#### **6. Niche model**

**6.1. Introduction**

**Object** Coexistence of two biological species

**Object clarification** coexistence – – with presence two types of habitat, niche model

**Foundation** Phase plane for the system of differential equations

**Aim** Definition of the law of change in the number of both species depending on the conditions of the process

**6.2. Niche model**

**General supposition** Two species that consume two types of food.

 The function *xi=xi*(*t*) describes the number of *i-*th species at the time *t*, *i=*1,2.

Consider two biological species located in a same area. We assume that none of them directly affects the other species. Lake competition model, they are consuming the same food, they certainly enter into intense competition between themselves in view of the limited amount of food. However, we have two types of food. Each species prefers a different type of food, but can also consume other foods.

Determine a mathematical model of the considered process. Obviously, the velocity of number change for *i*th species is proportional to the number of this species

 ** (1)

where *ki* is the growth of the number of this species, *i* = 1,2. If the quantity of foods is unbounded, then these coefficients are constant, and we can analyse these equations separatly. If the quantity of foods is bounded, then the growth coefficients are less and depend from the number of population. Note that both species consume two types of food. Now we get the following ***system of differential equations***

  (2)

where *ai* is the real coefficient of growth, and *bij* is a consumption of *j*thfood for *i*th species, *i*,*j* = 1,2. The formulas (2) are called the ***niche equations***.

For obtaining its uniqie solution, it is necessary to add the initial conditions. Suppose we now the initial numbers of species *x*10 and *x*20. Now we have theinitial conditions

 *xi*(0) = *xi*0, *i=*1,2. (3)

The Caushy problem (2), (3) id called the ***niche model***.

 **6.3. Equilibrium states for the system**

Find the equilibrium position for the system (1). Equating the right-hand sides of these equations to zero, we have two equalities

 (*a*1–*b*11*x*1–*b*12*x*2)*x*1 = 0, (4)

 (*a*2–*b*21*x*1–*b*22*x*2)*x*2 = 0, (5)

From the equality (4), it follows that *x*1=0 or *a*1–*b*11*x*1–*b*12*x*2=0. If the first of them is true, then the equality (5) takes the form (*a*2*–b*22*x*2)*x*2=0. Now we can find *x*2=0 or *a*2*–b*22*x*2=0. Therefore, we have two equilibrium positions *x*1=0, *x*2=0 and *x*1=0, *x*2=*a*2/*b*22. Analogically, from the equality (5), we find *x*2=0 or *a*2–*b*21*x*1–*b*22*x*2=0. If the first of them is true, then the equality (4) takes the form
(*a*1*–b*11*x*1)*x*1=0. Now we can have *x*1=0 or *a*1*–b*11*x*1=0. Therefore, we find two equilibrium positions *x*1=0, *x*2=0 and *x*2=0, *x*1=*a*1/*b*11. The first of them was be determined before. However, it is possible the case, where the first multipliers of both equalities (4), (5) are equal to zero. This corresponds to the system of algebraic equations

  (6)

Denote its solution by *x*1\*, *x*2\*. Hence, the considered system has four equilibrium positions

 *x*1=0, *x*2=0; *x*1=*a*1/*b*11, *x*2=0; *x*1=0, *x*2=*a*2/*b*22; *x*1=*x*1\*, *x*2= *x*2\*. (7)

First equilibrium state (the point *O*)is trivial that corresponds to the absence of both species. For the second equilibrium position (the point *A*1), we have the first species, and the second one is absent. For the third case (the point *B*2), we have the inverse situation with presence of the first species and the absence of the second one. For the fourth case (the point *C*), we have the presence of both species. However, we can have the degenerate case if the following equalities hold

 *a*1 /*b*11=*a*2/*b*21, *a*1/*b*21=*a*2/*b*22. (8)

Hence, all non-negative values *x*1,*x*2, satisfying the equality *b*11*x*1+*b*12*x*2=*a*1, correspond the equilibrium positions.

**6.4. Dividing of the phase space for the system**

Consider again the first quadrant of the plane. Then the value at the right hand-side of the first equality (2) is positive if the number *a*1–*b*11*x*1–*b*12*x*2 is positive, i.e., *k*1>0; see equality (1). This is true if *b*11*x*1+*b*12*x*2 is less than *a*1. Therefore, the derivative of the first unknown function is positive, and this function increases if the point (*x*1,*x*2) staies lower than the line *b*11*x*1+*b*12*x*2=*a*1, i.e., *k*1=0. Then the function *x*1 decreases if the point (*x*1,*x*2) staies upper than this line, i.e. *k*1<0.

Analogically, the value at the right hand-side of the second equality (2) is positive if the number *a*2–*b*21*x*1–*b*22*x*2=0 is positive, i.e., *k*2>0; see equality (1). This is true if *b*21*x*1+*b*22*x*2 is less than *a*2. Therefore, the derivative of the second unknown function is positive, and this function increases if the point (*x*1,*x*2) staies lower than the line *b*21*x*1+*b*22*x*2=*a*2, i.e., *k*2=0. The function *x*2 decreases if the point (*x*1,*x*2) staies upper than this line, i.e. *k*2<0.

Unlike the competition model, in this case the lines *k*1=0 and *k*2=0 are, generally speaking, not parallel. Thus, there are a greater number of options for the relative position of these lines, and behind each such option there is a special behavior of the system under study.

First, lines may or may not intersect in the first quadrant of the plane. In order to find out whether they intersect or not, it is enough to compare the points of intersection of the lines under consideration with the coordinate axes. Obviously, the line *k*1=0 intersects the *x*1-axis at the point *A*1 with coordinate (*a*1/*b*11,0), and *x*2-axis at the point *B*1 with coordinate (0,*a*1/*b*12). Analogically, the line *k*2=0 intersects the *x*1-axis at the point *A*2 with coordinate (*a*2/*b*21,0), and *x*2-axis at the point *B*2 with coordinate (0,*a*2/*b*22). Note that the points *A*1 and *B*2 are the equilibrium states of the system (2).

The lines under consideration do not intersect if both points of intersection of the first line with the coordinate axes *A*1 and *B*1 are located further from the origin of coordinates (see Figure 1) or both are further from it (see Figure 2) than the corresponding points *A*2 and *B*2 of the second line. If one of the indicated points of the first line is located closer to the origin of coordinates, and the other is further away than the corresponding points of the second line, then these lines intersect (see Figures 3 and 4). Finally, degenerate cases are possible when the lines intersect directly on the coordinate axes (the cases *A*1=*A*2 or *B*1=*B*2)or even coincide (the case *A*1=*A*2 and *B*1=*B*2).

Let the point *A*1 be located to the right of *A*2, and point *B*1 be located above *B*2, i.e., the line *k*1=0 is higher than *k*2=0. This first variant of the system evolution is true if the following inequalities hold

 *a*1/*b*11>*a*2/*b*21, *a*1/*b*21>*a*2/*b*22. (9)

Then the phase plane can be divided by three parts; see Figure 1. In this case, both functions decrease if the point (*x*1,*x*2) staies higher than both lines. Both functions decrease if this point staies lower than both lines. First finction increases, and the second one decreases if this point staies between these lines.



Figure 1. Directions of the system evolution.Variant 1.

Suppose, on the contrary, now the point *A*2 be located to the right of *A*1, and point *B*2 be located above *B*1, i.e., the line *k*2=0 is higher than *k*1=0. This second variant of the system evolution is true if the following inequalities hold

 *a*1/*b*11<*a*2/*b*21, *a*1/*b*21<*a*2/*b*22. (10)

Then the phase plane can be divided too by three parts; see Figure 2. In this case, both functions again decrease if the point (*x*1,*x*2) staies higher than both lines. Both functions decrease if this point staies lower than both lines. First finction decreases, and the second one increases if this point staies between these lines.



Figure 2. Directions of the system evolution. Variant 2.

Now consider the intersection of the lines k1=0 and k2=0. This is true if the point A2 be located to the right of A1, and point B1 be located above B2 or for the inverse situation. Let the first case is realized that is the third variant of the system evolution. This is possible under the conditions

 *a*1/*b*11>*a*2/*b*21, *a*1/*b*21<*a*2/*b*22. (11)

The plan is divided now by four parts. The corresponding directions of the system evolution depends on the location of the point relative to both curves under consideration (see Figure 3). The directions of system evolution (variant 4) when opposite inequalities

 *a*1/*b*11<*a*2/*b*21, *a*1/*b*21>*a*2/*b*22 (12)

are satisfied are shown in Figure 4.

We have also the corresponding degenerate cases. If the following conditions hold

*a*1/*b*11=*a*2/*b*21, *a*1/*b*21>*a*2/*b*22,

then we have the situation of Figure 1 with equality *A*1=*A*2. Inverse situation with conditions

*a*1/*b*11>*a*2/*b*21, *a*1/*b*21=*a*2/*b*22

correspond to the Figure 1 with equality *B*1=*B*2. The conditions

*a*1 /*b*11=*a*2/*b*21, *a*1/*b*21<*a*2/*b*22

correspond to the Figure 2 with equality A1=A2. Besides, the conditions

*a*1 /*b*11<*a*2/*b*21, *a*1/*b*21=*a*2/*b*22

correspond to the Figure 2 with equality B1=B2. Finally, we can have both equalities A1=A2 and B1=B2 with coincidence of two lines that is the fiveth variant of the system; see Figure 5.



Figure 3. Directions of the system evolution. Variant 3.



Figure 4. Directions of the system evolution. Variant 4.



Figure 5. Directions of the system evolution. Variant 5.

**6.5. Analysis of the system evolution. Variant 1.**

Suppose the inequalities (9) hold. The law of the system evolution depends from the initial state of the system. Let both initial states be small enough such that the point of start is lower than the lower line. In this case, both derivatives are positive, so both functions increase; see Figure 6, curve 1. Over time, the phase curve will reach the lower straight line. At this time, the derivative of the second function becomes zero, while the derivative of the first function remains positive. Thus, the movement in the direction of growth of the second function will stop, while the first function continues to increase. As a result, we find ourselves in the area between two straight lines. In this region, the second function begins to decrease, while the first function continues to increase. This is an analogue of the corresponding phase curve for the competition equation. As result, the system tends to the point *A*1that is the equilibrium position *x*1=*a*1/*b*11, *x*2=0.



Figure 6. Evolution of the system for Variant 1.

Suppose now both initial states be large enough such that the point of start is upper than the upper line. Then both functions decrease; see Figure 6, curve 2. Over time, the phase curve will reach the upper straight line. At this time, the derivative of the first function becomes zero, while the derivative of the second one remains positive. Thus, the movement in the direction of growth of the first function will stop, while the second function continues to decrease. As a result, we find ourselves again in the area between two straight lines. As we already know, in this case the system reaches an equilibrium position that is the point *A*1. However, a variant is possible when, in the process of decreasing function *x*2, we do not end up in the middle zone, but immediately find ourselves in an equilibrium position, see Figure 6, curve 3. This case is realized if the initial value of *x*2 was sufficiently small. Finally, the point of start can be between two lines; see Figure 6, curve 4. In this case the the first function is monotonically increasing, and the second is monotonically decreasing. This continues until an equilibrium position.

Thus, in this case, the only outcome will be the value *x*1=*a*1/*b*11, *x*2=0, which turns out to be a stable equilibrium position. The equilibrium positions *x*1=0, *x*2=0 and *x*1=0, *x*2=*a*2/*b*22 are unstable, and *x*1=*x*1\*, *x*2= *x*2\* is impossible for Variant 1.

We can have the analogical results if one of the inequalities (9) is changed by the corresponding equality.

**6.6. Analysis of the system evolution. Variant 2.**

Suppose the inequalities (10) hold. This situation is the opposite of that considered in the previous version. There are also four options for system evolution. However, in this case, the second type turns out to be the strongest and wins regardless of the initial state of the system. As a result, the system reaches an equilibrium position *x*1=0, *x*2=*a*2/*b*22, which corresponds to the point *B*2; see Figure 7. This is the stable equilibrium position, and the states *x*1=0, *x*2=0 and *x*1=*a*1/*b*11, *x*2=0 are non-stable. The equilibrium position *x*1=*x*1\*, *x*2= *x*2\* is impossible for Variant 2 too. We can have the analogical results if one of the inequalities (10) is changed by the corresponding equality.



Figure 7. Evolution of the system for Variant 2.

**6.7. Analysis of the system evolution. Variant 3.**

Suppose the inequalities (11) hold. Now we have many variants of the system evolution, which depend from the initial state of the system. If the initial point stays dawn the line *k*1=0, but upper *k*2=0, that corresponds the curve 8 of Figure 8, then the first function decreases and tends to zero, and the second one increases. Hence, the system moves to the equilibrium position *x*1=0, *x*2=*a*2/*b*22, which corresponds to the point *B*2. Inverse situation is the case, where the initial point stays dawn the line *k*2=0, but upper *k*1=0, that corresponds the curve 7 of Figure 8. Then the first function increases and tends to zero, and the second one decreases, so the system tends to the equilibrium position *x*1=*a*1/*b*11, *x*2=0, which corresponds to the point *A*1.



Figure 8. Evolution of the system for Variant 3.

Suppose now both functions are initialy small enough such that the point of start is dawn than both lines. Then both functions increase. We can have two different situations here. Maybe initial value of the first function is larger than second one, and with time, the system tends to the point *A*1; see the curve 1.However, we can have the inverse situation, and the system tends to the point *B*2; see the curve 2. Let now both functions be initialy large enough such that the point of start is upper than both lines. Then both functions decrease. We can have two different situations here too. If the initial value of the first function is larger than second one, then with time, the system tends to the point *A*1; see the curve 3. For the inverse case, the system tends to the point *B*2; see the curve 4. However, we have two cases extra. If both initial values are large enough, but the initial value of the second function is significantly less that the first one, then both functions decrease monotonously; and the second function tends to zero; see curve 6. For the inverse case, both functions decrease monotonously, but the first function tends to zero; see curve 5.

For Variant 3, the trivial equilibrium position and the state *x*1=*x*1\*, *x*2= *x*2\* are non-stable, but the equilibrium positions *x*1=*a*1/*b*11, *x*2=0 and *x*1=0, *x*2=*a*2/*b*22 are stable.

**6.8. Analysis of the system evolution. Variant 4.**

Suppose the inequalities (12) hold. If both functions are large enough at the initial time such that the point of start is upper than both lines, then both functions decrease and tend to the equilibrium position *x*1=*x*1\*, *x*2= *x*2\* that is the point *C*; see Figure 9. If both initial values are small enough such that the point of start is below than both lines, then then both functions increase and tend to the point *C* too. In the point of start is between the considered lines, besides the first value is small, and the second one is large enough, then the first function increases, and the second function decreases. The system tends to the point *C* again. For the inverse situation, the first function decreases, and the second in increases, but the system tends to the point *C*.



Figure 9. Evolution of the system for Variant 4.

For Variant 4, the equilibrium states *x*1=0, *x*2=0, *x*1=*a*1/*b*11, *x*2=0, and *x*1=0, *x*2=*a*2/*b*22 are non-stable, and the equilibrium position *x*1=*x*1\*, *x*2= *x*2\* is stable.

**6.9. Analysis of the system evolution. Variant 5.**

Suppose the equalities (8) hold, i.e., the lines *k*1=0 and *k*2=0 coincide, and we have the degenerate case.If the initial state is small enough, then the point of start is lower than the considered line. Hence, both derivatives of the state functions are positive, so these functions increase. As the phase curve approaches the indicated straight line, both derivatives in equalities (2) become smaller and smaller. Thus, this straight line is reached in the limit with an unlimited increase in time; see Figure 10, curves 1. The specific value of the equilibrium position on the segment is determined by the starting point.



Figure 10. Evolution of the system for Variant 4.

**6.10. Interpretation of results**

Niche model analysis has two levels, similar to the competition model. First of all, the outcomes of possible events should be explained, i.e. the system reaches a particular equilibrium position. Then, for each of the possible outcomes, the options for the evolution of the system should be described and the reason for this particular development of events should be explained.

Each of the described outcome options is determined by the relationships between the coefficients of the system of equations under consideration. The determining role here is played by values *ai*/*bij* that characterize the relationship between the growth of *i*th species and the consumption of *j*th type of food. The value of this value, as for the competition model, characterizes the viability of this species. However, unlike the competition model, there are two indicators of vitality due to the presence of two types of food.

The validity of conditions (9), i.e. inequalities

*a*1/*b*11>*a*2/*b*21, *a*1/*b*21>*a*2/*b*22,

means increased vitality of the first type over the second in terms of both indicators. As can be seen from Figure 6, in this case, regardless of the initial population size, the second species, which is weaker, dies out over time. The situation will not change if one of these relations is fulfilled in the form of equality. Indeed, this means an advantage of the first species in one of the indicators of vitality, with equal values of the other indicator in both species. The fulfillment of opposite inequalities (10) indicates increased vitality of the second type. As a result, as can be seen from Figure 7, he wins.

Inequalities (11) and (12) mean that each species is superior to another species in one of the indicators, but inferior to it in another indicator. The difference between these situations is that when conditions (12) are met, each species gives preference to “its own” type of food, and when inequalities (11) are met, to the “alien” type. In the first case, victory can go to any of the species, depending on the values of their initial numbers, while the other species is likely to become extinct; see Figure 8. If each species prefers its own type of food, then, regardless of the initial population size, both species survive, which corresponds to the niche effect; see Figure 9. This circumstance explains the diversity in nature of the animal and plant world. Finally, the degenerate case, characterized by inequalities (8), means that species have the same viability in both indicators, i.e. in fact, the population can be considered homogeneous. As can be seen from Figure 11, in this case, not one of the species can displace the competitor.

The evolution of the system in each specific case is determined by the relationship between the available constant amount of food and the changing need for it. When the population size is high, there is a shortage of food, and the number of the species decreases. If the number of a species is small, then there is enough food, which stimulates population growth.