Maria Magdoń-Maksymowicz
Andrzej Maksymowicz

ON THE EVOLUTION OF MIGRATING POPULATION WITH TWO COMPETING SPECIES

Abstract
A computer experiment study of population evolution and its dynamics is presented for two competing species (A and B) which share two habitats (1 and 2) of a limited environmental capacity. The Penna model of biological aging, based on the concept of defective mutation accumulation, was adopted for migrating population. In this paper, we assume and concentrate on the case when only one species (A) is mobile. For isolated habitats and for any initial population, we get at equilibrium spatial population distribution (A, B) in which A occupies location '1' only, while B-species is the ultimate winner in '2'. This is achieved by suitable choice of model parameters so habitat '1' is more attractive for species 'A' while location '2' is more advantageous to 'B'. However, population distribution begins to differ when migration between habitats is allowed. Initially stable distribution (A, B), becomes (A, A&B) with a mixed stationary population in location '2'. For a higher migration rate, initial (A, B) distribution goes to (A, A) distribution, in which A species is dominant also in a less friendly habitat '2'. However, a further increase in migration rate brings sequence (A, B) → (B, B). In short, for sufficiently high mobility of A-species, they eliminate themselves. Other scenarios not discussed here were also studied. They offer a rich variety of different sequences of population distribution regarding their size as well as other characteristics.

1. Introduction

In a standard approach, the equilibrium population n in an isolated habitat of limited capacity N is considered. So, population n always is less then capacity N, $n < N$. Age a distribution of the population, $n(a)$, is often used as basic information on the population structure. An alternative characteristic is mortality $\Delta n(a)/n(a)$, the relative ratio of members at age a that are eliminated from population pool, which may be seen as overall health condition of the population. A stable solution requires that the death rate d must be balanced against the birth rate b. Population $n(t)$ at time t is first diminished by Δn, which brings the population down to $n(t) - \Delta n$ after the first stage of the evolution process which eliminates some members. The survivors give birth at rate b, which completes one computation cycle, repeated at each time step. This brings population $n(t)$ to the next time step population at time $(t + 1)$, $n(t + 1)$.

Within the simplest logistic model of population evolution, we assume the elimination rate $d = \Delta n/n$ is composed of two terms,

$$\Delta n/n = h + n(t)/N.$$

The first constant term h may be associated with being hunted or eliminated by accidents, fishing, etc. The other term, known as the Verhulst factor [1], describes a death rate that grows linearly with the current population $n(t)$, thus preventing unlimited population growth. The Verhulst term expresses a limited environmental capacity N. Death happens more frequently for larger populations $n(t)$, and it guarantees a maximum population size $n < N$. This model, when applied to $h = 0$, gives the population after Verhulst elimination as $n = n(t) - n(t) \cdot n(t)/N$. Then, reproduction increases the population at the next time step $(t + 1)$ to $n(t + 1) = n + n \cdot b$. This brings us to an iterative map, taking us from population $n(t)$ to population $n(t + 1)$

$$n(t + 1)/N = (1 + b) \cdot n(t)/N \cdot (1 - n(t)/N)$$

better known as the logistic equation. The oversimplified logistic case with just two parameters (b, N), is still of interest because it offers analytical results that are easy to interpret. At equilibrium $n(t + 1) = n(t)$, this yields the fix single stable solution

$$n/N = b/(1 + b)$$

for $0 < b < 2$. The single solution changes into a cyclic one for bigger $b > 2$ when, at each bifurcation, we get cycle doubling from a single solution of cycle one to cycle two at $b = 2$. A further increase in b brings another bifurcation and transition from cycle 2 to cycle 4 at $b = 2.449771$; then consecutive doublings with cycles $4{\to}8{\to}16$, takes place at $b{=}2.5443, 2.5645$. At about $b{=}2.569946$, we enter a deterministic chaos regime with unpredictable values of n/N. The logistic case may still be useful as a reference or test when more advanced models, for example the Penna model

described below, are considered. Then results of computer simulation should be reduced to the logistic case for a suitable choice of the model parameters. The main criticism of the logistic model comes from the fact that it predicts unacceptable mortality at age a, the elimination rate $m(a) = \Delta n(a)/n(a)$, as age a-independent. This is far from the observed Gompertz law that claims exponential growth of mortality $m(a)$ with age,

$$m(a) = \Delta n(a)/n(a) = m(0) \cdot e^{ka}$$

for moderate ages a. The $m(a)$ dependence is explored by institutions such as insurance companies to estimate your expected survival time when you have had already reached age a. Better modeling of population evolution leads to alternative mechanism of biological aging and an individual's elimination. A review of some models and theories on biological aging and population evolution can be found in Stauffer et al. [2]. From the many suggested reasons for aging (oxygen free radicals, telomere shortening, accumulation of bad mutations, etc.), we concentrate on the Penna model [3, 4] which accounts for genetic death due to harmful mutations.

The competition aspect is widely studied; perhaps the best-known example is the Lotka-Volterra model [5, 6]. In a sense, it may be seen as a generalization of the standard logistic model by placing the two species in competition within a limited habitat. The logistic model parameters (b, N) now gain subscripts on the species and the effective capacity N depends on relative population sizes. The Lotka-Volterra model, for typical set of parameters, usually brings one of the species to extinction. The coexistence steady state is obtained if two species are at a low competitive mode. Another paper [7] of Ngoc et al. brings migration between locations, each governed by the Lotka-Volterra model. Asymmetric migration is considered, and a rich dynamic gives many outcome diagrams of the spatial structure of population. As mentioned earlier, in order to get an observed *age*-dependent mortality $m(a)$, it is necessary to go beyond models with *Verhulst* elimination mechanisms only. The Penna model, briefly described in the next section, offers expected $m(a)$ dependence. The Penna model of bad-mutations accumulation, however, lacks an analytical solution – apart from a very limited case of a single mutation threshold that kills. The Coe ([8]) et al. analytical results of the Penna model were also obtained in our earlier simulations [9]. Competition within the Penna model in a restricted habitat was studied in [10, 11]. The main result is essentially the same as in the Lotka-Volterra models. One species is the survivor, and the winner is the one with higher fertility b or lower bad mutation rate M. The values of M's *versus* b's control which species is favored. We want to enrich the model by introducing two competing species $S = A, B$ in a limited environment. Two locations $L = 1, 2$ of different characteristics are considered, and we allow for migration in between the habitats. A combination of competition and migration may bring new aspects to the problem of stable population structure and distribution.

2. Model of population evolution and its dynamics

In the simplest asexual version of the Penna model of bad mutations accumulation, two more model parameters are introduced: bad mutation rate M and threshold value T of resistance to active bad mutations. So now, we have a set of (b, M, T, N) model parameters. The advantage of the Penna model is the fact that it yields the correct age dependence of mortality $m(a)$, as given by the Gompertz exponential law. However, the Penna model was not solved analytically, and only a computer simulation makes the study of the model possible (with the exception of one special case of $T = 1$ when an analytical solution was obtained). Each individual in the population pool, labeled by index i, is characterized by age a and its genome represented by a bit-string with bit 1 at bit position (loci) which has bad mutation. Genetic death takes place when the number of active mutation of the i-th individual reaches threshold value T, $\mu(a) = T$, where $\mu(a)$ is the sum of bit 1 from bit position $q = 0$ to bit position $q = a$. In the computer experiment, we execute in the asexual version of the Penna model the following algorithm at each time step t:

- calculate current Verhulst factor $n(t)/N$,
- scan the population and eliminate each item with probability $n(t)/N$,
- if it survives, check for $\mu(a) = T$ to apply genetic death,
- if the item still exist, give birth at rate b, then
- child inherits parent's genome with M extra bad mutations per bit,
- increase item's age $a \rightarrow a + 1$ and time $t \rightarrow t + 1$.

With genetic death at age a at which $\mu(a) = T$, the life span of the individual is determined by the position q of the first critical bad mutation on genome. Still, death at an earlier age may be due to the Verhulst factor or any other mechanism of elimination. At every time step from time $t \rightarrow (t + 1)$, we scan the population and each individual is considered for possible elimination. If an individual survives, it gives the birth at rate b, and offspring with age $a = 0$ inherit its parent's genome - the parent's genome remains intact. The offspring is subject to extra mutations spelled over its genome randomly at a small rate M (per bit). After all members of the population are scanned, we complete the time loop step $t \rightarrow (t + 1)$. Obviously, only individuals without too many mutations $\mu(a)$ may produce enough offspring to sustain the population. Bad mutations at positions q above the critical q_c value, $q > q_c$, are irrelevant. So it leads, after the many iterations, to bad mutation accumulation at high bit positions which brings the idea of immortality to an impossibility.

A basic evolution algorithm is shown in Figure 1. The above algorithm, when applied to an isolated habitat and for an assumed set of model parameters (b, M, T, N), yields output population size, age-distribution of the population (for example, to see whether the Gompertz law is fulfilled), and other characteristics of the population at equilibrium. In a standard approach, a stable solution in an isolated system is discussed.
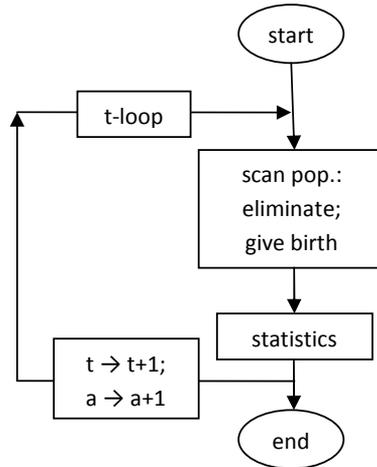
Figure 1. Basic flowchart of population dynamics simulation.

3. Algorithm of the simulation

In this paper, we consider 2 competing species A and B operating in two locations; '1' of environmental capacity N_1 and '2' of capacity N_2. We allow for possible migration between habitats. The set of model parameters was split into two categories; *species dependent* birth rate b and threshold T, then *habitat dependent* mutation rate M and environmental capacity N. We applied four sets of parameters (b, M, T, N) for 2 species $S = A, B$ and 2 locations $L = L_1, L_2$ specifically chosen so as to introduce handicapped conditions for one species A in the first location, while the other location should be advantageous to the other species B. We intend to study the effect of migration of, say, A-species. Would a coexistence with a mixed population be established in any of the habitats? The set for species A of high fertility b and low resistance T to illness meets a low mutation rate M in habitat '1' and a higher bad mutation rate in '2'. Species B has low fertility b, and B has a higher immunity to disease. The two species A and B are merged into 2 habitats: '1' of low bad mutation rate M and '2' of high mutation rate. The intensity of migration is controlled by one more parameter p, the probability of individuals migrating to the other habitat. All detailed information on input parameters (b, M, T, N) and p, initial population, conditions for termination of the iteration procedure, a list of several scenarios of the migration, how statistical data was collected, and other crucial (for computer people) details are offered in the next section. The flowchart of how population evolution was executed for this model with a migrating population is presented in Figure 2.

As mentioned in the previous section, we are studying two competing species (races or types) $S = A, B$, merged into one of two locations (habitats), $L = L_1, L_2$ –
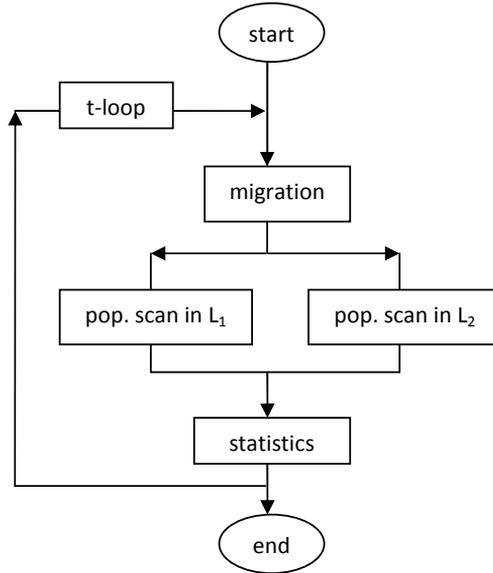
Figure 2. Flowchart of simulation for population dynamics with migration.

each of limited environmental capacity N_1 and N_2, respectively. Therefore, the set of (b, M, T, N) Penna model parameters, where

- b is the birth rate,
- M is bad mutation rate per bit, randomly spelled over newly born,
- T is critical number of activated bad mutations $\mu(a)$ that kills at age a,
- N is environmental capacity so that population is limited, $n < N$,
- p is the probability of the transfer of an item into the other location.

We split the components of the (b, M, T, N) set of parameters into species S-dependent and habitat-dependent ones. We propose b and T as characteristic to species, and we adopt the following values for simulation:

- $(b, T) = (0.25, 1)$ for $S = A$,
- $(b, T) = (0.20, 8)$ for $S = B$.

As it is seen, the more-fertile A species has a lower threshold T to genetic bad mutations compared to the B species that is less productive in terms of offspring. It is hard, therefore, to anticipate which species would take over in the limited and isolated habitat. Then, m and N are assumed to be location dependent,

- $(M, N) = (0.01, 1)$ for $L = 1$,
- $(M, N) = (0.04, 3)$ for $L = 2$.

The proposed parameters were carefully established to achieve the intended effect for isolated systems $p = 0$. We try to make species A dominant in location $L = 1$. A combination of high fertility b and low resistance T to illness, plus a low risk of bad

mutation M in $L = 1$, makes it is even more advantageous than the complementary combination of the parameters for the competing species B. As a result, only species A occupies the whole space in habitat '1'. This equilibrium is obtained for any initial ratio of A and B species. The opposite effect is reported in habitat '2' of higher bad-mutation rate. Here, B is the winner. In short, starting a simulation with any mixture of two species in two isolated habitats, we get at equilibrium separated species A in $L = 1$ and B in $L = 2$. Population n/N and any characteristics comply with the Penna model, yielding different characteristics of the population at equilibrium, corresponding to the assumed sets of the model parameters in each location. The results for $p = 0$ serve as a reference case for the study of how migration affects population characteristics. For the above set of parameters, we get

- $n/N = 0.167$ for species A in habitat '1', while logistic $n/N = b/(1 + b) = 0.200$,
- $n/N = 0.108$ for species B in habitat '2', while logistic $n/N = b/(1 + b) = 0.167$.

The two same values of $n/N = 0.167$ for the logistic model are accidental. It should be noticed that the Penna model always gives a smaller n/N for a stable population. This tendency is expected since, apart from the Verhulst elimination mechanism, we also account for genetic death in the Penna model. In typical runs, we need about 10^4 iterations to reach equilibrium when all monitored population characteristics (age distribution of the population, frequency of bad mutations 1 along bit string representing genome, and other characteristics) are stable, apart from statistical fluctuations. The final thousand or so last iterations are recorded to extract configuration averages of any monitored output data. The $N = 1$ environmental capacity is equivalent to memory size, which is able to accommodate about 10^8 members of the population at each location. We may increase the accuracy of calculation for larger N; the chosen N is a reasonable compromise between a higher accuracy of calculations and still-acceptable computation time.

When migration is taken into account, $p > 0$, we need to be more specific about how the migration takes place and how it is controlled. Several basic scenarios may be considered. For simplicity's sake, we assume that only the A species may migrate. We concentrate on a "one-way-ticket" migration policy in which a member of the A species moves from location $L = 1$ to $L = 2$ with probability p at each iteration time step. Examples of a few migration schemes between habitats i, j, with $i \neq j$, are listed below:

- "one way ticket" described above, $p = p(1 \rightarrow 2) = p(1, 2)$,
- "return visa" if A migrates between $L = 1, 2$ with same $p = p(i, j) = p(j, i)$,
- "cautious migrant" with p replaced by an effective $p_{eff}(i, j)$,

where $p_{eff}(i, j)$ is the $p(i, j)$ value modified by a factor that accounts for full or partial information available to the migrant on, for example, how much living space is left in the target destination and/or in the location from which the item is to move away. Details on how $p_{eff}(i, j)$ may be constructed will not be discussed here, as we intend to study only the simplest "one-way-ticket" basic scheme in this first approach. Some proposed $p_{eff}(i, j)$ may be found in our earlier work [12]. For instance,

$p_{eff}(i \rightarrow j) = p(i, j) \cdot (1 - n(A, j)/N_j)$ may describe the tendency to avoid migration if there is less free space in the target habitat. Here, $n(A, j)$ is the population of A-species in location j and the $(1 - n(A, j)/N_j)$ factor reduces the probability $p(i, j)$ of migration.

4. Results

For **no migration case**, $p = 0$, the sets of parameters (b, M, T, N) and initial data the same as indicated and used in the previous section, we always recover Penna model results for isolated systems. Species A is present in habitat $L = L_1$ while in $L = L_2$ species B is the only one. In terms of normalized to unity partial population $n(S, L)$, we get

- $n(A, 1)/N_1 = 0.167$ for $p = 0$,
- $n(B, 1)/N_1 = 0.000$ for $p = 0$,
- $n(A, 2)/N_2 = 0.000$ for $p = 0$,
- $n(B, 2)/N_2 = 0.108$ for $p = 0$.

Experimental demographic data on age distribution $n(a)$ of the population, or its other presentation in terms of mortality $\Delta n(a)/n(a)$, matches the Gompertz exponential law $\Delta n(a)/n(a) = m(0) \cdot e^{ka}$ valid for moderate ages a. A computer simulation of the Penna model confirms this distribution, see Figures 3.
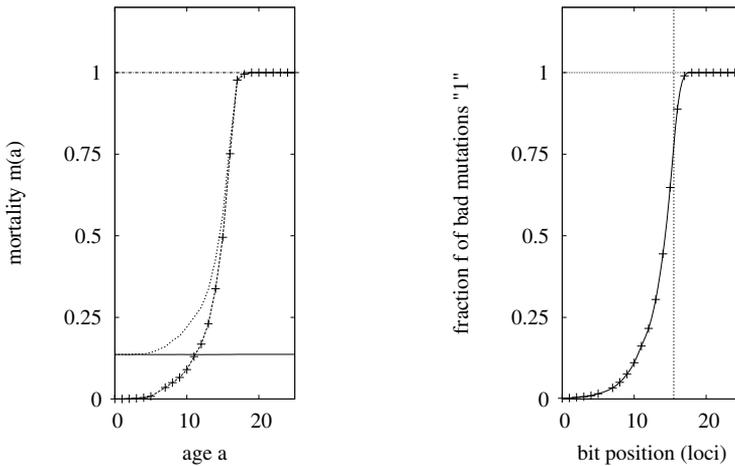

Figure 3. Age a distribution of mortality and mutation distribution on a genome.

Mortality may be split into two components; a constant component attributed to the Verhulst elimination, and a genetic death component (which is nearly zero for the youngest members yet rapidly grows for older members). Total mortality is roughly the sum of partial contributions. Life span is determined by the age a at which mortality $m(a)$ reaches 1. A complementary distribution of activated mutations with

age, or bit position (in the Penna model the genome, represented by a bit string, is read out bit by bit with age) is also seen in Figs.(3). It shows the essence of the bad mutation accumulation model where frequency of mutation grows with a.

For the **one way ticket** migration with $0 < p < p_1 = 0.001$, the A species move from location L_1 to L_2. Then population $n(A, 2)$ of emigrants A in location $L = 2$ grows linearly as it is shown in Figure 4. We have

- $n(A, 1)/N_1 = 0.167$ for $0 < p < p_1$,
- $n(B, 1)/N_1 = 0.000$ for $0 < p < p_1$,
- $n(A, 2)/N_2 = 0.108 \cdot p/p_1$ for $0 < p < p_1$,
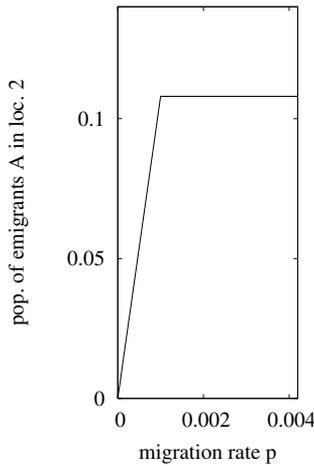- $n(B, 2)/N_2 = 0.108 \cdot (1 - p/p_1)$ for $0 < p < p_1$.

Figure 4. Population $n(A, 2)$ of A species in location 2 *versus* migration rate p.

Population $n(A, 1)/N_1 = 0.167$ stays the same, as losses due to migration are fully compensated by a high reproduction rate (which results in the free living space created by migration to be filled by newborns). Species B is repelled by A. In location $L = 2$, the emigrant population grows linearly with p as a result of a continuous supply of newcomers at a constant rate. The limited capacity of habitat $L = 2$ results in a decrease of population in species B, so the total population in habitat $L = 2$, $n(2) = n(A, 2) + n(B, 2)$ remains much the same. At $p = p_1 = 0.001$, population $n(A, 2)$ is saturated and population $n(B, 2)$ is extinct. A further increase in p brings no changes until another critical $p = p_2 = 0.020$.

For **p1 < p < p2 = 0.02** of more intense migration, we get a saturation

- $n(A, 1)/N_1 = 0.167$ for $p_1 < p < p_2$,
- $n(B, 1)/N_1 = 0.000$ for $p_1 < p < p_2$,
- $n(A, 2)/N_2 = 0.108$ for $p_1 < p < p_2$,
- $n(B, 2)/N_2 = 0.000$ for $p_1 < p < p_2$.

which describes a situation in which emigrants A in $L = 2$ take over territory $L = 2$ as result of a combination of two factors: a) high reproducibility, and b) a constant influx of its own species from $L = 1$. Simultaneously, the high reproduction rate of A in its native habitat $L = 1$ makes it possible to catch up with the losses due to massive migration. However, for a more-massive migration, $p_2 < p$, the final population distribution becomes unexpectedly reversed, with B species as overall survivals,

- $n(A, 1)/N_1 = 0.000$ for $p_2 < p$,
- $n(B, 1)/N_1 = 0.137$ for $p_2 < p$,
- $n(A, 2)/N_2 = 0.000$ for $p_2 < p$,
- $n(B, 2)/N_2 = 0.108$ for $p_2 < p$.

This time, the quick migration and outflow of A species from its habitat $L = 1$ makes the $n(A, 1)$ population very small soon after the initial fifty-fifty division of the environmental space between A and B. This is crucial for competing B in $L = 1$, and now B wins. All of the available space is now occupied by the B species, and the equilibrium 0.137 value (less than 0.167 population of A for the former case of moderate p reflects the relevant set of (b, M, T) parameters in this case. The situation in the $L = 1$ habitat holds serious consequences for the A-species in $L = 2$ location, where no longer a diminished supply of emigrants helps to keep up its population in the $L = 2$ environment. As a result, B species, which were dominant in $L = 2$ for $p = 0$, win in both habitats. A sketch of the space distribution in the two habitats ($L = 1$ is the leftmost one, $L = 2$ the rightmost) are disclosed in Figures 5 and 6. Actually, we used different capacities at the two locations, $N_2 = 3 \cdot N_2$. In short, we have the two-species-occupation distribution as follow:

- (A, B) in locations (1,2) for $p = 0$,
- $(A, A\&B)$ in locations (1,2) for $0 < p < p_1 = 0.001$,
- (A, A) in locations (1,2) for $p_1 < p < p_2 = 0.020$,
- (B, B) in locations (1,2) for $p_2 < p$.

So far, we discussed the one-way-ticket migration scheme. At the end of the results section, let us offer as a final touch how linear dependence of the $n(A, 2)$ as function of p is changed for a "return-visa" migration, see Figure 7.

Deviation from linearity is clearly seen. A smaller population of emigrants $n(A, 2)$ is expected since the population is reduced by the re-migrants that return to location $L = 1$. The deviation is significant for bigger p; small values of p cannot induce significant backwash. The ratio of migrants from $L = 1$ to $L = 2$ is of order of p, while the ratio of those who undertake migration and then return is of order of $p \cdot p$, which, for small p, may be negligible.

5. Conclusions

We conclude that the final balance of how densely the two locations are occupied, and in which proportions of A or B species strongly depend on migration intensity controlled by the $p(1 \rightarrow 2)$ parameter. Two critical values, p_1 and p_2, obtained in
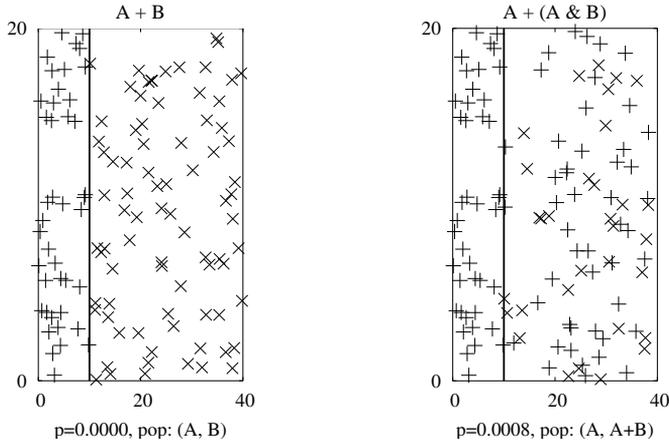
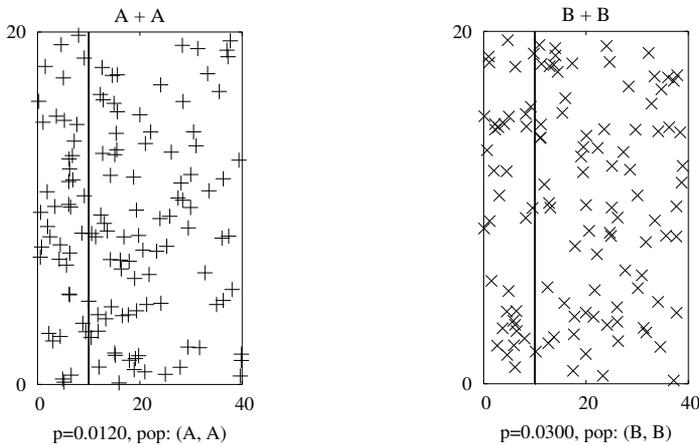**Figure 5.** Population distribution in locations 1, 2.

Figure 6. Population distribution in locations 1, 2.

numerical simulations, are rather sensitive with respect to the assumed values of birth rate b, probability of bad mutations M, and threshold T. With increasing p, we observe:

- for $p(1 \rightarrow 2) < p_1 = 0.001$, a dynamic equilibrium is reached with location L_2 shared by native B-species and emigrants A;
- for $p_1 < p(1 \rightarrow 2) < p_2 = 0.020$, a continuous supply of migrants in L_2 makes finally a takeover of the whole space by emigrants A;
- for $p_2 < p(1 \rightarrow 2)$, a rapid exodus of A makes L_1 free of species A and this time species B wins in both habitats (initial population consist of both A and B).
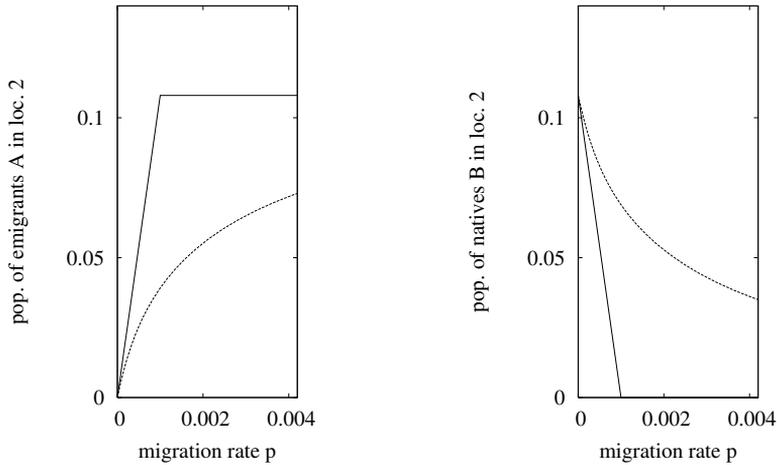
Figure 7. Population distribution in locations 1, 2.

The mobile A-species, if trying a more aggressive strategy of intense migration from location $'1'$ to the less-friendly habitat $'2'$, may lead to a rapid decrease of population of A in $'1'$, even leading to extinction of A-species. Then, the B-species take over and occupy both $'1'$ an $'2'$ locations. Critical values of p_1 and p_2 were obtained from computer simulations.

Acknowledgements

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Affiliations

Maria Magdoń-Maksymowicz

University of Agriculture, Krakow, Poland, `rrmagdon@cyf-kr.edu.pl`

Andrzej Maksymowicz

The School of Banking and Management, Krakow, Poland, `amax@agh.edu.pl`