

MIXED STRATEGIES AND NATURAL SELECTION IN RESOURCE ALLOCATION

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ABSTRACT. An appropriate choice of strategy for resource allocation may frequently determine whether a population will be able to survive under the conditions of severe resource limitations. Here we focus on two classes of strategies allocation of resources towards rapid proliferation, or towards slower proliferation but increased physiological and environmental maintenance. We propose a generalized framework, where individuals within a population can use either strategy in different proportion for utilization of a common dynamical resource in order to maximize their fitness. We use the model to address two major questions, namely, whether either strategy is more likely to be selected for as a result of natural selection, and, if one allows for the possibility of resource over-consumption, whether either strategy is preferable for avoiding population collapse due to resource exhaustion. Analytical and numerical results suggest that the ultimate choice of strategy is determined primarily by the initial distribution of individuals in the population, and that while investment in physiological and environmental maintenance is a preferable strategy in a homogeneous population, no generalized prediction can be made about heterogeneous populations.

1. Introduction. Interactions with resources often determine much of the dynamics of any population, since there are no unlimited resources available to any population, and since it is successful competition for the resource that will determine, whether individuals will be able to survive and reproduce. This consideration in turn raises a question of optimizing resource allocation strategies for fitness maximization under the constraint of different selective pressures that the population may be experiencing at each point in time. The two strategies that can be adopted by different species in response to different selective pressures that come from their environment are either to invest the resources into rapid proliferation, which has

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been suggested to be the preferable strategy in unstable environments, or into physiological maintenance and increasing environmental carrying capacity at the expense of rapid proliferation, which would allow maximizing fitness in more stable conditions [8, 19, 24]. The main criticism of this theory came from empirical studies: however intuitive the heuristic may seem, the adaptations that were predicted by either selective strategy were simply not observed in nature [28, 29, 30, 33].

The models that were used to make predictions about what environmental conditions could lead to the dominance of either type of resource allocation strategy often make the simplifying assumption of population homogeneity, or at least a level of heterogeneity that would not affect the dynamics of the overall system, since the choice of the dominant strategy is typically assumed to be determined solely by the environment (for a review of the existing theoretical models see [26]). This assumption may be valid if there is sufficient evidence to believe that the process that is being observed and described takes place on a sufficiently slow time scale, so that natural selection will simply have had no time to have any serious effect on population dynamics. In this case the assumption of homogeneity is a reasonable enough simplification. Otherwise, it is reasonable to believe that competition between individuals within the population poses as much, if not more selective pressures on the entire population than do interactions with the resources. That is, other members of the population are just as big a part of the environment as the resource, and if the population composition is changing, so can the final outcome of the individuals' interactions. However, this important aspect of population dynamics becomes buried under the assumption of homogeneity.

Examples of population heterogeneity and intra-species interactions driving the population towards one or the other strategy can be observed in many systems and on many levels of selection.

On the molecular level, Voytek and Joyce [32] reported that continuous *in vitro* evolution can be observed as 2 different species of RNA enzymes are made to compete against each other for common limited resources (in this case substrates). In the described experiment, the substrates were necessary for amplification of RNA. The authors observed that as the system evolved, so did the enzymes, whose biochemical characterization revealed distinct differences in their strategies: enzymes that invested in being efficient rather than proliferative, reacted with the substrate nearly hundredfold faster than the other; highly proliferative selected enzymes, while not as reactive, produced 2-3 times more progeny.

Elser et al. [9] investigated the question of resource management at the cellular level, looking particularly at competition for the common resource among different types of tumors. The authors found that in some tissues, such as in colon and lung, the microenvironment seems to promote selection of most rapidly proliferating clones, while conditions in other organs may favor the clones with lower mortality rate. This suggests that even within the same patient, different microenvironmental conditions in different organs might favor evolution of the overall tumor composition towards different strategies. This, of course, is only possible in the case of sufficient tumor heterogeneity, i.e., the fact that tumors are composed of populations of genetically diverse cells [12, 21, 31] that in addition to competing for the common resources also impose selective pressures on each other.

Another example of selection on the cellular level has been demonstrated in the work done by Chikatsu et al. [4]. The authors studied two types of rat embryo fibroblasts and were able to observe that not only did conditions in the culture

affect selection in cell clones with respect to growth strategy but also that presence of one type of clones affected fitness of another type of clones under the same environmental conditions.

On the organismal level, distinct resource allocation strategies have been observed to emerge in unicellular organisms like bacteria. Deneff et al. [7] observed that in natural acidophilic biofilm communities two genotypic groups of *Leptospirillum* bacteria are unequally represented in the bacterial population during different stages of colonization. At the early stages of colonization, the environmental resources (compatible solutes) are allocated primarily towards osmoprotection (physiological maintenance at the expense of rapid proliferation), while in the successive stages more resources are allocated for metabolism and increased fecundity. The importance of intra-species variation and its effects on biodiversity has also been documented in multicellular organisms, such as forest trees [5], malaria mosquitoes [27], hylid frogs [1], Eurasian badgers [20], as well as in human social ecological systems [10].

In this paper we construct and study a consumer-producer type model based on two models previously proposed in [17], where the individuals within a population differ in their choice of what proportion of the common renewable resource is allocated for rapid proliferation, or for increased physiological and environmental maintenance achieved at the expense of rapid proliferation, in order to investigate the question of whether either strategy can become intrinsically dominant if a heterogeneous population is allowed to evolve over time. In order to investigate these questions, we turn to two models proposed by Krakauer et al. [17], where the authors look at a large number of competitor species interacting with a single, collectively constructed niche from the point of view of life history trade-offs. That is, they assume that time and energy that is invested by the species, or individuals within a single species, in increasing the common environmental carrying capacity (the 'common niche') is subtracted from time and energy invested in proliferation. From an evolutionary point of view, one should not expect evolution to select for individuals that invest in increasing environmental carrying capacity, since immediate benefits of 'fecundity construction' are larger. This conundrum is referred to as 'construction dilemma'. The authors investigate both models of niche and fecundity construction and conclude that niche construction can be selected for if the species are allowed to actively monopolize their niche. In this paper we construct a joined model based on the two models of niche and fecundity construction proposed by Krakauer et al. [17] in order to investigate whether 'construction dilemma' can be resolved not through niche monopolization but solely through introduction of sufficient population heterogeneity. We use the model to address the questions of strategy selection under the conditions of both resource availability and limitation, and consider a possibility of resource over-consumption by individuals within the populations. We hypothesize that one cannot predict which strategy will come to dominate over time without understanding both the rules that govern the dynamics of the system and knowing the initial composition of the population.

It is important to note that the purpose of this work is not to test what birth, death, competition or any other rates would render either strategy more or less optimal for maximizing the populations fitness when consuming a dynamic resource, or to provide a case study for a specific biological system. Instead, we want to construct a conceptual theoretical framework, where we investigate how the distribution of individuals that can adopt different strategies evolves over time depending

on the initial state of the system. The asymptotic distribution will show what strategy (if any) will be selected in the process of natural evolution of the system. The resulting insights can then be fine-tuned and applied to more specific biological, social or economical systems.

This paper is organized as follows: first the formulation of the mathematical model is given. Then, a parametrically homogeneous system is analyzed in order to identify the possible dynamical regimes of the model. Next, parametric heterogeneity with respect to strategy choice is introduced. The resulting infinitely-dimensional system is then reduced to low dimensionality using the Reduction theorem [14, 15]. The changes in population composition over time are investigated numerically under the assumption of different initial distributions of individuals within the population with respect to strategy choices. The paper concludes with a discussion of results and conclusions.

2. Model Description. Consider a population of individuals $x(t)$, whose survival and proliferation are dependent on their ability to colonize and exploit common collectively constructed 'niche' z . Within the frameworks of the proposed model, 'niche' is considered to be an abstract generalized 'extrinsic resource', which can be used by each individual either for increased proliferation (denoted here as r-strategy for rapid proliferation) or for increased physiological and environmental maintenance (denoted here as s-strategy for slow proliferation). Each individual is assumed to also possess some kind of abstract 'inner resource', such as time, energy, or in case of financial systems, money, than can be converted to the 'extrinsic resource'. An example of such a situation could be an ant colony, where individual ants spend time and energy on constructing the collective nest; another such example could be beavers building dams.

The dynamics of $z(t)$ is determined by a natural restoration rate γ and decay/loss rate $\delta z(t)$, which can be interpreted as loss, or natural decay of the extrinsic resource, such as the damage that is done to the beaver-constructed dam as a result of natural processes. Resource utilization and restoration is accounted for by the term $e(1-c)\frac{x/z}{1+x/z}$, where the common extrinsic resource is restored proportionally to each individual's investment. Parameter e accounts for inter-conversion of each individual's 'intrinsic' resource to commonly available 'extrinsic' resource. Noticeably, in the case when $c \geq 1$, one can observe resource over-exploitation, i.e., a situation, when an individual consumes more of the common resource than they invested in it; within the frameworks of the proposed model, such individuals are referred to as over-consumers; their importance will be discussed later in the paper.

In order to enable us to investigate how different strategies can be selected over time, let us introduce parameter $\alpha \in [0, 1]$, which is intrinsic to each individual $x(t)$ (from now on denoted as $x_\alpha(t)$) and which represents the probability with which an individual uses either r-strategy, used with probability α , or s-strategy, used with probability $(1 - \alpha)$, for resource allocation. By construction, the closer α is to zero, the more likely the individual is to use r-strategy for resource allocation, and the larger the value of α , the more likely they are to use s-strategy. Since in this model formulation, the only difference between the individuals is the value of parameter α , we find it appropriate to refer to them as α -clones.

When $\alpha = 0$, each individual of this clone type use the available resources for rapid proliferation; the per capita growth rate is described by $r(c_2 \frac{z}{N+z} - \phi)$, where ϕ is the individuals average death rate, $N(t) = \int_\alpha x_\alpha d\alpha$ is the total population size,

and where population growth is proportional both the current population size and the amount of total available extrinsic resource.

When $\alpha = 1$, each individual of this clone type uses available resources for physiological and environmental maintenance at the expense of rapid proliferation. In this case, the per capita growth rate is described by the functional form $r(c_1 - \frac{bN}{kz})$, where the carrying capacity is not constant but is rather determined by the currently available amount of $z(t)$. If the individual uses both strategies with the probabilities α and $(1 - \alpha)$ respectively, i.e., uses some of the “extrinsic resource”, for rapid proliferation and some for physiological maintenance, which is more realistic than using just one pure strategy, then the per capita growth rate of each α -clone is

$$\alpha r(c_1 - \frac{N(t)}{kz(t)}) + (1 - \alpha)(\frac{c_2 z(t)}{N(t) + z(t)} - \phi).$$

The dynamics of the resource are determined by a natural restoration rate γ and decay/loss rate $\delta z(t)$. Consumption-restoration process is accounted for by the term $e \frac{N(t)(1-c)}{z(t)+N(t)}$. It is assumed that each individual attempts to restore e units of resources per unit time, which is mitigated by spatial limitations and intra-population competition, accounted through $z(t) + N(t)$. One can also view this fractional relationship is in terms of mass action law, or ratio-dependence, i.e. as $e(1-c) \frac{N/z}{1+N/z}$. As the number of consumers x_{alpha} increases, the amount of resource z will increase or decrease depending on the value of the parameter $c \geq 0$.

For the purposes of initial analysis, let us first consider the case, when the parameter α is fixed, so that the entire population consists of a single α -clone. (It can be interpreted as follows: if natural selection has had sufficient time to act upon the population, the final outcome can be seen as there being an “optimal proportion” of each strategy within the population, if such a proportion exists). This assumption will be relaxed later in the paper.

In this case, $N(t) = x_\alpha(t)$, i.e., the population is monomorphic and homogeneous with respect to α . The resulting system becomes:

$$\begin{cases} \frac{dN}{dt} = rN(t)(\alpha(c_1 - \frac{bN(t)}{kz(t)}) + (1 - \alpha)(\frac{c_2 z(t)}{N(t)+z(t)} - \phi)), \\ \frac{dz}{dt} = \gamma - \delta z(t) + eN(t)(\frac{\alpha(1-c_1)}{N(t)+z(t)} + \frac{(1-\alpha)(1-c_2)}{N(t)+z(t)}). \end{cases} \quad (1)$$

The case, where $\alpha = 1$, was analyzed completely in [16]. The case, where $\alpha = 0$, is briefly discussed in the Appendix (this particular model loses biological relevance for $c_0 > 1$ because trajectories fall outside the positive quadrant for a wide range of initial values). The values of $z(t)$ are guaranteed to remain in the positive quadrant for $e > \frac{\gamma}{c_2 - 1 + \alpha(c_1 - c_2)}$.

3. Analysis. Bifurcation analysis performed on System (1) (see Appendix A) revealed seven possible topologically non-equivalent types of phase-parameter portraits in the positive half-plane (N, z) and $(c_2, c_1 > 0, \alpha \in [0, 1])$ -parameter space for different fixed values of parameters ϕ, e, γ, δ . Results are summarized in Figure 1, which schematically depicts three slices of $(c_2, c_1, \alpha \in [0, 1])$ - parameter portraits (Figure 1a-c) and respective phase (N, z) -plane portraits (see Figure 1,d).

First, we fix α and study the dynamics of the model with respect to variations of parameter c_1, c_2 , holding all other parameters in the system constant. In Domain 1 of the phase parameter portrait (when no over-consumption of the resource is

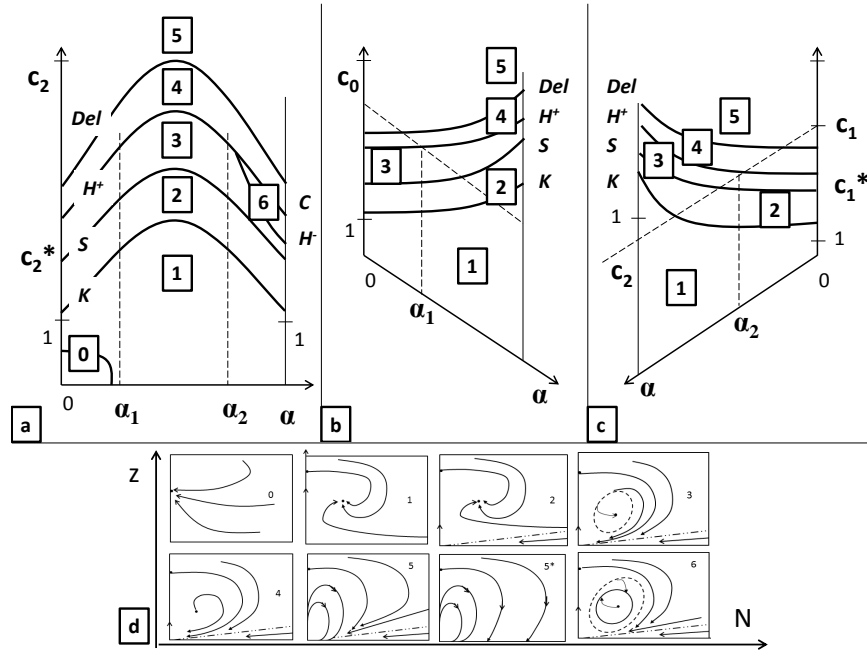


FIGURE 1. Bifurcation diagram of the System (1). (a),(b),(c) present schematically (c_1, c_2, α) parameter portraits for fixed values of $\gamma, \delta, e = 1$ and (d) represents the corresponding typical phase portraits. In Domain 1 there exists a non-trivial globally attracting equilibrium point A_α . Domains 2 and 6 are the regions of bistability; in Domain 2, there is a nontrivial stable node, while in Domain 6 there exists a stable oscillatory regime. In these regions population survival is conditional on the initial population size and the initial amount of resource. In Domain 3, an unstable limit cycle is formed around the point A_α , shrinking the range of possible initial conditions that will lead to sustainable population survival. In Domain 4, point A_α is unstable, so any perturbation will lead to population collapse. In Domain 5, an elliptic sector appears, which implies that a population is bound for extinction regardless of initial conditions. Finally, Domain 0 corresponds to the case, when only trivial equilibrium $B(0, \frac{\gamma}{\delta})$ is globally attractive, which is of no biological interest. Domains are separated by bifurcation boundaries K, S, H, C, Del and $Al = 0$ that correspond, respectively, to the appearance of attractive sector in a vicinity of O , appearance of unstable heteroclinic cycle, loss of stability of A_α (Hopf bifurcation), merging of stable and unstable cycles containing A_α inside and disappearance of positive nontrivial equilibrium. When $c_2^* = H^+$ ($\alpha=0$) and $c_1^* = H^+$ ($\alpha=1$) are end points of the Hopf boundary H^+ , the following scenarios can be realized: (a) when $c_2 > c_2^*, c_1 > c_1^*$, the system can sustainably exist for $\alpha \in [\alpha_1, \alpha_2] \subset (0, 1)$; (b) when $c_2 > c_2^*, c_1 < 1$, the system can sustainably exist for $\alpha \in [\alpha_1, 1]$; (c) when $c_0 < 1, c_1 > c_1^*$, the system sustainably exist for $\alpha \in [0, \alpha_2)$.

allowed, i.e., when $c_1 < 1$, $c_2 \in (\phi, 1)$, the equilibrium point

$$\hat{N}_\alpha = \frac{1}{\delta K_\alpha} \left(\gamma + \frac{e(1 - \alpha c_1 - c_2(1 - \alpha))}{1 + K_\alpha} \right), \hat{z}_\alpha = \frac{1}{\delta} \left(\gamma + \frac{e(1 - \alpha c_1 - c_2(1 - \alpha))}{1 + K_\alpha} \right),$$

$$K_\alpha = \frac{(1 - \alpha)\phi + \alpha(c_1 - 1)}{2(\alpha c_1 + (1 - \alpha)(c_2 - \phi))} + \frac{\sqrt{((1 - \alpha)\phi + \alpha(c_1 - 1))^2 + 4\alpha(\alpha c_1 + (1 - \alpha)(c_2 - \phi))}}{2(\alpha c_1 + (1 - \alpha)(c_2 - \phi))} \quad (2)$$

is a global attractor, and the general set of trajectories tend to this point with time. That is, a niche, which is defined here as a state of sustainable coexistence with a common renewable resource, will successfully be formed regardless of the initial population size or initial amount of resource available.

Domain 1 always exists when $c_1 < 1$, $c_2 \in (\phi, 1)$ and may continue to exist for $c_2, c_1 > 1$ for certain values of other parameters. Increasing parameters c_2 and/or c_1 , one moves into Domain 2, which is a region of bistability (see Figure 1 d2). In Domain 2, population survival is going to be possible only depending on the appropriate initial conditions: if the initial population is too large or the initial amount of the resource is too small, the population will go extinct. Further increases in c_2 and/or c_1 moves the system behavior to Domain 3, where an unstable limit cycle exists around the stable equilibrium point A_α , thus further shrinking its domain of attraction and consequently decreasing the range of initial conditions that permit sustainable coexistence of the population and the resource. In Domain 4, the limit cycle merges with the equilibrium point A_α , making it unstable. This implies that any small perturbation from the state of equilibrium will cause population extinction. Further increasing c_2 and/or c_1 causes point A_α to move closer and closer to the origin, finally merging with it in Domain 5, which results in the appearance of an elliptic sector (see Figure 1, d5) and thus inevitable, albeit delayed, population extinction. Moving into Domain 5 could be interpreted as “the tragedy of the commons, when overly efficient consumers exhaust the ‘common resource’, thereby eventually causing extinction of the entire population [11, 22, 23]. Within Domain 6, a regime of stable oscillatory behavior is possible. In Domain 6, one can observe a paradoxical effect of increased resource decay having a stabilizing effect on the system. More details for the case $\alpha = 1$ can be found in [16]. Note also that for all parameter values, the System has a non-hyperbolic trivial equilibrium $O(0, 0)$ and equilibrium $B(N = 0, z = \frac{\gamma}{\delta})$, which is a saddle if $Al \equiv c_2(1 - \alpha) - \phi + \alpha(c_1 + \phi) > 0$ and a stable node if $Al < 0$. Domain 0 is bounded by $Al = 0$; in this Domain point A_α does not exist, and only point B is stable. Therefore, Domain 0 appears to be biologically irrelevant, since it corresponds to the case, when the ‘extrinsic resource’ grows and decays independently of consumers, which within the frameworks of this model can only happen if the population size is close to 0. Note, that for $\alpha = 0$, condition $Al < 0$ reduces to $c_2 < \phi$.

The dynamical behaviors described above are realized under variation of either one of c_2, c_1 for fixed α . It is also worth noting that while the location of the boundaries changes for different α, c_2 and c_1 , the order in which the described dynamical regimes appear remains unchanged (see Figure 1 a-c.).

The boundary lines presented in the phase-parameter portraits of Figures 1 a-c correspond to bifurcations of co-dimension 1 in the System, and points of intersections of the lines correspond to bifurcations of higher co-dimensions. Specifically,

boundary K corresponds to the appearance of an attracting parabolic sector in a vicinity of the origin; boundary S corresponds to the appearance of an unstable limit cycle from heteroclinics, composed of separatrices of points O and B ; boundary H corresponds to the change of stability of point A_α (Hopf bifurcation), where H^+ determines the appearance of an unstable limit cycle and H^- determines the appearance of a stable limit cycle. Boundary C corresponds to the merging of stable and unstable cycles and, finally, Del corresponds to the merging of point A_α with O . Note now that boundaries $H^+ \cup C$ are dangerous because their intersection will cause population extinction. Also, Domain 6, which is bounded by boundary C , exists for a narrow range of parameters δ and γ (natural rates of resource decay and restoration), and only when α is closer 1 than to 0.

Let us look in more detail at the boundary H^+ . Let $c_2^* = H^+(\alpha = 0)$ and $c_1^* = H^+(\alpha = 1)$. Then we can observe the following dynamical regimes that can be realized in System (1) and which are also depicted in Figure 1, a-c:

1) If $c_2 > c_2^*, c_1 > c_1^*$, then for $0 < \alpha < 1$, the population can sustainably coexist with the common resource for some mixed strategy $\alpha \in (\alpha_1, \alpha_2) \subset (0, 1)$; however, population goes extinct for the critical cases of pure strategies, i.e., when $\alpha=0$ and $\alpha=1$, see Figure 1a;

2) If $c_2 > c_2^*, c_1 < 1$ (or $c_0 < 1, c_1 > c_1^*$) then the population can sustainably coexist with the common resource for $\alpha \in (\alpha_1, 1]$, see Figure 1b,c;

3) The population can sustainably coexist with the common resource and exhibits qualitatively equivalent stable behavior for $\alpha \in [0, 1]$ if both $c_2, c_1 < 1$, see Figure 1a-c.

This bifurcation diagram can be used conceptually to not only understand the possible dynamical regimes but also to make predictions about possible implications of changes in population composition, as well as changes in intrinsic properties of individuals within the population.

4. Modeling parametric heterogeneity. Until now we have been acting upon the assumption of a fixed proportion of clones that adopt either strategy in the population, i.e., that α is a constant. It can happen if the system has already had time to evolve and reach a steady state, concentrating near the average parameter value. However, the dynamics cannot be so easily predicted if the selection process is still ongoing or if there exists no 'optimal' proportion of each strategy within the population, and consequently the population tends to a distribution of strategies.

In order to enable us to visualize evolutionary trajectories of a system that may still be experiencing ongoing selective pressures, or the one that has been significantly perturbed, assume that the population is composed of many α -clones $x_\alpha(t)$, where the parameter $\alpha \in [0, 1]$ represents the probability with which an individual uses s-strategy (and hence $1-\alpha$ represents the probability of using r-strategy) in the α -clone. The initial state of such a polymorphic population can be described through the distribution of the parameter $\alpha \in [0, 1]$, where $P_\alpha(0) = \frac{x_\alpha(0)}{N(0)}$. In this case, instead of the 2-dimensional parametrically homogeneous System (1), we consider the following infinitely dimensional parametrically heterogeneous System:

$$\begin{cases} \frac{dx_\alpha}{dt} = rx_\alpha(\alpha(c_1 - \frac{bN(t)}{kz(t)}) + (1-\alpha)(\frac{c_2z(t)}{N(t)+z(t)} - \phi)), \\ \frac{dz}{dt} = \gamma - \delta z(t) + e(E^t[\alpha](1-c_1) + (1-E^t[\alpha])(1-c_2))\frac{N(t)}{N(t)+z(t)}. \end{cases} \quad (3)$$

The last equation in System (3) can be deduced from the last equation of System (1) by integrating over α ; here we denote to $E^t[\alpha]$ as the mean value of α over the current distribution of clones, $P_\alpha(t) = \frac{x_\alpha(t)}{N(t)}$.

If the selective pressures acting upon the population are sufficiently strong, then, we should expect to see the distribution of clones, $P_\alpha(t) = \frac{x_\alpha(t)}{N(t)}$ to change over time, and the question of what the final distribution will be, or what the transitional regimes that could be observed as the system stabilizes, does not have an intuitive and predictable answer. This is due to the fact that now the state of the environment in which the population evolves is determined not only on the amount of 'resources' that the individuals have to compete for but also by the population composition and individuals themselves; consequently, different types of clones can impose different selective pressures on each other, over time further affecting overall system dynamics. The effects of intra-population selective pressures on system dynamics cannot be captured without taking into account population heterogeneity.

The proportion of each type of clone within the population can be tracked through the expected value of the parameter α , which in the homogeneous system was just a constant but in a parametrically heterogeneous system becomes a function of time.

Each individual tries to maximize his or her own fitness through allocating their resources either towards increased proliferation or increased physiological maintenance, in such a way as to maximize their fitness, which in the framework of ODEs is measured as the growth rate per individual, i.e., $\frac{dx_\alpha}{dt} / x_\alpha$. If only two clones adhering to two pure strategies were interacting, the predominant strategy would be determined only by the relative value $\frac{dx_\alpha}{dt}$ of each clone at each time point (see Figure 2). However, if many clones are interacting, it is not immediately clear, which strategy will come to dominate through natural selection, since both population composition and the amount of extrinsic resources available would be changing.

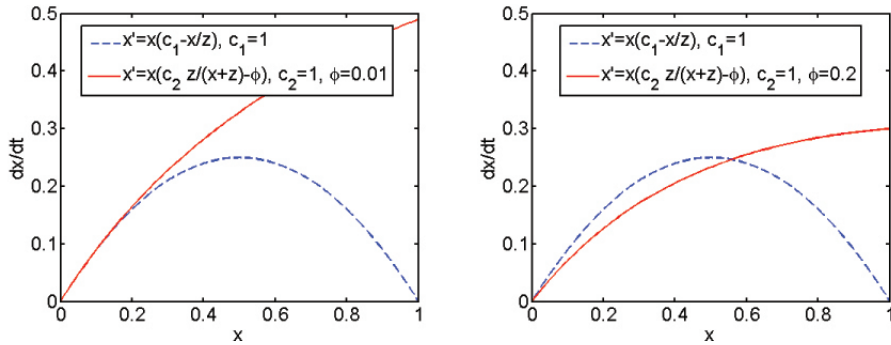


FIGURE 2. Relative positions of the growth curves for the two strategies under fixed z (a) $c_1 = c_2 = 1, \phi = 0.01$ (b) $c_1 = c_2 = 1, \phi = 0.2$.

In order to investigate this question, let us introduce auxiliary variables $q(t)$ and $g(t)$ such that

$$\begin{cases} \frac{dq(t)}{dt} = \frac{z(t)}{z(t)+N(t)}, \\ \frac{dg}{dt} = \frac{bN(t)}{kz(t)}. \end{cases} \tag{4}$$

Then the equation for the rate of change of the frequency of each clone can be written as

$$x_\alpha(t)' = rx_\alpha(t)(\alpha(c_1 - g(t)') + (1 - \alpha)(c_2q(t)' - \phi)). \tag{5}$$

The solution to Equation (5) is

$$x_\alpha(t) = x_\alpha(0)e^{[r((\alpha c_1 - (1-\alpha)\phi)t + (1-\alpha)c_2q(t) - \alpha g(t))]} \tag{6}$$

Then the total population size $N(t)$ becomes:

$$\begin{aligned} N(t) &= \int_\alpha x_\alpha(t)d\alpha = N(0) \int_\alpha e^{r(c_2q(t) - \phi)t} \cdot e^{r\alpha((c_1 + \phi)t - c_2q(t) - g(t))} P_0(\alpha)d\alpha \\ &= N(0)e^{r(c_2q(t) - \phi)t} \cdot M_0[r((c_1 + \phi)t - c_2q(t) - g(t))], \end{aligned} \tag{7}$$

where $N(0)$ is initial population size, and M_0 is the moment generating function (mgf) of the initial distribution $P_0(\alpha)$; the mgf is defined by the formula $M_0(\delta) = \int_\alpha e^{\delta\alpha} P_0(\alpha)d\alpha$. The distribution of clones over time is given by

$$P_\alpha(t) = \frac{x_\alpha(t)}{N(t)} = \frac{e^{\alpha\Omega(t)}}{M_0[\Omega(t)]}, \tag{8}$$

where $\Omega = r((c_1 + \phi)t - c_2q(t) - g(t))$. The mean value of α at time t is

$$E^t[\alpha] = \int \alpha P_t(\alpha)d\alpha = \int P_0(\alpha) \frac{\alpha e^{\alpha\Omega}}{M_0(\Omega)} d\alpha = \frac{M_0'(\Omega)}{M_0(\Omega)}. \tag{9}$$

Putting together all the expressions that have been obtained as a result of these transformations, we obtain the following system of equations:

$$\begin{cases} \frac{dz}{dt} = p - dz(t) + re(E^t[\alpha](1 - c_1) + (1 - E^t[\alpha])(1 - c_2)) \frac{N(t)}{z(t) + N(t)}, \\ \frac{dq}{dt} = \frac{z(t)}{z(t) + N(t)}, \\ \frac{dg}{dt} = \frac{bN(t)}{kz(t)}, \end{cases} \tag{10}$$

where $N(t)$ is defined in System (7) and $E^t[\alpha]$ is the mean value of the parameter α , which can be calculated from Equation (9).

The auxiliary variables $q(t)$ and $g(t)$, which were not present in the original model, are actually the keystone quantities that govern the system dynamics and determine all of its statistical characteristics. More details on this approach for studying replicator equations can be found in [14, 15].

4.0.1. *Differences in intrinsic properties of the population.* In order to investigate, how such a heterogeneous system can evolve over time and to visualize evolutionary trajectories with respect to different parameter values, we consider two different initial distributions of clones within a population: uniform and truncated exponential (of which uniform distribution can be considered a special case). The choice of truncated exponential distribution can be justified through the principle of maximum entropy (MaxEnt): if the mean value of the random variable is the only quantity that can be estimated from observations or other data, then the most likely distribution of the variable is exponential with the estimated mean [13]. Given that is bounded on the interval [0,1], then, according to MaxEnt principle, we should choose the truncated exponential in this interval as the initial distribution.

Parameter values for the trajectories, illustrated in Figure 3a and 3c were chosen explicitly to fall into Domain 1. The two figures differ only in the value of parameter ϕ , which is taken to be $\phi = 0.09$ in Figure 3a and $\phi = 0.14$ in Figure 3c. Nevertheless, one can already observe that the population evolves towards different expected values of α . This is most evidently reflected in the graph for how the distribution of clones changes over time in Figures 3b and 3d, which in turn suggests that even a small change in the intrinsic properties of individuals within the population can have critical effect on which way a heterogeneous population will evolve.

However, the mean value of α does not always reach an equilibrium value, i.e., the population does not always tend towards some fixed strategy, whether pure or mixed. Starting in Domain 6, we can observe that not only do the population size and amount of extrinsic resource start oscillating (which corresponds to the system entering inside the domain of attraction of the stable limit cycle) but so does the $E^t[\alpha]$. In this case, as the system evolves, no final distribution of clones becomes fixed over time (Figure 4). This suggests that the standard approach using a fixed value of the parameter α (or its mean value) can yield incorrect predictions within this domain of the model parameters and, hence, is not justified in general case.

4.0.2. *Differences in initial composition of the population.* Now we would like to investigate how the changes in initial distribution of clones will affect the direction in which the population will evolve. That is, we want to investigate the changes in evolutionary trajectories in the case when the intrinsic properties of the individuals within the system are fixed (such as birth, death and resource consumption rates) but the initial population composition, and consequently the set of selective pressures experiences by each individual within the population, is different. In other words, we want to investigate how the evolution of the population as a whole can be affected by the strategic choices made by individuals within it.

In Figures 5 and 6, one can observe the changes in the population size $N(t)$, resource amount $z(t)$ and the mean value $E^t[\alpha]$ over time under different initial distributions, given that all other initial conditions were the same for both cases. In Figure 5, part (a) corresponds to initial uniform distribution, part (b) to initial truncated exponential distribution with parameter $\mu = 1.1$, and part (c) to initial truncated distribution with parameter $\mu = 10.1$. One can see that the trajectories look strikingly different as the population evolves, passing through different regions of the phase-parameter space. Noticeably, in Figure 5b, the population size crashed at $t = 32$, while in parts (a) and (c) one could observe stable coexistence with the resource. This effect is due to the trajectory moving outside of domain of attraction of the non-trivial equilibrium point A_α in Figure 5b.

5. **Discussion.** In situations when resource availability is crucial for population survival and expansion, the question of most efficient resource allocation becomes of vital importance. Considered in this work are two general 'pure' strategies for resource allocation that the individuals can use for optimizing their fitness: investing the resources primarily in rapid proliferation or in physiological and environmental maintenance and the expense of rapid proliferation, with a full spectrum of possible intermediate strategies. The two pure strategies were analyzed separately in [17], where the authors considered a situation, in which either different species, or individuals within the same species, interact with a collectively constructed niche, on which depends their overall survival. The authors focused specifically on what is known as a 'construction dilemma', i.e., a question of why investment of basic life

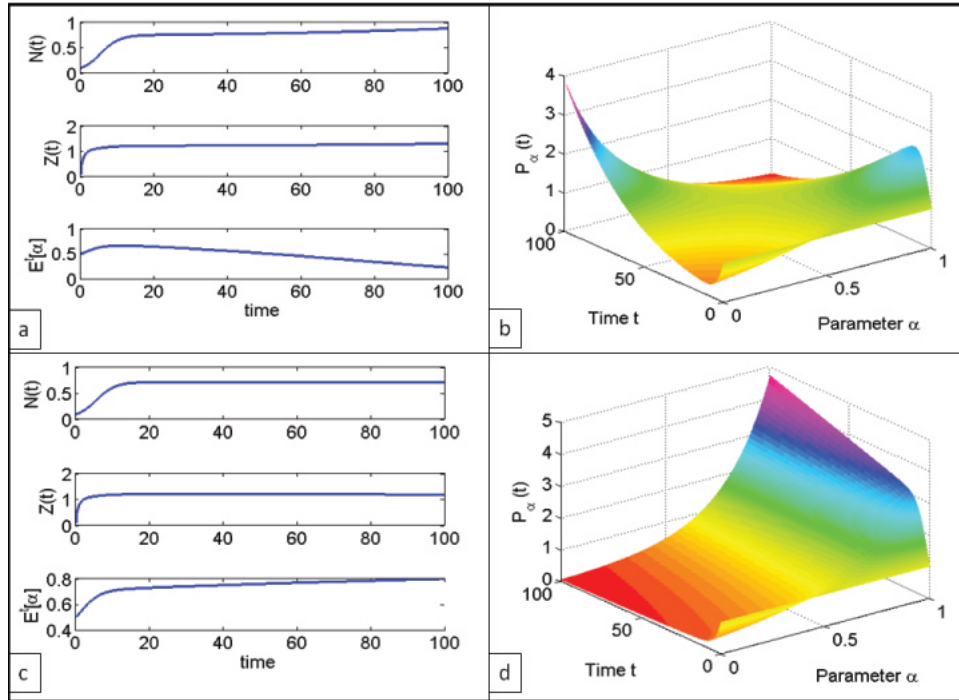


FIGURE 3. Trajectories and distribution of clones throughout the completely altruistic population (starting in Domain 1). Even a very slight change in the value of an intrinsic parameter ϕ (natural death rate of individuals that invest primarily in fecundity) causes the system to evolve towards the dominance of one or the other strategy (investment in fecundity in the top case and investment into carrying capacity in the bottom case). The total population size and the total amount of resource are virtually the same in both cases. All parameters held constant at $r = 1$, $e = 1$, $b = 1$, $k = 1$, $N_0 = .1$, $c_2 = .2$, $c_1 = .6$, $d = 1$, $p = 1$, $\phi = 0.09$. (c-d): all parameters held the same, except $\phi = 0.14$.

history trade-offs, such as energy, time, or, in the case of financial systems, money, into physiological and environmental maintenance could be selected for if the immediate benefits of investment into rapid proliferation are greater. They came to the conclusion that the construction dilemma can be resolved through 'niche monopolization', which can be achieved either through spatial proximity, or through preferential access to the resources. In this paper we challenge the authors' conclusion, suggesting that even within the proposed simplified conceptual framework of a consumer-resource type system construction dilemma can be resolved if the population is heterogeneous with respect to the initial strategy choice.

In order to investigate the question of natural selection in strategies for resource allocation, we constructed a mathematical model based on models introduced in [17], which captures the dynamics of a consumer-resource type of a system, where

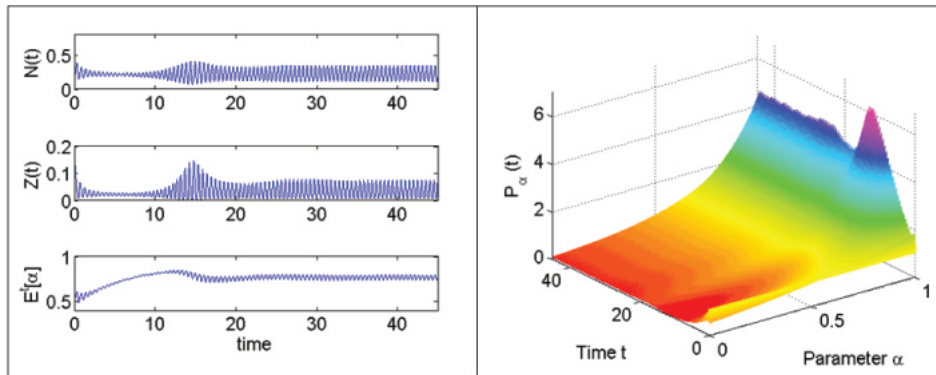


FIGURE 4. Trajectories and distribution of clones throughout the population. In this case, one not only observes stable oscillatory behavior in the amount of resource and total population size but also a shift between the two strategies. That is, the population evolves not towards eventual dominance of just one pure strategy but shifts between two strategies. Initial distribution is uniform. Initial conditions are such as to fall within Domain 6. Parameters are $r = 1$, $e = 1$, $b = .9$, $k = 1$, $\phi = 1.2$, $N_0 = .1$, $c_2 = 8.75$, $c_1 = 9$, $d = 24$, $p = 7.72$.

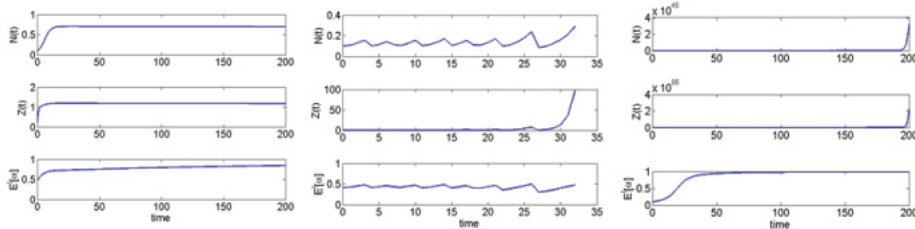


FIGURE 5. The effects of difference in the initial composition of the population with respect to different strategies. Different initial distributions were chosen to be (a) uniform initial distribution (b) truncated exponential initial distribution, with parameter $\mu = 1.1$ (note: population crashes after time $t = 32$) and (c) truncated exponential initial distribution, with parameter $\mu = 10.1$. Initial conditions are such as to fall within Domain 1. All parameters held constant at $r = 1$, $e = 1$, $b = 1$, $k = 1$, $N_0 = .1$, $c_2 = .2$, $c_1 = .6$, $d = 1$, $p = 1$, $\phi = 0.14$. One can see that the initial composition of the population can have dramatic effects on the direction in which the population will evolve over time. (Note: the values of μ were chosen arbitrarily for illustrative purposes).

the individuals can allocate the extrinsic resources that are available to them either for rapid proliferation (here termed r-strategy) or for slow proliferation but increased physiological and environmental maintenance (here termed s-strategy).

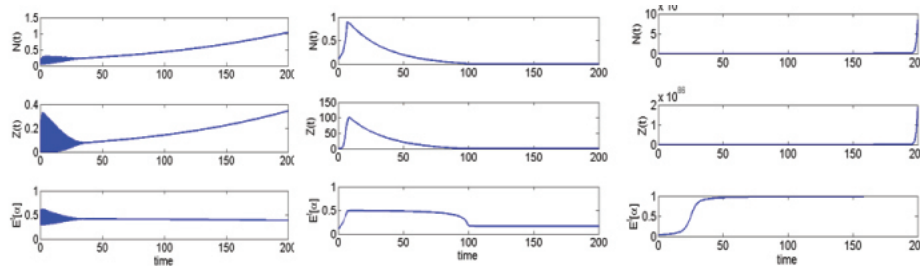


FIGURE 6. The effects of difference in the initial composition of the population with respect to different strategies. Different initial distributions were chosen to be (a) uniform (b) truncated exponential with parameter $\mu = 10.1$ and (c) truncated exponential with parameter $\mu = 30.1$. Other parameters held constant at $r = 2$, $e = 2$, $b = 1$, $k = 1$, $N_0 = .1$, $c_2 = .2$, $c_1 = 2$, $d = 1$, $p = 1$, $\phi = 0.05$.

We also allow for the existence of 'over-consumers', i.e., individuals that are capable of drawing more from the common resource pool than they restore. Each individual in the population is characterized by a value of parameter α , which corresponds to the probability of an individual allocating the resources according to either strategy ($\alpha = 1$ corresponds to pure s-strategy and $\alpha = 0$ corresponds to pure r-strategy); a set of individuals characterized by the same value of the parameter are referred to here as α -clones. The 'success' of either strategy, whether pure or mixed, is determined by the overall growth rate of the set of individuals that choose it. Examples of populations, where individuals within the same population can switch between different resource allocation strategies, range from bacteria [6, 25] to cancer cells [9] to forest trees [5] to socio-economical systems [10]. While we can observe the current state of the system and the corresponding distribution of strategies, identification of mechanisms that could have led to it, and speculation about other possible evolutionary trajectories that the system could have taken, is rarely possible. In this paper we propose but one way to try and explore this question.

At first, full bifurcation analysis was performed on the model, where the population was assumed to be parametrically homogeneous, i.e., the value of α was fixed. This was done to identify all possible dynamical regimes in the system to create a framework, within which to then evaluate the effects of natural selection on a parametrically heterogeneous population. The obtained bifurcation diagram describes the possible dynamical regimes of a population that is homogeneous with respect to α .

An important conclusion from the bifurcation analysis is that the main qualitative regimes of behaviors and also the sequence in which they appear as the parameters of (over-)consumption change are very similar for both models, i.e., when the individuals in the population use only pure r- or s-strategies. We want to emphasize that namely the regimes of qualitative behaviors, not particular phenomenological equations, determine, whether the model corresponds to a real system of interest. The bifurcation analysis shows that both pure strategy models can be applied to describing the dynamical behaviors of the same system, which suggests that mixing

the two strategies in different proportions to describe the dynamics of a population is also mathematically justified by the similarity of their qualitative behavior.

In order to investigate how a heterogeneous population will behave, and in particular, which strategy can be selected purely through the process of natural selection without any specific assumptions imposed on the environment in which the selection process occurs, we applied the Reduction theorem [14, 15], which allows reducing an otherwise infinitely dimensional System (3) to a 3-dimensional system of non-autonomous ODEs. The approach can be summarized as follows: assume each individual within the heterogeneous population is characterized by their own intrinsic value of the parameter α . Assume also that the individuals can be grouped in such a way as to fall into some distribution that is known at the initial time moment. Overall dynamics in such a system is then governed not by the constant average value of α but by the expected value of α at each time moment, which can be tracked through the moment generating function of the initial distribution. In this case one can observe the mean of α moving across, or 'traveling' through the phase parameter portrait as the population evolves, which is why obtaining a full bifurcation diagram of the original parametrically homogeneous system was beneficial. This approach to studying the dynamics of the parametrically inhomogeneous system was justified by the Reduction theorem.

Several interesting effects were observed that allow answering, at least in part, the questions posed in the beginning of this work. We were able to demonstrate that while the direction in which the population will evolve is largely determined by what domain in the phase parameter space one starts in, this was never the sole determining factor and that varying initial population composition had a larger impact on final population composition. We also showed that the strategy towards which the population eventually evolves is not always a pure strategy but can be a mixture of strategies. Moreover, we have been able to observe regimes when the mean value of α oscillates sustainably, as do population size and amount of resource. (Interestingly, one frequently can observe oscillatory behavior before a strategy stabilizes and the mean of α reaches an equilibrium. However, increasing amplitude of oscillations can also signal that population collapse is approaching, since this most often occurs when the trajectory passes through Domain 2 (unstable limit cycle), entering Domain 4 (unstable node), and from there traveling either directly to the origin (immediate extinction), or to Domain 5 (elliptic sector) in Figure 1).

We were also able to show that starting with different initial distributions, even within the same domain on the phase-parameter space, can lead to different system behaviors and different strategies being favored by natural selection in the long run. We could observe it by calculating numerical solutions of the system, with uniform initial distribution of strategies within the population, and truncated exponential initial distribution (parameter α bounded on the interval $[0,1]$) with different parameters of the distribution. As one can see in Figures 4 and 5, even when everything else is equal, the direction in which the system will evolve depends greatly on the initial distribution.

Therefore, when one is trying to predict the direction in which the system will evolve, just knowing the rules that govern its dynamics might not be enough to make a more or less accurate prediction. One needs to also know the composition of the population that is playing by these rules. This is true even in the case of perfect information, i.e., when every individual in the population knows the rules and plays to maximize his or her own fitness.

Appendix A. Analysis.

A.1. Equilibria. In order to simplify analysis, let us first make the following change of variables: $\frac{dt}{z(N+z)} \rightarrow d\tau$, yielding a system of equations that for any $\alpha \neq 0$ is topologically equivalent to System (1) for $N \geq 0$, $z > 0$:

$$\begin{cases} \frac{dN}{dt} = N(\alpha(c_1 z - N)(N + z) + (1 - \alpha)z(c_2 z - \phi(N + z))) \\ \quad \equiv F(N, z) = Nf(N, z), \\ \frac{dz}{dt} = z((\gamma - \delta z)(N + z) + e(\alpha(1 - c_1) + (1 - \alpha)(1 - c_2))N) \\ \quad \equiv G(N, z) = zg(N, z), \end{cases} \quad (11)$$

where parameters $\gamma \geq 0$, $c_1, c_2, e, \phi, \delta > 0$, $\alpha \in [0, 1]$.

For any α , System (11) has trivial equilibria $O(0, 0)$ and $B(0, \frac{\gamma}{\delta})$. The system can also have one positive non-trivial equilibrium $A_\alpha(\hat{N}_\alpha, \hat{z}_\alpha)$, where coordinates $(\hat{N}_\alpha, \hat{z}_\alpha)$ satisfy equations

$$\begin{cases} \alpha(c_1 z - N)(N + z) + (1 - \alpha)z(c_2 z - \phi(N + z)) = 0, \\ ((\gamma - \delta z)(N + z) + e(\alpha(1 - c_1) + (1 - \alpha)(1 - c_2))N) = 0. \end{cases} \quad (12)$$

The first equation of System (12) is homogeneous. Letting

$$\begin{cases} z = K_\alpha N \end{cases} \quad (13)$$

we get equation for K_α :

$$(\alpha c_1 + (1 - \alpha)(c_2 - \phi))K_\alpha^2 - ((1 - \alpha)\phi + \alpha(c_1 - 1))K_\alpha - \alpha = 0, \quad (14)$$

which has the unique positive solution

$$K_\alpha = \frac{(1 - \alpha)\phi + \alpha(c_1 - 1)}{2(\alpha c_1 + (1 - \alpha)(c_2 - \phi))} + \frac{\sqrt{((1 - \alpha)\phi + \alpha(c_1 - 1))^2 + 4\alpha(\alpha c_1 + (1 - \alpha)(c_2 - \phi))}}{2(\alpha c_1 + (1 - \alpha)(c_2 - \phi))} \quad (15)$$

if the following condition is satisfied:

$$\alpha c_1 + (1 - \alpha)(c_2 - \phi) > 0. \quad (16)$$

From Equations (12), (13) and (15), we can obtain the coordinates of the non-trivial equilibrium expressed with K_α

$$\hat{N}_\alpha = \frac{1}{\delta K_\alpha} \left(\gamma + \frac{e(1 - \alpha c_1 - c_2(1 - \alpha))}{1 + K_\alpha} \right), \hat{z}_\alpha = \frac{1}{\delta} \left(\gamma + \frac{e(1 - \alpha c_1 - c_2(1 - \alpha))}{1 + K_\alpha} \right). \quad (17)$$

Remark 1. Note, that for critical cases,

$$K_{\alpha=0} = \frac{\phi}{c_0 - \phi}, \hat{N}_{\alpha=0} = \frac{c_2 - \phi}{\delta \phi} \left(\gamma + \frac{(1 - c_2)(c_2 - \phi)}{c_2} \right), \hat{z}_{\alpha=0} = \frac{1}{\delta} \left(\gamma + \frac{(1 - c_2)(c_2 - \phi)}{c_2} \right)$$

and $K_{\alpha=1} = \frac{1}{c_1}$, $\hat{N}_{\alpha=1} = \frac{c_1}{\delta} \left(\gamma + \frac{c_1(1 - c_1)}{1 + c_1} \right)$, $\hat{z}_{\alpha=1} = \frac{1}{\delta} \left(\gamma + \frac{c_1(1 - c_1)}{1 + c_1} \right)$.

A.2. Structure of non-trivial equilibria. Jacobian $J_\alpha = (a_{ij}), i, j = 1, 2$ of System (11) consists of elements

$$\begin{cases} a_{11} = \alpha(c_1z - N)(N + z) + (1 - \alpha)z(c_2z - \phi(N + z)) + \\ \quad + N(\alpha(c_1z - N) - \alpha N - (1 - \alpha)\phi z), \\ a_{12} = N(2c_2z - \phi(N + 2z) + \alpha((c_1 + \phi - 1)N + 2(c_1 + \phi - c_2)z)), \\ a_{21} = z(\gamma - \delta z + e(\alpha(1 - c_1) + (1 - \alpha)(1 - c_2))), \\ a_{22} = ((\gamma - \delta z)(N + z) + e(\alpha(1 - c_1) + (1 - \alpha)(1 - c_2))N) + \\ \quad + z((\gamma - \delta z) - \delta(N + z)) \end{cases}$$

It is easy to verify that

$$Det(J_\alpha(B)) = -\frac{(\alpha c_1 + (1 - \alpha)(c_2 - \phi))\gamma^4}{\delta^3}$$

and

$$Trace(J_\alpha(B)) = \frac{(\alpha c_1 + (1 - \alpha)(c_2 - \phi) - \delta)\gamma^2}{\delta^2}.$$

Thus point B is a saddle if $Det(J_\alpha(B)) < 0$ and a stable node if $Det(J_\alpha(B)) > 0$.

Due to condition (16), we can state that B is a saddle if the System has positive equilibrium A_α , and can be a stable node if positive A_α does not exist. Therefore, surface

$$Al : \{ \alpha \in [0, 1], c_1, c_2, \phi, \gamma, e > 0, \alpha c_1 + (1 - \alpha)(c_2 - \phi) = 0 \}$$

is a boundary of Domain 0 where the System has no positive non-trivial equilibrium A_α (see Figure 1). Remark that for $\alpha = 0$, this Domain can exist only if $c_2 < \phi$; also, noticeably, for $\alpha = 1$ the System does not realize that behavior.

The expressions for $Det(J_\alpha(A_\alpha))$ and $Trace(J_\alpha(A_\alpha))$ are very complex but they can be simplified using the following Lemma:

Lemma A.1. *If the system of differential equations $N' = Nf(N, z), z' = zg(N, z)$*

(a) has non-zero equilibrium $A(N_0, z_0)$ such that $f(N_0, z_0) = 0, g(N_0, z_0) = 0$, and

(b) function $f(N, z)$ is homogeneous of order n with respect to N, z , then

$$Det(J(N_0, z_0)) = Nf_N(zg_z + Ng_N)|_{(N,z)=(N_0,z_0)},$$

$$Trace(J(N_0, z_0)) = Nf_N + zg_z|_{(N,z)=(N_0,z_0)} = z(g_z - f_z)|_{(N,z)=(N_0,z_0)},$$

where $J(N, z)$ is the Jacobian matrix of the system.

Proof. The Jacobian of the System at point A is

$$\begin{aligned} \begin{pmatrix} f + Nf_N & Nf_z \\ zg_N & g + zg_z \end{pmatrix}_{(N,z)=(N_0,z_0)} &= \begin{pmatrix} N_0f_N(A) & N_0f_z(A) \\ z_0g_N(A) & z_0g_z(A) \end{pmatrix} = \\ &= \begin{pmatrix} N_0f_N(A) & \frac{-N_0^2}{z_0}f_N(A) \\ z_0g_N(A) & z_0g_z(A) \end{pmatrix} \end{aligned} \tag{18}$$

The first equality follows from the condition (a). The second equality follows from the Euler property for a homogeneous function $f(N, z)$ of power n , i.e. that $f(N, z) : Nf_N(N, z) + zf_z(N, z) = nf(N, z)$, and again from condition (a): since $f(N_0, z_0) = 0$, then $N_0f_N(N_0, z_0) = -z_0f_z(N_0, z_0), f_z(N_0, z_0) = \frac{-N_0}{z_0}f_N(N_0, z_0)$.

Statements are proven. □

Applying Lemma A.1 to the expression for the Jacobian $J_\alpha(A_\alpha)$, we obtain $Det(J_\alpha(A_\alpha))$ and $Trace(J_\alpha(A_\alpha))$. Combining the obtained results we prove the following

Theorem A.2. For any $\alpha \in [0, 1]$, if condition (16) holds, the nontrivial equilibrium $A_\alpha(\hat{N}_\alpha, \hat{z}_\alpha)$, whose coordinates are given in (17), is a positive non-saddle point. It appears\disappears as an unstable node at the fold surface $\Delta_\alpha : Det(J_\alpha(A_\alpha)) = 0$

$$\Delta_\alpha : \gamma/e = \frac{-(1 - \alpha c_1 - c_2(1 - \alpha))}{1 + K_\alpha} \tag{19}$$

and changes stability at the Hopf surface $H_\alpha : Trace(J_\alpha(A_\alpha)) = 0$

$$H_\alpha : \gamma/e = \frac{-(1 - \alpha c_1 - c_2(1 - \alpha))(Y + \delta K_\alpha) + aZ}{(1 + K_\alpha)(Y + \alpha Z)} \tag{20}$$

where K_α is given in (15), $Y = \delta + \phi + \delta K_\alpha$, $Z = 2 - K_\alpha(c_1 + \phi - 1)$.

Slices of the Hopf boundary H to the (c_1, c_2) -plane for different fixed α and to the (c_2, α) -plane for different fixed c_1 are shown in Figure 7.

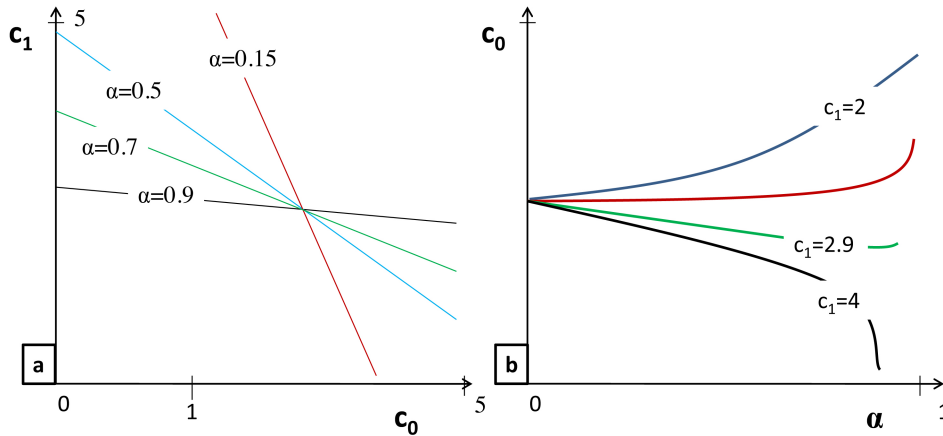


FIGURE 7. Slice of Hopf boundary H to the (c_1, c_2) -plane for different fixed $\alpha \in (0, 1]$ (a), to the (c_2, α) -plane for different fixed c_1 . (b) In both cases $e = 1, \phi = .2, \gamma = 1.58, \delta = .85$.

Remark 2. For $\alpha = 1$ fold and Hopf surfaces are of the form $\Delta_{\alpha=1} = 0 : \frac{\gamma}{e} = \frac{c_1(c_1-1)}{c_1+1}, H_{\alpha=1} : \frac{\gamma}{e} = \frac{c_1(c_1-1)(c_1+2\delta+c_1\delta+c_1^2)}{(c_1+1)^2(c_1+\delta)}$;

For $\alpha = 0$ fold and Hopf surfaces are of the form $\Delta_{\alpha=0} = 0 : \frac{\gamma}{e} = \frac{(c_2-\phi)(c_2-1)}{c_2}, H_{\alpha=0} : \frac{\gamma}{e} = \frac{(c_2-\phi)(c_2-1)((\delta-\phi)\phi+c_2(\delta+\phi))}{c_2(-\phi^2+c_2(\delta+\phi))}$.

A.3. Non-hyperbolic equilibrium $O(0, 0)$. For analysis of topological and asymptotical structure of the equilibrium O in the first quadrant of the (N, z) -plane we use methods described in [3]. Let us apply the following change of variables (also known as the “blowing-up” transformation) to System (11):

$$(N, z) \rightarrow (N, u = z/N), N \neq 0,$$

transforming point $(0, 0)$ to the axis u , and changing the independent variable to $Ndt = d\tau$, which results in the following system of equations:

$$\begin{cases} \frac{dt}{N} = N^2(\alpha(1 + u)(c_1u - 1) - (1 - \alpha)u(\phi - (c_2 - \phi)u)), \\ \frac{du}{d\tau} = u((e(1 - \alpha c_1 - (1 - \alpha)c_2 + \gamma(1 + u)) + N(-\delta u(1 + u) - \\ -\alpha(1 + u)(c_1u - 1) + (1 - \alpha)u(\phi - (c_2 - \phi)u))) \end{cases} \tag{21}$$

System (21) has two equilibrium points at axis $N = 0$: $u_1 = 0$ with eigenvalue $\lambda_1^1 = (1 - \alpha c_1 - (1 - \alpha)c_2) - \gamma$ and $u_2 = -e(1 - \alpha c_1 - (1 - \alpha)c_2) / \gamma$ with eigenvalue $\lambda_1^2 = -\lambda_1^1$. Although the second eigenvalue is zero for both points ($\lambda_2^1 = \lambda_2^2 = 0$), their structure can be strictly defined in the positive (N, z) -quadrant using the method described in [3]. Denote

$$E = e(1 - \alpha c_1 - (1 - \alpha)c_2) + \gamma \tag{22}$$

If $E > 0$, then only equilibrium $(0, u_1)$ belongs to the first quadrant, where it has an attractive node sector; if $E < 0$, then two equilibria $(0, u_1)$ and $(0, u_2)$ belong to the first quadrant; $(0, u_1)$ is a saddle and $(0, u_2)$ can be a saddle, as well as an attractive node. $E = 0$ corresponds to merging $u_1 = u_2 = 0$.

The second change of variables

$$(N, z) \rightarrow (v = N/z, z), z \neq 0 \tag{23}$$

maps point $(0, 0)$ to the axis v , and through changing time using transformation $zdt = d\tau$, System (11) becomes:

$$\begin{cases} \frac{dv}{d\tau} = v(-\gamma - (e(1 - \alpha c_1 - (1 - \alpha)c_2) + \gamma)v + ((1 + v)(\delta + \alpha(c_1 - v) + \\ + (1 - \alpha)(c_2 - \phi(1 + v))))z, \\ \frac{dz}{z} = z(-(e(1 - \alpha c_1 - (1 - \alpha)c_2) + \gamma)v - \delta(1 + v)z) \end{cases} \tag{24}$$

The equilibrium $(v = 0, z = 0)$ is a saddle ($\lambda_1 = \gamma, \lambda_2 = -\gamma$) Applying the same set of transformations to System (11) with $\alpha = 0$, and then returning to the initial variables, we prove the following statement:

Proposition 1. *In System (11) for all $\alpha \in (0, 1]$ and the specified values of other parameters $c_1, c_2, \phi > 0, \gamma \geq 0, 0 < e \leq 1$ there exist only three different phase-parameter portraits in the neighborhood of equilibrium point O , which are topologically equivalent to the portraits that are shown in Figure 8a, and only two different phase-parameter portraits for $\alpha = 0$, which are shown in Figure 8b.*

B4. Equilibria “at infinity”. The structure of equilibrium points “at infinity” will be studied using the Poincaré sphere [2].

(a) The change of variables

$$(N, z) \rightarrow (u = 1/N, v = z/N), N \neq 0 \tag{25}$$

and

$$dt = u^2 d\tau \tag{26}$$

transforms System (1) to

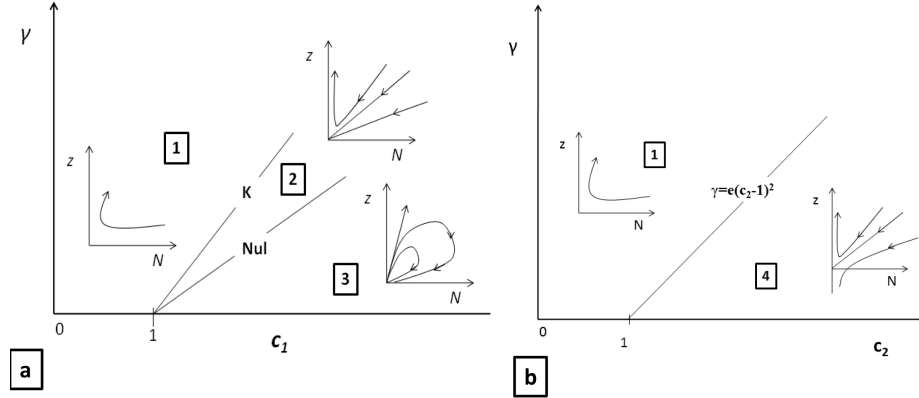


FIGURE 8. A schematic bifurcation diagram of the non-hyperbolic equilibrium point O in (N, z) - phase plane and (a) (c_1, γ) -parameter plane for $\alpha \in (0, 1]$, (b)

(c_2, γ) -

parameter plane for $\alpha = 0$; other parameters of the System (11) are positive. (a) The parameter plane is divided into three Domains, 1, 2, 3; the vicinity of O in these Domains contains a hyperbolic sector, hyperbolic and attractive parabolic sectors and an elliptic sector, respectively. (b) The parameter plane is divided into two Domains, 1 and 4; Domain 1 is as above, in Domain 4, some trajectories can leave positive quadrant, making the system biologically irrelevant for these initial conditions.

$$\begin{cases} \frac{du}{d\tau} = u(v(\phi(1+v) - c_2) - \alpha((c_1 + \phi - 1)v - 1 + (c_1 + \phi - c_2)v^2)), \\ \frac{dv}{d\tau} = v(v(\phi(1+v) - c_2) - \alpha((c_1 + \phi - 1)v - 1 + (c_1 + \phi - c_2)v^2) + (1+v)(\gamma u - \delta v) - eu(\alpha(c_1 - c_2) + c_2 - 1)) \end{cases} \quad (27)$$

Equilibrium points of Systems (27) for $u = 0$ are $v = 0$ satisfy the equation:

$$(\alpha c_1 + \delta + (1 - \alpha)(c_2 - \phi))v^2 - (\alpha(1 - c_1 - \phi) + \phi - \delta)v - \alpha = 0 \quad (28)$$

Lemma A.3. Only one of the roots of Equation (30), $v = v^*(\alpha)$, can be positive for $0 < \alpha \leq 1$; at $\alpha = 0$, $v^*(\alpha = 0) = 0$.

Proof. Rewrite Equation (28) in the form: $B(\alpha)v^2 - A(\alpha)v - \alpha = 0$, where $A(\alpha) = \alpha(1 - c_1 - \phi) + \phi - \delta$, $B(\alpha) = \alpha(c_2 - c_1 - \phi) + \phi - \delta - c_2$. The validity of Lemma (A.3) is evident if $B(\alpha) > 0$. If $B_\alpha = 0$, then $\alpha = \frac{c_2 - \phi + \delta}{c_2 - \phi - c_1}$, and $\alpha \in [0, 1] \Leftrightarrow c_2 - \phi + \delta \leq 0$ for $c_1, c_2, \delta, \phi \geq 0$. So, Equation (28) has no positive roots if $\alpha \neq 0$. \square

It can be verified that eigenvalues of $u = v = 0$ are $\lambda_1 = \lambda_2 = \alpha$, and eigenvalues of $u = 0, v = v_1(\alpha)$ are

$$\lambda_1(\alpha) = \delta v_1(\alpha)(1 + v_1(\alpha)) > 0,$$

$\lambda_2(\alpha) = -v_1(\alpha)(\delta - \phi + \alpha(c_1 + \phi - 1) + 2(c_2 + (\delta - \phi) + \alpha(c_1 + \phi - c_2))v_1(\alpha))$
 Therefore, point $u = 0, v = v_1(\alpha) > 0$ is a saddle.

Remark 3. For $\alpha = 1, v_1 = \frac{1}{c_1 + \delta}$ and the eigenvalues are $\lambda_1 = \frac{\delta(c_1 + \delta + 1)}{(c_1 + \delta)^2}, \lambda_2 = -\frac{c_1 + \delta + 1}{c_1 + \delta}$. For $\alpha = 0, v_1 = \frac{\phi - \delta}{c_2 - \phi + \delta}$. If $\phi > \delta$, then $v_1 > 0$. The corresponding eigenvalues are $\lambda_1 = \frac{\delta c_2(\phi - \delta)}{(c_2 + \delta - \phi)^2}, \lambda_2 = \frac{-(\phi - \delta)^2}{(c_0 + \delta - \phi)}$.

Note that System

$$\begin{cases} \frac{du}{d\tau} = u((\phi(1 + v) - c_2v), \\ \frac{dv}{d\tau} = e(1 - c_2)u + (1 + v)(\gamma u - \delta v) + v(\phi - (c_2 - \phi)v), \end{cases} \tag{29}$$

which was obtained from the System (11) through the change of variables (25) and (26), does not have an equilibrium point at $u = v = 0$ for $\phi < \delta$. For $\phi = \delta$, equilibrium $u = v = 0$ is not hyperbolic; it contains a hyperbolic sector for positive u, v .

(b) Making the transformation

$$(N, z) \rightarrow (u = 1/z, w = N/z), z \neq 0 \tag{30}$$

and putting it together with expression (26), we obtain the following System:

$$\begin{cases} \frac{du}{d\tau} = u(\delta(1 + w) - u(\gamma(1 + w) - ew(\alpha c_1 - 1 + c_2(1 - \alpha))), \\ \frac{dw}{d\tau} = w(\delta(1 + w) + c_2 - \phi - \gamma u(1 + w) - \phi w - euw(1 - c_2) \\ + \alpha((\phi - w)(1 + w) + (c_1 - c_2)(1 + euw))) \end{cases} \tag{31}$$

This System has the only one new equilibrium (when compared with equation (27)): $(u = 0, w = 0)$. Eigenvalues at this point, namely $\lambda_1 = \delta, \lambda_2 = \alpha c_1 + (1 - \alpha)(c_2 - \phi + \delta)$, are positive. Thus, it is an unstable node for all α . Combining the results, we get the following proven statement:

Proposition 2. For $\alpha \in (0, 1]$ in the first quadrant of (N, z) -plane, System (11)

- 1) has a source at the end N -axis,
- 2) has a source node at the end z -axis and a saddle point at the end of the axis, where $v_*(\alpha)$ is a non-negative root of Equation (28) if $\alpha(c_2 - c_1 - \phi) + \phi - \delta - c_2 > 0$,
- 3) has a saddle point at the end z -axis if $\alpha(c_2 - c_1 - \phi) + \phi - \delta - c_2 < 0$.

Typical structures of the System behaviors in the first quadrant of (N, z) -plane are shown in Figure 9. For all initial values of trajectories do not leave the first quadrant.

A.4. Heteroclinis, homoclinics and limit cycles.

A.4.1. *Heteroclinis and homoclinics.* An attractive parabolic sector in the positive vicinity of the non-hyperbolic point O appears when separatrix of O coincides with the separatrix of the saddle point in the equator of the Poincaré sphere (“at infinity”), creating the heteroclinics at (N, z) phase plane. The boundary K corresponds to this bifurcation in the parameter portrait; it divides the Domain into sections, where a parabolic sector exists, and where it does not (see Figure 10a).

Another important heteroclinic connection forms, when the outgoing separatrix of saddle equilibrium B coincides with the incoming separatrix of equilibrium O .

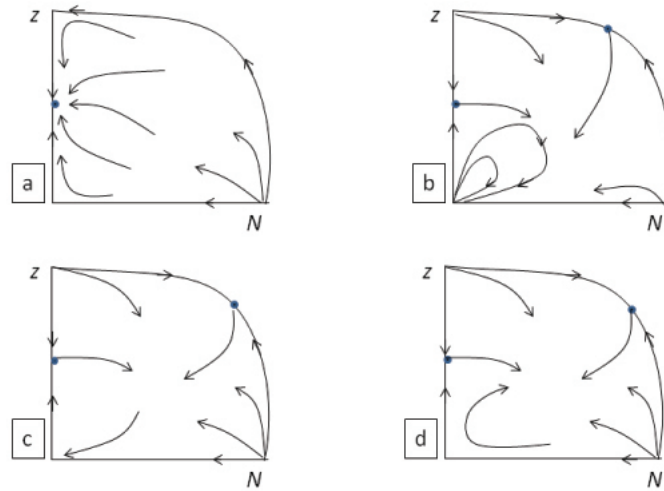


FIGURE 9. (a) Only equilibrium B is attractive, (b) equilibrium O is attractive and repelling (contains an elliptic sector in its vicinity), no more attracting equilibria, (c) equilibrium O is attractive, other attractive manifolds have to exist, (d) O is repelling a saddle, attractive manifold(s) have to be present in a bounded part of the first quadrant.

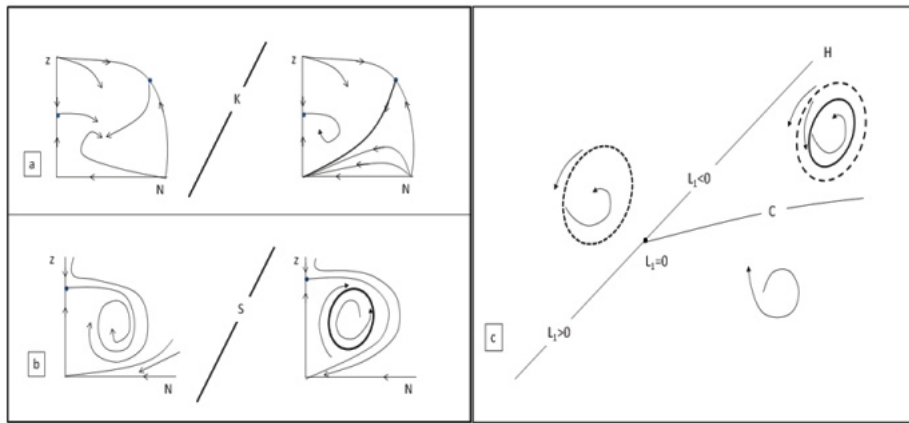


FIGURE 10. Schematic bifurcation diagrams of heteroclinics- and Hopf bifurcations in the System (11): (a) appearance/disappearance of attractive parabolic sector in the vicinity of the origin; (b) appearance/disappearance of unstable limit cycle containing A_α , and (c) generalized Hopf bifurcation $L_1(H) = 0$ in a neighborhood of A_α .

The unstable limit cycle is generated, containing nontrivial equilibrium A_α (see, Figure 10b, where parametric boundary S corresponds to this bifurcation).

Elliptic sector in the vicinity of point O , is shown in Figure 8, Domain 3 and in Figure 9b, consists of a family of homoclinics tending to O with $t \rightarrow \pm\infty$

A.4.2. *Hopf bifurcations.* Equilibrium A_α of System (11) can change stability via Hopf bifurcation for a range of parameter values that belong to the surface H_α (see Equation (20)). To understand whether the bifurcation is sub- or supercritical, we compute the first Lyapunov value L_1 [2].

For $\alpha = 1$, $H_{\alpha=1} : \frac{\gamma}{e} = \frac{c_1(c_1-1)(c_1+2\delta+c_1\delta+c_1^2)}{(c_1+1)^2(c_1+\delta)}$, and the first Lyapunov value is $L_1(H_{\alpha=1}) \cong \frac{(c_1-1)^6 c_1^6 \delta (c_1^2+c_1+2\delta-c_1\delta)}{(c_1+1)^{10}(c_1+\delta)^5}$. Thus, $L_1 > 0$ for $(c_1^2+c_1+2\delta-c_1\delta) > 0$ and $L_1 < 0$ for $(c_1^2+c_1+2\delta-c_1\delta) < 0$. Since $\frac{dTr(A)}{d(\gamma/e)} \neq 0$, the former case corresponds to the subcritical Hopf bifurcation, and the latter case corresponds to the supercritical Hopf bifurcation (see [18]).

The case $L_1(H_{\alpha=1}) = 0$ corresponds to Bautin (generalized Hopf) bifurcation of co-dimension 2. It happens in the System (11), $\alpha = 1$ for large δ ; the schematic bifurcation diagram is presented in Figure 10c. Next, we analyze the Hopf bifurcation for $\alpha = 0$.

Proposition 3. *Equilibrium A_α of System (11) with $\alpha = 0$ changes stability only via subcritical (catastrophic) Hopf bifurcation.*

Proof. $H_{\alpha=0} : \frac{\gamma}{e} = \frac{(c_2-\phi)(c_2-1)(c_2(\delta+\phi)+\phi(\delta-\phi))}{c_2(c_2\delta+\phi(c_2-\phi))}$, $N_0(\alpha = 0) = \frac{(c_2-\phi)^2 e(c_2-1)}{c_2(c_2\delta+\phi(c_2-\phi))}$. The sign of the first Lyapunov quantity L_1 is calculated using the formula given in [2]. We have shown that $L_1 = l\hat{L}$, where l is a positive constant, and $\hat{L}_1 = \delta(-(c_2-\phi)(c_2-\phi+\delta) + c_2(c_2-\phi+2\delta))((c_2-1)(c_2-\phi)^2 e - c_2\delta N_0)$. It is easy to verify that $\hat{L}_1 = 0$ for $\delta = 0$ and $\delta = -\frac{\phi(c_2-\phi)}{c_2+\phi}$ that are non-positive for positive N_0 . $\hat{L}_1 = 0$ also for $\delta = -\frac{\phi(c_2-\phi)}{c_2-1}$, which is negative for the required $c_2 > \phi$ and $c_2 > 1$; if $c_2 < 1$, then $\frac{\gamma}{e} = \frac{(c_2-\phi)(1+\phi)(c_2-1)}{c_2} < 0$. Thus, $L_1(H) > 0$.

The statement is proven. □

Summarizing, we have shown that for some parameter values $L_1(H) = 0$ for $\alpha = 1$, and $L_1(H) \neq 0$ for $\alpha = 0$. Due to the continuity arguments, there have to exist $\alpha^* \in (0, 1)$, such that System (11) has a stable limit cycle if $1 \geq \alpha > \alpha^*$, and has no one if $0 \leq \alpha < \alpha^*$.

A.5. Bifurcation diagrams of System (11) and interpretation of model dynamics.

A.5.1. *Phase portraits of the System.* In Figure 11 five phase portraits of System (11), $\alpha = 0$ are presented. Phase portraits of System (11) for $\alpha = 1$ were presented in [16]. The sequences of dynamical behaviors that are depicted in these portraits are realized in the System for fixed $0 < \alpha \leq 1$ with variation of parameters c_0 and/or c_1 , or for fixed c_0 and/or c_1 with variation of $0 < \alpha \leq 1$. Note that the phase-parameter portraits of System (11) with $\alpha = 0$ were topologically similar to those obtained at $\alpha = 1$ with the addition of Domain 0 and exception of Domain 6. In the original formulation of the model with $\alpha = 0$ [17] some trajectories left the first quadrant for certain initial values, thus causing the model to lose biological relevance. However, the change of variables $\frac{dt}{z(N+z)} \rightarrow d\tau$ allowed to

investigate the smooth System (11), which is topologically equivalent to System (1) for $N \geq 0, z > 0$.

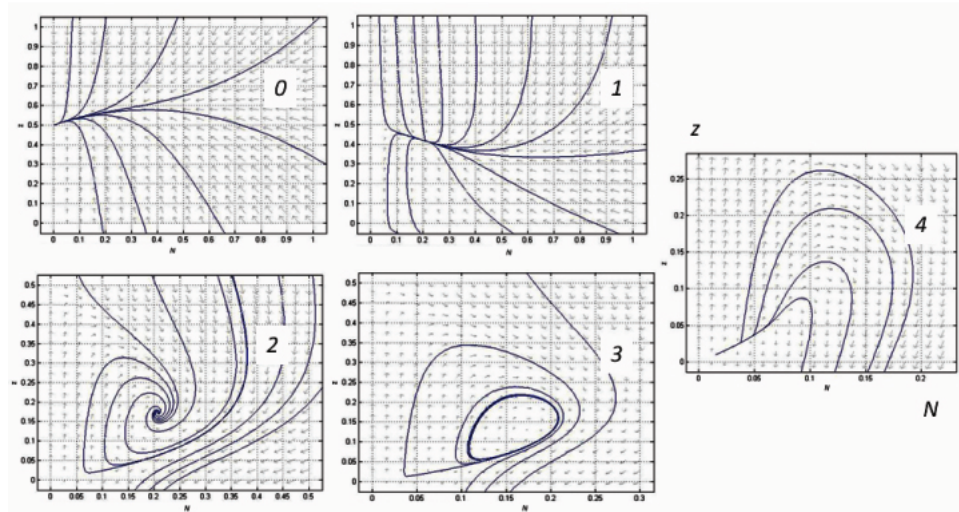


FIGURE 11. Phase-parameter portraits of System (11) for $\alpha = 0$. In Domain 0 (where $0 < c_2 < \phi$), only the trivial equilibrium B is an attractor. In Domain 1, non-trivial equilibrium point A_α is a global attractor. Domain 2 is a region of bistability: there are two attracting points, A_α and origin O , whose basins of attraction are divided by separatrix of point O . In Domain 3, an unstable limit cycle is formed around stable point A_α , further decreasing its basin of attraction. In Domain 4, the limit cycle shrinks, sits on the point A_α , making it unstable. Starting from Domain 2, some trajectories in fact travel outside of the first quadrant, predicting positive population size for negative amount of resources, thus rendering the model biologically irrelevant in this region of phase-parameter space.

A.5.2. *Bifurcation diagram.* Based on results formulated in Propositions (1) - (3) we are able to construct the schematic bifurcation diagram of System (11):

Theorem A.4. (1) For any $\alpha \in [0, 1]$, positive $c_1, c_2, e, \delta, \gamma$ -parameter space of System (11), can be divided into seven domains of topologically non-equivalent phase portraits with non-negative coordinates (N, z) :

(2) In Domain 0, $c_2 \in (0, \phi)$, only point $B(N = 0, z = \frac{\gamma}{\delta})$ is attractive (see Figure 9a). In Domain 1, the only non-trivial equilibrium point $A_\alpha(\hat{N}_\alpha, \hat{z}_\alpha)$ is attractive; its coordinates are given in Equation (17). In Domains 2 and 3, point A_α shares basins of attraction with equilibrium point O at the origin. The separatrix of O and the unstable limit cycle that contains point A_α serve correspondingly as the boundaries of the basins of attraction. In Domain 4, only equilibrium O is globally attractive; it contains attractive parabolic sector. Equilibrium A_α is positive and unstable. In Domain 5, only point O is globally attractive. It contains an elliptic sector in its positive neighborhood. In this region, there is no non-trivial positive equilibrium.

Domain 6 exists only for $1 \geq \alpha > \alpha^* > 0$ (i.e., when α is closer to 1 than to 0). It is a domain of bistability. In it there are two attractive manifolds: a stable limit cycle, h contains an unstable equilibrium point A_α , and an equilibrium point O at the origin.

(3) Boundaries between Domains correspond to the following bifurcations in System(12): K and S correspond to heteroclinic connection between point O , an infinitely removed saddle point (see Figure 10a,b), and point B . Boundary H corresponds to the Hopf bifurcation (H^+ and H^- correspond to sub- and supercritical bifurcations respectively). $Nul \equiv \Delta = 0$ corresponds to the appearance of an unstable point A in the positive quadrant. Boundary C corresponds to the fold bifurcation of limit cycles.

Note that parameter portraits in Figure 1 demonstrate the schematic slices of complete bifurcation portrait, projected to the planes (α, c_2, c_1) and (N, z) . The boundary lines correspond to bifurcations of co-dimension 1, and points of intersections of the lines correspond to bifurcations of higher co-dimensions.

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