**A Metapopulation Colonization – Extinction Model: How does Genome Wide Heterozygosity in subpopulations change with the amount of migration?**

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**Abstract**

Understanding the impact of migration on genetic diversity within metapopulations has critical implications for conservation biology. Especially in decisions between conserving one large habitat versus multiple smaller patches. This study investigates how varying migration and extinction rates affect genome-wide heterozygosity within subpopulations in a simulated metapopulation of interconnected demes. Using an extended form of the basic extinction-colonization model in SLiM, we simulated a metapopulation with 10 equally sized, interlinked demes. We analyzed the genome-wide heterozygosity as a proxy for population health, across a range of migration rates (0.000001 to 0.5) and extinction rates (0 to 0.1).

The results reveal that increased migration enhances genetic diversity within subpopulations. Extinction risk gets reduced with increased migration, even if the population has a high extinction rate. These insights support conservation strategies that prioritize habitat connectivity to facilitate gene flow, especially in fragmented landscapes.

The model's assumptions, including equal migration for all demes and neutral mutations, present limitations, though they also establish a baseline for further investigation.

**Introduction**

Biological Question

Our biological question is*: What is the Effect of different Migration Rates on Genome Wide Heterozygosity (within Subpopulation Diversity) in the different Subpopulations of one Metapopulation?*

Motivation

In conservation biology, the question of whether one should protect one large habitat, or multiple small patches often arises. With this dilemma in mind, we wanted to see how migration influences population dynamics in a metapopulation with several demes. Specifically, we wanted to see how the genetic variation in the subpopulations changes, depending on different migration rates. We did this with the assumption that genetic variation is a proxy for the health of the population, i.e. having large genetic variation prevents the species from extinction / detrimental stochastic events (Pannell & Charlesworth 2000).As a metric for the genetic variation, we chose heterozygosity of the entire genome of the subpopulations.

In addition, we were also interested in how different rates of extinction influence the amount of genetic variation and the survival of the metapopulation. What is the probability of extinction when looking at different rates of migration and extinction?

Background

The term metapopulation is used to describe a group of subpopulations which are connected to each other by having a certain amount of gene exchange. Metapopulation dynamics, as originally defined by Levins, consist of two main processes, being extinction and colonization. It is suggested by theory that these processes can influence, among others, the genetic variation within a metapopulation (Pannell & Charlesworth 2000).

There are multiple metrics to determine the genetic variation of a population, the most general one being heterozygosity which shows a biological importance. Moreover, there are well-established theories that predict levels of heterozygosity (Hedrick & Gilpin 1997). This measure is, apart from the FST, widely used in metapopulation studies. As mentioned above, we chose to assess the genetic variation to have a proxy for the health of the population, with the justification that there is theory as well as empirical evidence that loss of genetic diversity leads to reduction in fitness (Vandewoestijne et al. 2008).

A diagram of trees and a network

Description automatically generatedModel and outcomes

Our model is based on the basic Metapopulation Extinction – Colonization Model that the SLiM manual provides. It is a neutral model in discrete time. We examine a non-Wright Fisher population consisting of diploids. Extinction in this model is both density dependent and locally random. We decided that our metapopulation consists of 10 demes with the same carrying capacity, each one connected with the others and all having the same migration rate. We expect heterozygosity (=genetic variation) to increase with the amount of migration, since a mutation can spread more easily with movement of the individual. We also expect that the heterozygosity will plateau at very high migration rates (0.2 – 0.5). We therefore chose to look at more values in the range of 0-0.2, since with higher migration rates (0.2-0.5), the population almost behaves like one large population. We considered values larger than 0.5 as unrealistic for metapopulations, which is why our maximum migration rate equals 0.5.

Figure 1: A graphical representation of our model made in BioRender, Oktober 2024.

**Model & Methods**

*Table of parameters and variables*

Fixed parameters:

* + N: number of Subpopulations (=10)
  + K: Carrying capacity (=size) of each deme (=1000 individuals)
  + Starting population = K
  + tmax: 2000 Generations
  + Mutation Rate (=1e-7)
  + Recombination Rate (=1e-8)
  + Mutation type: m1 (m1 has dominance coefficient 0.5 and is neutral (fitness 0.0))
  + Genomic element type: g1 (initialized with mutation type m1, base mutation rate and a length of 10’000 bases)

Variable Parameters:

* + m: migration rate (0.000001, 0.00001, 0.0001, 0.001, 0.01, 0.015, 0.1, 0.15, 0.2, 0.3, 0.4, 0.5)
  + e: extinction rate (0, 0.0001, 0.001, 0.01, 0.1): density dependent and locally random
  + Number of migrants per generation: Poisson distributed & dependent on population size and migration rate

Outputs:

* + The mutation type, when (in which generation) and where (on which allele) it arose, as well as the number of individuals carrying this mutation, in SLiM
  + From this we calculated the allele frequencies and therefore also the heterozygosity in R.

Methods:

For our model, we used two different coding languages, R (Version 4.4.1) and SLiM (Version 4.3).

1. In SLiM, we used the recipe for the “A metapopulation extinction-colonization model” (Haller & Messer 2016) as our basic code and adjusted it to our means. We soft coded (using configurable parameters to enable easy modification) the migration rate and how many runs we want per rate, added an if loop to make sure that if there is no migration, no individuals will be chosen to migrate and included a stop command, which ended the simulation if the metapopulation went extinct.
2. In R, we coded the variable parameters (m and e) which we needed to send to SLiM. We did this by coding a “code block” which was then sent to SLiM via Terminal (bash command in R). This gave SLiM all the information it needed to run the simulation and output the data. (Chunk 1 in our code)
3. After this, we read in all the data and sorted it into one data table with all the metrics we wanted to analyse (Migration rate, Seed, Heterozygosity in each deme, mean heterozygosity and mean of mean heterozygosity). (Chunk 2 in our code)
   1. Calculation of Allele Frequencies:

To assess the allele frequency of every new mutation which occurred in a subplot during our simulation, we divided the number of individuals in a subplot carrying this mutation (numbers of alleles showing the mutation is an output from SLiM) by 2000. We did this, because the carrying capacity of a deme was set to 1000 individuals and we are working with a diploid organism, which shows two copies of every allele.

* 1. Calculation of Heterozygosity:

Having the allele frequencies of the different loci allows us to calculate the heterozygosity per locus. This was done with the formula , with allele frequency representing p and q defined as (Kirby 1984).

From the heterozygosity of the different loci, it is possible to calculate the genome wide heterozygosity. For this we took the mean over all the heterozygosity values per loci including the individuals which show no mutation. As a result, we then have the genome wide heterozygosity per deme for every simulation. To compare the outcomes across different simulations, we calculated the mean genome-wide heterozygosity for each migration rate, resulting in twelve mean heterozygosity values for the metapopulation—one for each of the twelve migration rates.

1. Further we started to visualize and plot the data.
2. After doing this for one extinction rate, we continued with 4 others. We did not soft code it, since the idea came towards the end of the practical. But this might be a practical extension of our code for future usage.

**Results**

The data generated with our model was analysed in R studio, version 4.4.1.

Figure 2 shows the extinction probability of metapopulations with different extinction rates, depending on different migration rates. For all extinction rates, the fraction of extinction decreases with higher migration rates, except for e = 0.0001 where there is no extinction at all.

When having an extinction rate of 0.1 (unrealistically high), the extinction probability is 100 percent for migration rates up to 0.0001. Only when having higher rates of migration, rescue of the population is possible (for migration rate 0.001 a possibility of 50 percent, increasing to 100 percent of rescue for migration rate of 0.01). The metapopulation never goes extinct when the extinction rate is set to 0.0001 or lower, even if the migration rate is small (0.000001). One can also see, that with a migration rate of 0.01 or higher, the metapopulation always gets rescued, no matter how high the extinction rate is.

**Figure 2**

A graph of migration rates

Description automatically generated

Figure 2: This graph shows the extinction probability of a metapopulation depending on different migration rates. The x Axis shows the different migration rates on a logarithmic scale and the y Axis the fraction of simulations which ended in extinction. The five colours represent the different extinction rates which we used for different runs of our model. The data points are represented as coloured points, connected with a dashed line. For each shown extinction rate (4 values), we looked at 12 different migration rates. This was then simulated 20 times, yielding 960 simulations.

Figure 3 highlights the genome wide mean heterozygosity of the metapopulation for each migration rate, depending on a fixed extinction rate. With an extinction rate of 0 (blue line), the metapopulation never goes extinct. The mean heterozygosity increases after a migration rate of 0.0001, but plateaus after a migration rate of 0.01. An extinction rate of 0.0001 behaves similar as one of 0, all metapopulations survive. The remaining extinction rates show a similar pattern of increased heterozygosity with increasing migration rate. The higher the extinction rate, the more migration is needed for the population to survive, i.e. the less data points are visible on the plot.

Apart from the simulation with e = 0.1, all metapopulations reach about a maximum heterozygosity of 0.002 when having high migration rates. Extinction of 0.1 leads to a maximum mean Heterozygosity of around 0.0015.

**Figure 3:**

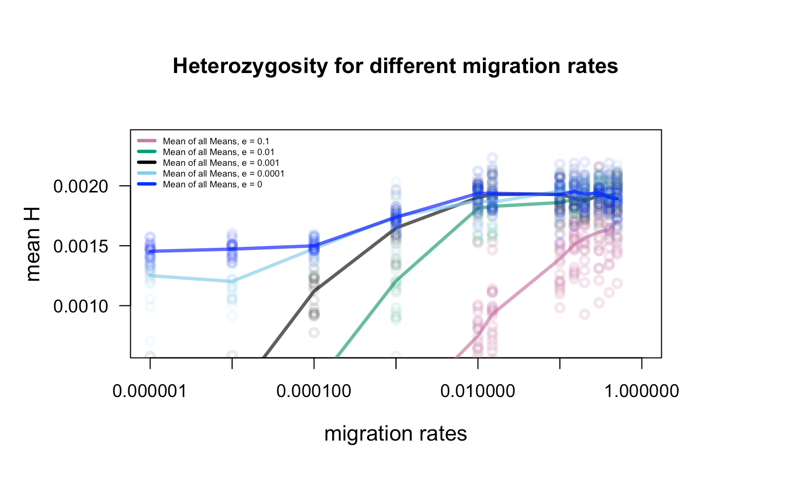


Figure 3: The x axis shows the different migration rates on a logarithmic scale and the y axis the genome wide mean heterozygosity of the different simulations. The output of different extinction rates is visible in different colours, as mentioned in the legend. The points show the mean Heterozygosity of every simulation, while the line indicates the mean of those means. For each shown extinction rate (5 values), we looked at 12 different migration rates. This was then simulated 20 times, yielding 1200 simulations.

**Discussion**

The results clearly show that an increased migration rate within one metapopulation leads to an increase of the genome wide heterozygosity within the subpopulations. Already low migration rates can help a population to persist. This might be linked to the fact that a higher amount of genetic variation leads to a more stable metapopulation, eventually preventing it from extinction. As already mentioned, populations with higher genetic variation tend to be “healthier” and more protected against detrimental stochastic events such as genetic drift, which in small populations can lead to extinction (Spielman et al. 2004).

A study on lesser kestrels, conducted by Ortego et al., showed that individuals born in a smaller and spatially isolated population show lesser genetic diversity than individuals born in a bigger and better-connected habitat. These patterns of heterozygosity can be explained by reduced gene-flow and the small population size, which is consistent with the low number of migrants these populations get. They also observed a poorer reproductive performance as well as a reduced long-term persistence of the small, isolated populations. This might be due to the detrimental consequences of reduced genetic diversity, which was observed in several species (Ortego et al. 2008). This all goes hand in hand with the predictions of our model.

Findings from Pannell and Charlesworth (1999) emphasize how important migration is in maintain genetic variation and highlight that recolonization dynamics play an important role in genetic outcomes. Recurrent local extinction and recolonization which our model allows, was found to reduce both within-deme and total metapopulation genetic diversity. Thus, preventing a subpopulation from local extinction with a continuous flow of migration, will lead to a higher genetic variation for both within-deme and total metapopulation genetic diversity (Pannell & Charlesworth 1999).

Our analysis also highlights, that an increased migration rate influences the extinction probability. Even if the populations are highly endangered (unrealistic extinction rate of 0.1), they can persist if the migration rate is high enough. These findings can be implemented in conservation biology, as they show how important it is to make sure migration is guaranteed, in order to prevent a species from extinction. Since the heterozygosity values tend to plateau after a specific migration rate, we do not always have to aim for the highest possible migration rate. Looking at Figure 2, an intermediate migration rate can have the same effects on genetic variation without necessitating maximal migration. In addition, our study shows that the probability of rescue is higher for populations which show high amount of migration but have rather high extinction rates, than for populations which show small extinction rates but are not connected to other habitats.

To summarize, our analysis reveals that higher amount of migration within a metapopulation leads to a higher genetic variation within the different subpopulations. As stated in the introduction, higher genetic variation can be seen as a measure for the health of a population, decreasing their probability of extinction.

Implications and Limitations

Concerning the implications of our results, our analysis suggests that designing a reserve as one large habitat would be the most effective strategy for maintaining genetic diversity and reducing extinction risk. However, if this is not possible, multiple smaller habitats work as well, with the condition that there is sufficient migration to ensure connectivity among subpopulations and therefore prevent extinction. This is supported by the findings from Schultz and Crone (2005), who revealed that small, well-connected patches can play an equally significant role as large, isolated ones in metapopulation persistence (Schultz and Crone, 2005). To further improve our conclusions, our model could incorporate variable carrying capacities to illustrate the different patch sizes in reserve planning. Moreover, one could add migration barriers by implementing probabilities for dispersal. This could provide more insights into how isolation affects population persistence. Schultz and Crones’ study on the Fender’s blue butterfly demonstrated that patches in the range of 1 km were more likely to be colonized than patches further away, highlighting the importance of spatial connectivity over patch size in certain contexts (Schultz and Crone, 2005).

At this point, our model assumes constant migration rates across all patches. This is likely to be an oversimplification of real-world dynamics. The inclusion of spatially explicit migration rates, like Schultz and Crone (2005) did, could help simulate more realistic reserve designs. Including these points would provide our model with the ability to be more precise in identifying conditions under which small, connected patches or large isolated ones contribute the most to conservation.

Our model can be seen as a Null Model, from where one can manipulate different variables that might be of interest. For instance, the model assumes a neutral mutation. Furthermore, there is an equal amount of migration between the demes and migration is possible from every deme to all the other demes. Additionally, all the demes have the same carrying capacity, implementing same size. These parameters could be adjusted with real values, observed in a population. If you know the extinction rate as well as the connectivity between the subpopulations of an endangered species, you could assess the amount of migration needed for rescue with the help of our model.

To illustrate this idea of a valuable null framework that could be extended, one can look at a study conducted by DiLeo et al. (2024). This study asked the question under which conditions one can expect to find an association between genetic diversity and extinction in nature. They addressed this by linking genetic data form the Glanville fritillary butterfly (*Melitaea cinxia)* with ecological data from hundreds of local populations. The results demonstrated that genetic diversity is a strong predictor of population extinction risk but highlighted that this association is highly context dependent. Their findings underline that associations between genetic diversity and extinction can vary across populations, influenced by confounding factors like demographic history, environmental conditions and population connectivity. DiLeo et al. found that extinction risk declined with increasing heterozygosity in large populations but not in small ones, unless these have recently undergone a decline (DiLeo et al. 2024). In summary, a possible addition to our model would be to incorporate different ecological factors to make the model more realistic. A further point is that we did not calculate different measures of diversity. Evaluating the heterozygosity between the subpopulations would be a nice extension of the model, showing how different they are. It would, for example, be practical to calculate the FST*.* This is a metric, many researchers use, which therefore would help to compare our results to other studies. Moreover, according to Hedrick & Gilpin (1997), measuring or evaluating the change, more specifically loss, of heterozygosity is of importance in conservation biology. In our model, we simply assess the mean heterozygosity at the end of 2000 Generations and do not look at how it changes over time, which could also be very interesting.

Take-home messages

As expected, migration plays an important role in conserving populations since it increases genetic variation. With higher genetic variation, the chance of extinction decreases. Even with a relatively low amount of migration, populations that are exposed to high amount of extinction are more likely to persist and increase in genetic variation.

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**Author Contributions**

Conceived and designed the analysis: Jasper Russel, Emma Ochsner, Lena Witschi (with the help of ChatGPT November 2024, regarding some specific commands in R).

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