeled in accordance with the Ricker's equation.

Let d_1 and d_2 be the dispersal rate of the first species, d_3 and d_4 be the dispersal rate of the second species characterized by (A_1, J_1) and (A_2, J_2) respectively. Where r_1 and r_2 are the reproduction rate for both populations respectively. The Ricker's equation for the scramble-scramble competition is given by

$$J_1(n+1) = (1-d_1)A_1(n)e^{r_1-A_1} + d_2A_2(n)e^{r_2-A_2(n)} \quad (8)$$

$$A_1(n+1) = (1-d_3)J_1(n) + d_4J_2(n)$$

$$J_2(n+1) = (1-d_2)A_2(n)e^{r_2-A_2(n)} + d_1A_1(n)e^{r_1-A_1(n)} \quad (9)$$

$$A_2(n+1) = (1-d_4)J_2(n) + d_3J_1(n).$$

3.2.1 Graphical Analysis of Scramble-Scramble competition

As shown in section[2], for the single species we were able to calculate fixed points and stability mathematically. However, in this section a graphical analysis of our system is more efficient. Denoting P_1 and P_2 the population of both species respectively, we produce a graphical analyzation of the effects of dispersion.

First, we consider two local patches under scramble competition regime, where both patches are on stable period four cycles (without dispersal). With

sufficiently large symmetric dispersal between the two patches, the metapopulation follows the local dynamics and lives on a period four cycle.

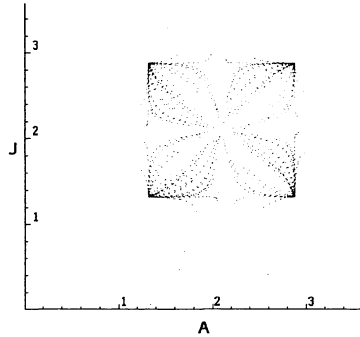


Figure 9: Period-4 Trajectory for P_1

When the dispersal rate from Patch 2 to Patch 1 is fixed while we increase the dispersal rate from Patch 1 to 2, a remarkable bifurcation occurs. The metapopulation has a positive fixed point while the local dynamics live on period four attractors.

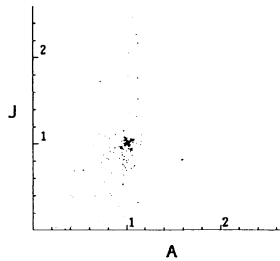


Figure 10: Trajectory graph for P_1 at fixed point.

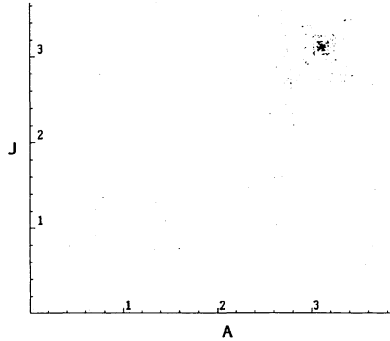


Figure 11: Trajectory graph for P_2 at fixed point.

Local patches governed by Rickers's Model have two coexisting chaotic attractors with fractal basin boundaries of attraction whenever $r = 2.7$ and there is no dispersal.



Figure 12: Basin of Attraction for a Single Patch at $r = 2.7$

With symmetric dispersal, the metapopulation follows the single patch dynamics and has two coexisting chaotic attractors with fractal basin boundaries. However, the metapopulation dynamics is on a fixed point whenever the dispersal rate from one patch to another is high. In other words, dispersion between two initially chaotic patches results in having much simpler dynamics. In our case, this occurs at $d1 = .7$ and $d2 = .1$

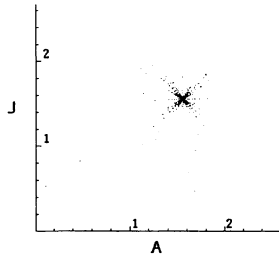


Figure 13: Trajectory graph of fixed point for P_1 chaotic attractor as local dynamics.

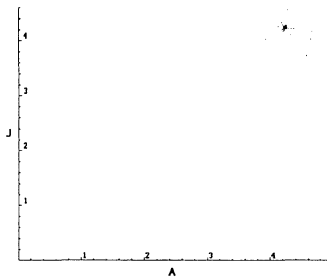


Figure 14: Trajectory graph of fixed point for P_2 chaotic attractor as local dynamics.

At intermediate values of dispersal rates, the metapopulation changes from chaotic dynamics to simple periodic dynamics. For example, at $d_1=4$, we have both patches experiencing four cycle dynamics.

3.3 Scramble-Contest competition

Now we study a two patch system that is modeled in accordance with the combination of the Verhulst's and Ricker's equations.

Denoting d_1 and d_2 as the dispersal rate of the first species, which is governed by the Ricker's equation, and d_3 and d_4 be the dispersal rate of the

second species, which is governed by the Verhulst equation, characterize by (A_1, J_1) and (A_2, J_2) respectively. Denoting r_1 and r_2 are the carrying capacity of population for the first and second species, and s_1 and s_2 are the fraction capacity of juveniles becoming adults for the first and second species respectively. The parameter b represents the growth speed ratio of the second species. The equations of motion for the scramble-contest competition is given by

$$J_1(n+1) = (1-d_1)A_1(n)e^{r_1-A_1(n)} + d_2 \frac{A_2(n)r_2}{A_2(n)+b} \quad (10)$$

$$A_1(n+1) = (1-d_3)J_1(n) + d_4J_2(n)$$

$$J_2(n+1) = (1-d_2) \frac{A_2(n)r_2}{A_2(n)+b} + d_1A_1(n)e^{r_1-A_1(n)} \quad (11)$$

$$A_2(n+1) = (1-d_4)J_2(n) + d_3J_1(n).$$

3.3.1 Graphical Analysis of Scramble-Contest competition

Denoting the population of first species, the scramble population, as P_1 and the population of second species, the contest population, as P_2 , we graphically examine the Scramble-Contest system.

First, we examine one-dimensional dispersion from P_1 to P_2 . We have previously found that if our initial value of the reproduction rate for P_1 is set to certain values our local dynamics becomes a period-4 oscillation. We couple a period-4 scramble population with a contest population where $r_1 > b$, i.e. a surviving contest population. It is noticed that as dispersal from P_1 to P_2 is increased both populations approach a stable fixed point. This fixed point occurs when the dispersal rate is greater than .5. We also couple a chaotic attracting scramble population with a surviving contest population. The value of the reproduction rate for the scramble population is 2.8. The characteristics of this coupling is similar to the previous example. Here, we move from a chaotic attractor (Figure 15) to a period-eight oscillation and so on until we reach a stable fixed point. Our stable fixed point also occurs when the value of the reproduction rate is greater than .5 (Figure 16). Generally, in the couple of scramble population, governed by the Ricker's model, and a contest population, governed by the Verhulst's model, with dispersion from the scramble population to the contest population, an increase of dispersion is equivalent to adjusting parameters and analyzing local dynamics for the scramble population. In this population the decrease of dispersal

has the same effect as increasing the reproduction rate in its local dynamics. The contest competition gains the ability to handle multiple attractors where as before it could not. Figure 17 shows the system dynamics as dispersion varies.

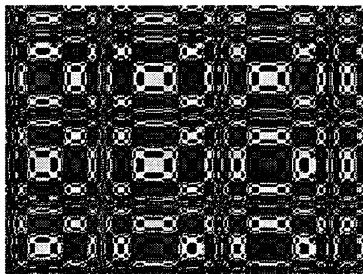


Figure 15: Basin of attraction for chaotic attractor.

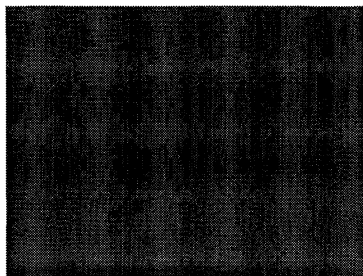


Figure 16: Stable fixed point at $d_1 = .51$

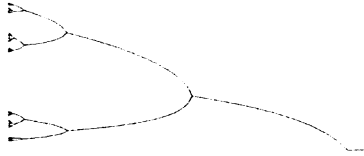


Figure 17: Bifurcation about d_1

Here, there is dispersal from the contest competition population P_2 into the scramble competition population P_2 . This dispersal effects the size of P_1 but not the actual periodic oscillations in P_1 . The competition population decreases when dispersal is introduced and dies out soon after.

Now we look at two-dimensional dispersion. First, we have the case of symmetric two-dimensional dispersal. Symmetric dispersals behaves the same as one way dispersal from P_1 to P_2 . As dispersals are increased symmetrically a stable fixed point is approached. Fixed points also occur for values of the dispersal rate greater than .5 (see Figure 15 and 16).

The introduction of asymmetric two-dimensional dispersion between P_1 and P_2 is similar to the introduction of symmetric dispersion. There is change in system dynamics as before, but there is a different range of dispersals in which the populations approach a fixed point. As seen in figure 18, which is a bifurcation about the dispersion from patch2 d_4 , while fixing the value of the dispersion from patch1 d_1 at .1, the system does not approach a fixed point. In figure 19 d_1 has been increased to .7. Now we see that the system approaches a stable fixed point.



Figure 18: Bifurcation about d_4 with $d_1 = .3$



Figure 19: Bifurcation about d_4 with $d_1 = .7$

4 Conclusion

Using our analysis of the two patch systems we can conclude:

- In a single patch system: contest intraspecific competition local dynamics show that the population at any initial condition can either die or survive, however in scramble regime under different variation of the reproductive rate either the population persists, or global stability, Hoft bifurcation, or multiple attractors with basin boundaries.
- In two-patch systems with dispersal the local dynamics for contest-contest competition are similar to those of a single patch contest regime if the reproduction rate (r) is either greater or smaller than the speed

ratio (*b*). However, we coupled one living patch with one dying patch and increase dispersal, the results show that population in patch one is decreasing and patch two are increasing. This effect is known as the "Rescue Effect".

- The Scramble-Scramble coupled dynamics show that dispersion rate can severely affect the dynamics of the system. If we couple two chaotic patches, and have an intense net dispersion rate from one patch to the other, both patches contain a fixed point. If the dispersion rate decreases, we can have both patches in period four cycles. Thus, as the dispersion rate decreases from one patch to another, both locally chaotic patches head toward stability.
- For the coupled Scramble-Contest system the addition of both one-dimensional and two-dimensional dispersal has an effect on the individual patches. Most importantly, we show that we are able to couple a scramble population, with local dynamics of periodic oscillations or a chaotic attractor, with a surviving contest population and find fixed points of the system for various values of dispersion. In such systems there are also cases where the contest population can handle periodic oscillations.

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