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## **MATHEMATICAL MODELING AND SIMULATION OF MULTIALLELIC MIGRATION-SELECTION MODELS**

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### **Abstract**

Population ecology is concerned with the growth and decay of specific populations. This field has a variety of applications ranging from evolution and survival at the environmental level to the spread of infectious disease at the cellular and molecular levels. Many ecological circumstances require the use of mathematical methods and reasoning in order to acquire better knowledge of the issue at hand. This study considered and analyzed multiple different mathematical models of population dynamics along with their purposes. This foundation was then applied in order to explore the migration of populations from one isolated region to another along with the relationships that those populations have. The following research paper presents the theoretical base, analysis, and specific simulations of this study along with application. The study resulted in a complete classification and analysis of an existing Ecological model with migration added along with proven coexistence with a given migration-selection model.

### **Introduction**

Ecology is an old discipline christened in 1866 by Ernst Haeckel [K]. This field is formally defined as the study of the interrelationships of organisms with each other and with their physical environment [V]. Essentially, Ecology is simply concerned with investigating the way all living things interact and survive. This is a very broad science and as a result has a wide range of application. Common examples of application include agriculture, fisheries, forestry, medicine, and urban development.

There are multiple sub disciplines of Ecology, many of which require the use of mathematical analysis and modeling. The specific subset of Ecology that this research is concerned with is Population Ecology, also known as Autecology [K]. This field deals with the dynamics and relationships of species populations with respect to an environment. Mathematical modeling is an essential tool in this field. There are many models that exist in Population Ecology in order to gain a better understanding of specific phenomenon. The main results that are desired from these models are coexistence and survival. With this area of Ecology, one concept that hasn't been thoroughly explored is that of migration. This research considers this idea of migration through multiple models along with analysis and simulation.

The goal of this study was to analyze and classify all cases of an existing migration-selection model. Basic analysis of an existing Ecological model with migration applied was utilized in order to reach this goal. The two key properties of coexistence and conditional survival are attempted to be found and analyzed completely.

## Survey of Literature

In order for the results of this study to be interesting and significant, the concept of migration had to be initially paired with another model of Population Ecology. The reason for this is because it was discovered early on with this study that migration alone without a relationship between the species of certain population produces trivial results. Many different models were investigated, but the one that was chosen was the classic Lotka-Volterra Competition model. The reason this model was chosen is because it is well explored and offers interesting interaction between species. The Lotka-Volterra model was initially developed in 1932 [K] and as a result this model's dynamics and characteristics are well known. Given this, it is convenient to extend this model into something more complex. This section will introduce the classic Lotka-Volterra model along with common analysis.

The Lotka-Volterra competition model is known as an interference or interspecific competition model. That is, two species are assumed to diminish each other's per capita growth rate by direct interference [K]. In simplest terms, this type of competition involves two species utilizing the same resource within an environment. The exact model is as follows,

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{k_1} - \alpha_{12} \frac{N_2}{k_1}\right) \\ \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{k_2} - \alpha_{21} \frac{N_1}{k_2}\right) \end{cases} \quad (1)$$

$N_i$  = population of species  $i$

$r_i$  = intrinsic growth rate of species  $i$

$k_i$  = carrying capacity of species  $i$

$\alpha_{ij}$  = strength of effect of species  $j$  on species  $i$

where  $r_i$ ,  $k_i$ , and  $\alpha_{ij}$  are positive constants with  $N_i(0) > 0$  [V].

As with the analysis of any system of differential equations, we are concerned with the critical points of system (1). That is, the conditions where

$$\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$$

are a topic of interest. These critical points along with their orientation determine the general behavior of the system. Some simple algebraic manipulation shows that the points  $(0,0)$ ,  $(N_1,0)$ ,  $(0,N_2)$ , along with the solution to the following system

$$\begin{cases} N_1 = k_1 - \alpha_{12} N_2 \\ N_2 = k_2 - \alpha_{21} N_1 \end{cases} \quad (2)$$

are all zeros of this competition model. Each linear equation of (2) is known as a zero growth isocline. Figure 1 describes the behavior that each isocline induces.

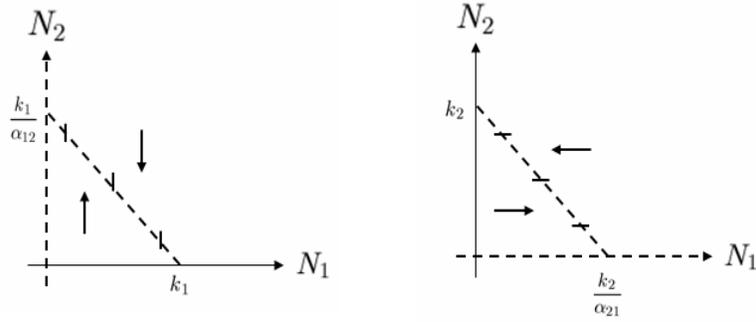


Figure 1: Zero growth isoclines with behavior

The above critical points determine the general behavior of this model. As a result, the manipulation of the parameters of the two isoclines (2) creates all possible classifications of behavior of this model. Considering this, there will be four classifications of this system. If one simply considers the intercepts of each isocline, it is clear why there are four possibilities. Figure 2 shows all possible cases and Figure 3 describes the orientation of each.

	1	2	3	4
$\frac{k_1}{k_2} \circ \alpha_{12}$	>	<	>	<
$\frac{k_2}{k_1} \circ \alpha_{21}$	<	>	>	<

Figure 2: Classic competition model isocline intercept cases

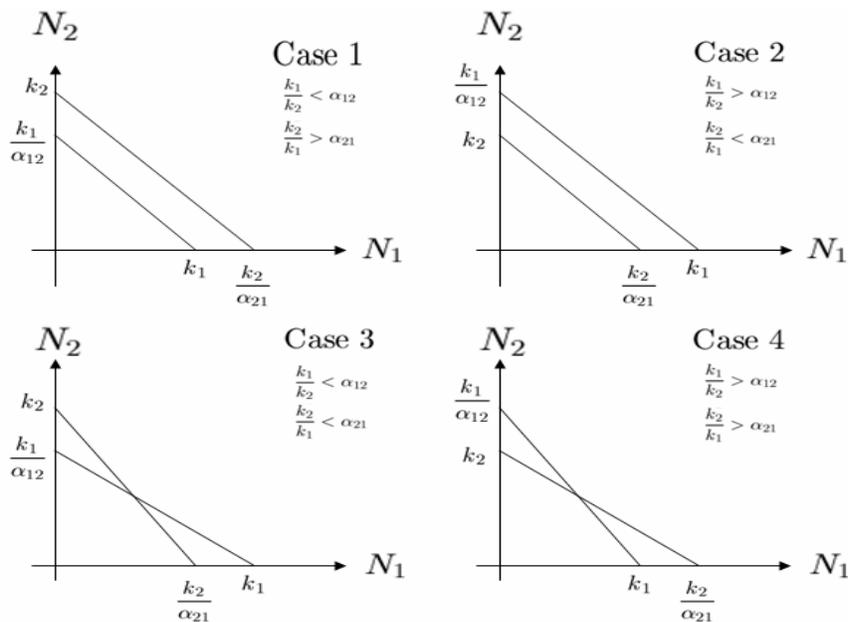


Figure 3: All possible orientations of classic competition model isoclines

Since the classic Lotka-Volterra competition model is of two dimensions, it is natural to analyze these four cases by plotting the phase portrait of each. Figure 4 contains all of these plots. Case 1 and Case 2 represent a larger competition effect on one species and a smaller competition effect on the other. That is, one species competes at a higher level for the needed resources, resulting in dominance of the other species. Interpretation of the phase portraits for these two cases shows that regardless of initial conditions, the weaker competitor will be extinguished. Case 3 represents a large competition effect created by both species. This results in saddle point behavior of this case which is illustrated in Figure 5. What this means is depending on the initial populations of the given species, one will survive and the other will be extinguished. It is also important to note that coexistence is possible in this case but is extremely rare. This will also be referred to as a conditional coexistence case. Case 4 represents a low competition rate for both species. This case ensures coexistence of both species regardless of initial species population values. For this reason, Case 4 is considered to be the most significant of all cases biologically speaking.

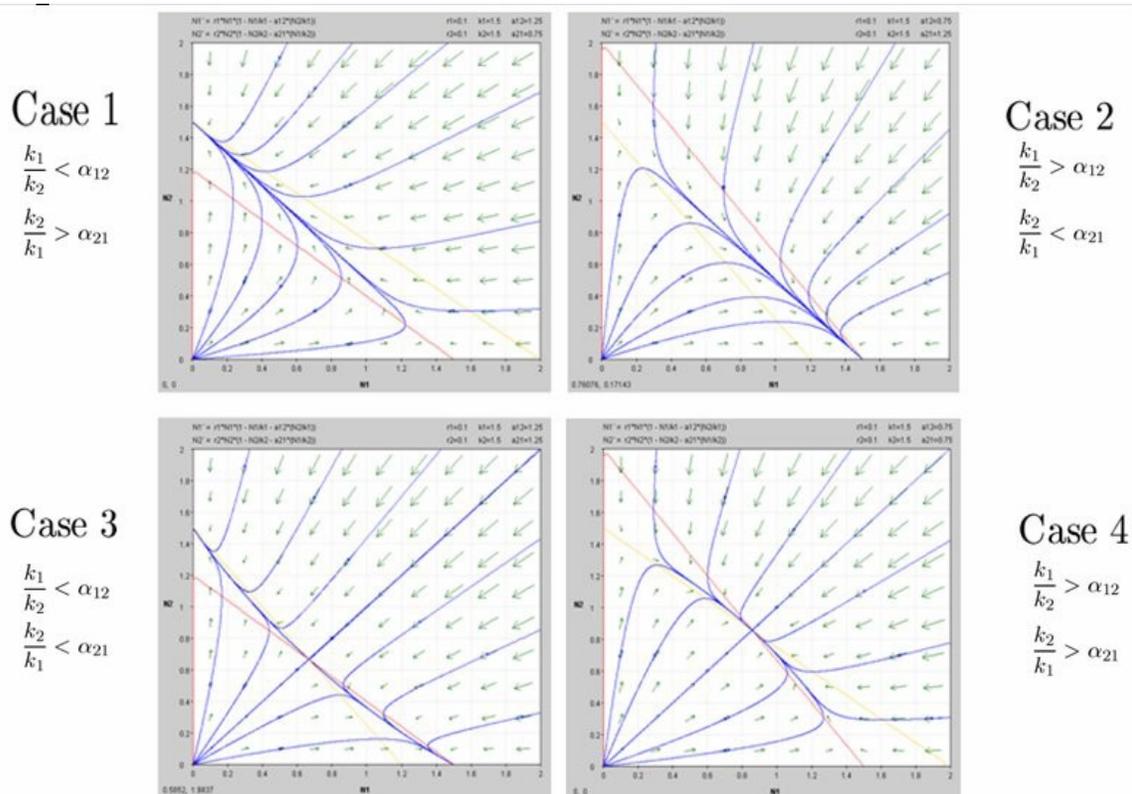
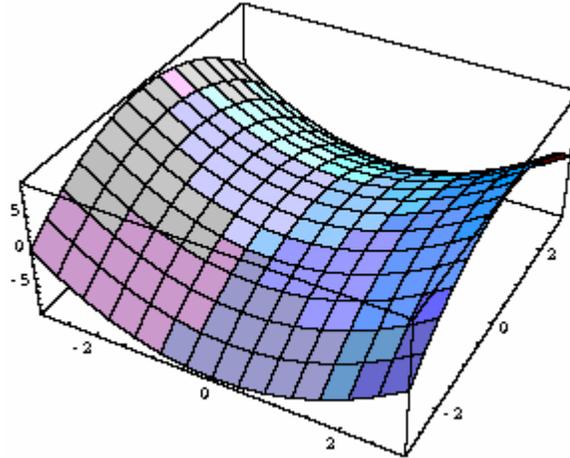


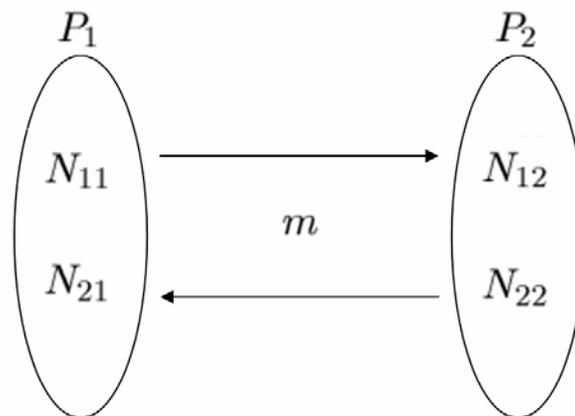
Figure 4: Phase portraits of all cases generated with PPlane



**Figure 5:** Saddle point behavior illustration

## Methods

The first model that this study examines is the modified Lotka-Volterra competition model with migration. The classic Lotka-Volterra competition model describes two different species sharing one habitat. This modification of the classic model implements migration. That is, multiple discrete patches of population are considered instead of one only. The basic case of this modified model considers two species migrating between two different population patches at a certain rate. Figure 6 is the conceptual diagram of the basic case of this model.



$P_i$  = patch  $i$   
 $N_{ij}$  = population of species  $i$  in patch  $j$   
 $m$  = migration rates of individual species

**Figure 6:** Conceptual diagram of modified competition model with migration

The system of differential equations of this model is as follows,

$$\begin{cases} \frac{dN_{11}}{dt} = (m_{12}N_{12} - m_{11}N_{11}) + r_{11}N_{11}\left(1 - \frac{N_{11}}{k_{11}} - \alpha_{11,21}\frac{N_{21}}{k_{11}}\right) \\ \frac{dN_{21}}{dt} = (m_{22}N_{22} - m_{21}N_{21}) + r_{21}N_{21}\left(1 - \frac{N_{21}}{k_{21}} - \alpha_{21,11}\frac{N_{11}}{k_{21}}\right) \\ \frac{dN_{12}}{dt} = (m_{11}N_{11} - m_{12}N_{12}) + r_{12}N_{12}\left(1 - \frac{N_{12}}{k_{12}} - \alpha_{12,22}\frac{N_{22}}{k_{12}}\right) \\ \frac{dN_{22}}{dt} = (m_{21}N_{21} - m_{22}N_{22}) + r_{22}N_{22}\left(1 - \frac{N_{22}}{k_{22}} - \alpha_{22,12}\frac{N_{12}}{k_{22}}\right) \end{cases} \quad (3)$$

$P_i$  = patch i

$N_{ij}$  = population of species i in patch j

$m$  = migration rates of individual species

$r_{ij}$  = intrinsic growth rate of species i in patch j

$k_{ij}$  = carrying capacity of species i in patch j

$\alpha_{ij,kl}$  = strength of effect of species  $N_{ij}$  on species  $N_{kl}$

where  $m_{ij}$ ,  $r_{ij}$ ,  $k_{ij}$ , and  $\alpha_{ij,kl}$  are positive constants with  $N_{ij}(0) > 0$ . It is clear that this model consists of the Classic Lotka-Volterra model paired with the concept of migration between population patches

Analysis of the modified competition model with migration (3) is more complex than the analysis of the classic competition model (1). Since the basic case of this modified model is of four dimensions, the phase plane analysis that was previously explored cannot be used. Instead, the different cases developed are tested and classified through the use of a simulation software package called Berkeley Madonna. Berkeley Madonna is a general purpose differential equation solver developed by the University of California at Berkeley. The code used for testing is included in the appendix of this paper. Following is the analysis of this model.

As with the analysis of the classic competition model, the goal is to determine and manipulate the critical points of this system of equations. That is, we are concerned with the places where

$$\frac{dN_{11}}{dt} = \frac{dN_{21}}{dt} = \frac{dN_{12}}{dt} = \frac{dN_{22}}{dt} = 0$$

occurs. Through some basic algebraic manipulation, one can see that (0,0,0,0) is a critical point along with the following isoclines described in Figure 7. Manipulation of the intercepts of these four isoclines generates 16 different classifications of behavior. Each of case was then simulated and tested thoroughly within the Berkeley Madonna software. Multiple tests considering differing parameters were performed in order to ensure consistency. All were shown to result in the same general outcome.

$$N_{11} \text{ zero growth isoclines: } N_{11} = 0 \ \& \ N_{12} = -\alpha_{21,11} \frac{m_{11}}{m_{12}} N_{21} + k_{11} \frac{m_{11}}{m_{12}}$$

$$N_{21} \text{ zero growth isoclines: } N_{21} = 0 \ \& \ N_{22} = -\alpha_{11,21} \frac{m_{21}}{m_{22}} N_{11} + k_{21} \frac{m_{21}}{m_{22}}$$

$$N_{12} \text{ zero growth isoclines: } N_{12} = 0 \ \& \ N_{11} = -\alpha_{22,12} \frac{m_{12}}{m_{11}} N_{22} + k_{12} \frac{m_{12}}{m_{11}}$$

$$N_{22} \text{ zero growth isoclines: } N_{22} = 0 \ \& \ N_{21} = -\alpha_{12,22} \frac{m_{22}}{m_{21}} N_{12} + k_{22} \frac{m_{21}}{m_{22}}$$

**Figure 7:** Zero growth isoclines of modified competition model with migration

The strategy for testing each classification is as follows. First, certain initial conditions were chosen and fixed for the following variables:  $m_{ij}$ ,  $r_{ij}$ , and  $k_{ij}$ . The variable  $\alpha_{ij,kl}$  was then manipulated in order to examine the trends of each classification. The reason for this is because the competition coefficients were found to be the only independent parameters for each inequality. This strategy proved to be the simplest way to test each case. Once a classification was generated, the initial population of each species was altered in order to test conditional coexistence, unconditional coexistence, and species survival trends.

These tests produced the classification of one unconditional coexistence case and five conditional coexistence cases leaving the remaining ten cases as being dominant by one species or the other. Biologically, this is interpreted as being one situation in which both species considered will survive together regardless of initial populations. As with the classic competition model, this occurs when the competition coefficient is relatively small, but migration factors also play a significant role. The five conditional coexistence cases display the unstable saddle point behavior previously discussed. That is, coexistence is possible, but extremely rare. Most likely, depending on the initial population values, one species will die out completely while the other will survive. Lastly, there are ten cases in which one species is ensured to die off while the other survives. The following table in Figure 8 describes each of these cases along with the classification obtained.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
$\frac{k_{21}}{k_{12}} \circlearrowleft \alpha_{11,21} \frac{m_{21}}{m_{22}}$	>	<	>	>	>	<	<	<	>	>	>	<	<	<	>	<
$\frac{k_{11}}{k_{22}} \circlearrowleft \alpha_{21,11} \frac{m_{22}}{m_{21}}$	>	>	<	>	>	<	>	>	<	<	>	<	<	>	<	<
$\frac{k_{22}}{k_{11}} \circlearrowleft \alpha_{12,22} \frac{m_{11}}{m_{12}}$	>	>	>	<	>	>	<	>	<	>	<	<	>	<	<	<
$\frac{k_{12}}{k_{21}} \circlearrowleft \alpha_{22,12} \frac{m_{12}}{m_{11}}$	>	>	>	>	<	>	>	<	>	<	<	>	<	<	<	<
	**					*	*	*	*	*						*

\*\* unconditional coexistence  
 \* conditional coexistence (unstable)

Figure 8: All 16 possible orientation cases of modified competition model isoclines

The second model analyzed with this study considers is a migration-selection model developed by Thomas Nagylaki. This model is discussed in much of Nagylaki’s current research, but a correct classification of each case has yet to be researched. The exact system is described as follows [N2].

$$\frac{dP_{ik}}{dt} = q \sum_l (m_{kl} P_{il}) + \gamma P_{ik} \left( \sum_j (r_{ijk} P_{jk}) - \sum_{ij} (r_{ijk} P_{ik} P_{jk}) \right) \quad (4)$$

$P_{ik}(t)$  = gene frequency of Allele  $A_i$  in deme  $k$  at time  $t$

$m_{kl}$  = probability that an individual in deme  $k$  migrates from deme  $l$

$\gamma$  = selection factor

$q$  = migration factor

$r_{ijk}$  = viability of Alleles  $A_i A_j$  in deme  $k$  ( $r_{ijk} = r_{jik}$ )

Note:

$$\sum_l m_{kl} = 1 \quad \text{each } k$$

$r_{ijk} = s_{ik} + s_{jk}$  where  $s$  = dominance of individual Allele

This model is described at the genetic level simply because its application lies with Population Genetics, a sub discipline of Population Ecology.

As with the analysis of the modified competition model, the basic case was considered. That is three species migrating two discrete population patches were explored. The reason three species were chosen instead of two is a consequence of selection. Selection is only interesting for three or greater species. If only two were implemented, only trivial results were produced. Considering the basic case of three species and two patches, this is the resulting model.

$$\left\{ \begin{array}{l} \frac{dP_{11}}{dt} = q \sum_l (m_{1l}P_{1l}) + \gamma P_{11} ( \sum_j (r_{1j1}P_{j1}) - \sum_{ij} (r_{ij1}P_{i1}P_{j1}) ) \\ \frac{dP_{21}}{dt} = q \sum_l (m_{2l}P_{2l}) + \gamma P_{21} ( \sum_j (r_{2j1}P_{j1}) - \sum_{ij} (r_{ij1}P_{i1}P_{j1}) ) \\ \frac{dP_{31}}{dt} = 1 - P_{11} - P_{21} \\ \frac{dP_{12}}{dt} = q \sum_l (m_{1l}P_{1l}) + \gamma P_{12} ( \sum_j (r_{1j2}P_{j2}) - \sum_{ij} (r_{ij2}P_{i2}P_{j2}) ) \\ \frac{dP_{22}}{dt} = q \sum_l (m_{2l}P_{2l}) + \gamma P_{22} ( \sum_j (r_{2j2}P_{j2}) - \sum_{ij} (r_{ij2}P_{i2}P_{j2}) ) \\ \frac{dP_{32}}{dt} = 1 - P_{12} - P_{22} \end{array} \right. \quad (5)$$

The strategy for analysis of this model was the same as the previous models. The null points of this system were found and analyzed. Isoclines were considered along with the intercepts they generated. Due to the complexity of this system, each individual case wasn't able to be classified. There proved to be too many parameters which didn't allow for a simplification of each case. That is, when the strategy applied to the modified competition model was used with this migration-selection model, complete testing through simulation within Berkeley Madonna was unsuccessful.

Even though this is true, some meaningful results were still found. Through simulation and experimentation, coexistence with this model was shown to occur. One example of this is displayed in the appendix. This coexistence displays the saddle point behavior seen in the previous models. That is, this case of coexistence is quite unstable. Biologically this is significant. This mathematically proves that under certain conditions all three alleles can stably coexist within a migration-selection model.

## Conclusions

This study provided some significant results with regards to Population Ecology and migration. First, each case of the modified competition model with migration was successfully analyzed and classified. This classification provides a complete knowledge of the dynamics and behavior of this specific model. Analysis was also reinforced and confirmed through the use of

simulation and numerical experimentation. It was shown that unconditional coexistence is possible and conditional coexistence also can occur.

The second set of results was produced through analysis of the migration selection model. It was shown that coexistence for this model is possible, but complete classification of each case was not accomplished. All of the coexistence cases found were found to be unstable and could be considered as a conditional coexistence case. This is primarily a result of the complexity of this model.

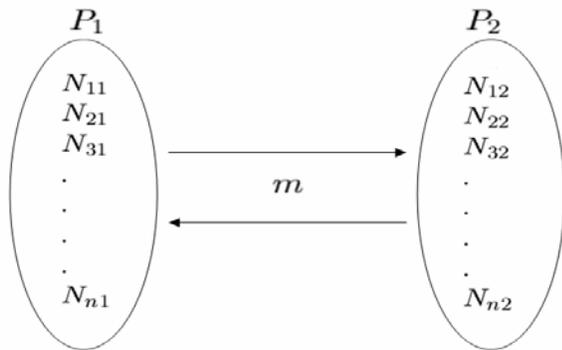
## Discussions

The results found can be interpreted to have significant meaning. The first results drawn show the complete classification of the modified competition model with migration. That is, when considering a population model involving only interspecific competition and migration there is a complete understanding of the dynamics involved. This is useful when one either wants to predict the exact outcome or engineer a specific outcome of a population which fits this model.

The second analysis performed considered Nagylaki's migration-selection model. Even though a complete classification wasn't reached, it was shown that coexistence is possible with the basic case of three species and two discrete population patches. This is significant because exact conditions were discovered that ensure coexistence. Again, if one wishes to engineer coexistence of a population of genes which fits this model, it is shown to be possible.

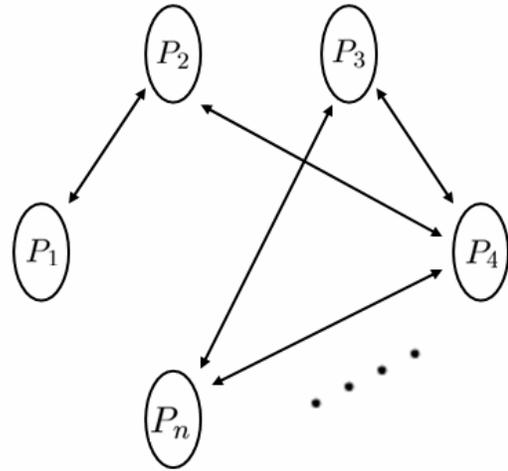
These results are not only helpful when considering migration and competition or migration and selection with certain ecological situations, but it also suggests that migration can be paired and analyzed with other Ecological models. With Population Ecology, it isn't useful to simply consider one or even two models with a study. Often multiple models are combined to include all biological phenomena in order to develop a more accurate and significant system. The results of this study show that migration can be combined with other models in order to offer meaningful outcomes.

There are multiple areas to go from here when considering future study. Since only the basic case for the modified competition with migration model and the migration selection model were considered, more complex cases can be examined. For example, analysis can be extended to  $n$  different populations or even  $n$  discrete population patches in either of these cases. Combinations of these two can also be explored. Figure 9 and figure 10 displays these possibilities. Also, as previously suggested, migration could be applied to multiple existing Population Ecology models as desired. This depends on the specific Ecological situation considered. Lastly, the complete classification of the migration-selection was not complete. In order for the strategies used with this research to be successful, the migration-selection model itself needs to be simplified. Otherwise, another analysis technique could be used in order to accomplish this.



$P_i$  = patch  $i$   
 $N_{ij}$  = population of species  $i$  in patch  $j$   
 $m$  = migration rates of individual species

**Figure 9:** A given migration model considering  $n$  species



**Figure 10:** A given migration model considering  $n$  discrete population patches

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## Appendix 1

Berkeley Madonna code:

### Classic Lotka-Volterra Competition Model

```

METHOD RK4

STARTTIME = 0
STOPTIME=100
DT = 0.02

{competition model with 1 patch and 2 species}
d/dt(N1) = r1*N1*(1 - N1/k1 - a12*(N2/k1))
d/dt(N2) = r2*N2*(1 - N2/k2 - a21*(N1/k2))

{initial values of species N1 and N2}
init N1 = 50
init N2 = 12

{growth rates}
r1 = 0.2
r2 = 0.15

{competition rates}
a12 = 0.1
a21 = 0.15

{carrying capacities}
k1 = 30
k2 = 20

```

### Modified Competition Model with Migration

```

METHOD RK4

STARTTIME = 0
STOPTIME=100
DT = 0.02

{competition model with 2 patches and 2 species with species Nij, ith species jth patch}
d/dt(N11) = (m12*N12 - m11*N11) + r11*N11*(1 - N11/k11 - a11_21*(N21/k11))
d/dt(N21) = (m22*N22 - m21*N21) + r21*N21*(1 - N21/k21 - a21_11*(N11/k21))

d/dt(N12) = (m11*N11 - m12*N12) + r12*N12*(1 - N12/k12 - a12_22*(N22/k12))
d/dt(N22) = (m21*N21 - m22*N22) + r22*N22*(1 - N22/k22 - a22_12*(N12/k22))

{initial values of species N11, N21, N12, and N22}
init N11 = 1.5
init N21 = 1.5

init N12 = 1.5
init N22 = 1.5

{growth rates}
r11 = 0.1

```

r21 = 0.1  
 r12 = 0.1  
 r22 = 0.1

{competition rates}  
 a11\_21 = 0.5  
 a21\_11 = 0.5  
 a12\_22 = 0.5  
 a22\_12 = 0.5

{carrying capacities}  
 k11 = 1.5  
 k21 = 1.5  
 k12 = 1.5  
 k22 = 1.5

{migration rates}  
 m11 = 0.1  
 m21 = 0.1  
 m12 = 0.1  
 m22 = 0.1

## Migration-Selection Model

```
{ 3 Alleles, 2 patches model }
{ d/dt(p_i,k)=sum_{j}( m_k,j*p_i,j ) + r*p_i,k*[sum_{j}( r_ij,k*p_j,k ) - sum_{l,j}( r_lj,k*p_l,k*p_j,k )] }

method RK4 starttime=0 stoptime=30 dt=0.005

init p11=0.5
init p21=0.3
{ p31 = 1-0.5-0.3 }
init p12=0.1
init p22=0.2
{ p23 = 1-0.1-0.2 }

{ q=migration, r=selection factors }
r=50 q=1

{ migration - selection model }
d/dt(p11) = q*(m11*p11 + m12*p12) + r*p11*( (r111*p11 + r121*p21 + r131*p31) - mr1)
d/dt(p21) = q*(m11*p21 + m12*p22) + r*p21*( (r211*p11 + r221*p21 + r231*p31) - mr1)
p31 = 1 - p11 - p21
d/dt(p12) = q*(m21*p11 + m22*p12) + r*p12*( (r112*p12 + r122*p22 + r132*p32) - mr2)
d/dt(p22) = q*(m21*p21 + m22*p22) + r*p22*( (r212*p12 + r222*p22 + r232*p32) - mr2)
p32 = 1 - p12 - p22

{ continued selection model }
mr1=(r111*p11 + r211*p21 + r311*p31)*p11 + (r121*p11 + r221*p21 + r321*p31)*p21 + (r131*p11 + r231*p21 +
r331*p31)*p31
mr2=(r112*p12 + r212*p22 + r312*p32)*p12 + (r122*p12 + r222*p22 + r322*p32)*p22 + (r132*p12 + r232*p22 +
r332*p32)*p32

{ migration probabilities by patch }
m11=- 0.5 m12= 0.5
m21= 0.5 m22= -0.5

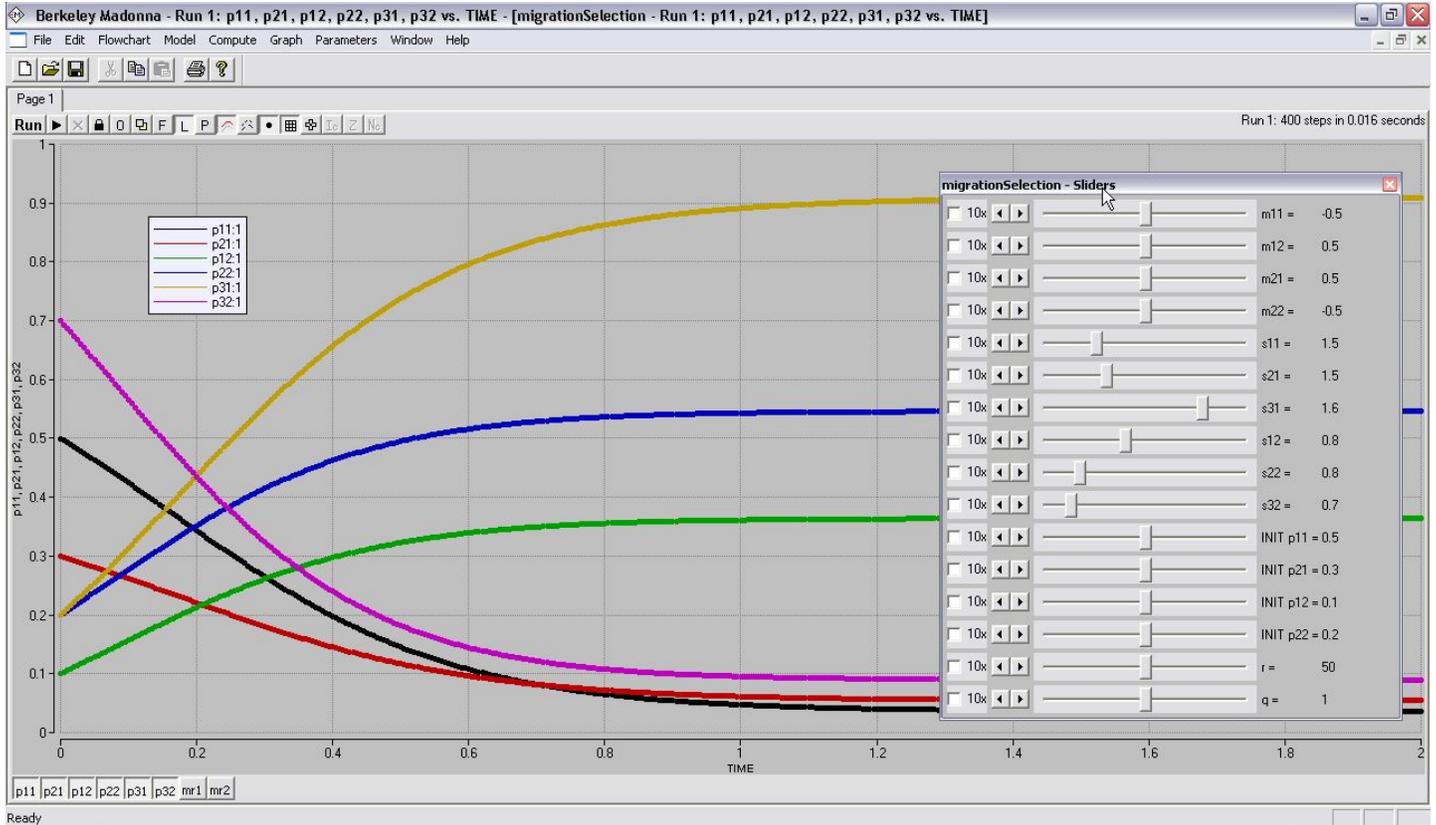
{ rijk: viability of AiAj in deme k }
r111=s11+s11 r121=s11+s21 r131=s11+s31
r211=s21+s11 r221=s21+s21 r231=s21+s31
r311=s31+s11 r321=s31+s21 r331=s31+s31

r112=s12+s12 r122=s12+s22 r132=s12+s32
r212=s22+s12 r222=s22+s22 r232=s22+s32
r312=s32+s12 r322=s32+s22 r332=s32+s32

{ dominance of individual alleles }
s11=1.5 s21=1.5 s31=1.6
s12=0.7 s22=0.7 s32=0.6
```

## Appendix 2

### Example of coexistence with Migration-Selection model



### **Author Biography**

Chad Vidden is a senior undergraduate student at Minnesota State University, Mankato. He is majoring in Mathematics with a minor in Computer Science. Chad is active in numerous clubs and honors societies on campus including being an officer of the Math and Honors Clubs. After graduation in May of 2007, he will be beginning the Applied Mathematics PhD program at Iowa State University. After earning a graduate degree, Chad hopes to teach as a university and conducting further research.

### **Faculty Mentor Biography**

Dr. Namyong Lee earned a PhD in Mathematics at the University of Minnesota, Minneapolis in 1998. He is currently a professor in the Mathematics Department at Minnesota State University, Mankato. Besides teaching courses, Dr. Lee conducts his own research, attends national conferences, advises undergraduate students, and also advises the Math Club.