A Metapopulation Colonization – Extinction Model: How does Genome Wide Heterozygosity in subpopulations change with (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 change, 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.[1] 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.[1]

There are multiple ways to determine the genetic variation of a population, the most general one being heterozygosity. It shows a biological importance and there are well-established theories that predict levels of heterozygosity.[2] This measure is, apart from the F_{ST}, 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.[3]

Model and outcomes

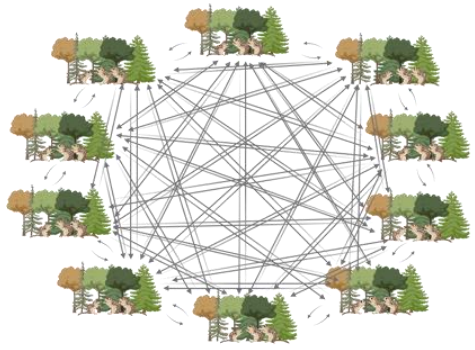

Figure 1: A graphical representation of our model made in BioRender, Oktober 2024.

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 each 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.

Model & Methods

Table of parameters and variables

Fixed parameters:

- N: number of Subpopulations (=10)
- K: Carrying capacity (=size) of each deme (=1000)
- Starting population = K
- t_{max}: 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)
- Number of migrants per generation: Poisson distribution & dependent on Population Size and migration rate

Outputs:

- The mutation type, when and where it arose in SLiM.
- From this we calculated the allele frequencies and therefore also the heterozygosity in R.

<u>Methods:</u>

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" [4] as our basic code and adjusted it to our means. We soft coded 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)
    a. 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 (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.
    b. 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 $H = 2pq$, with allele frequency representing p and q defined as $1 - p$. [5]
       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.

4. Further we started to visualize and plot the data.
5. 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

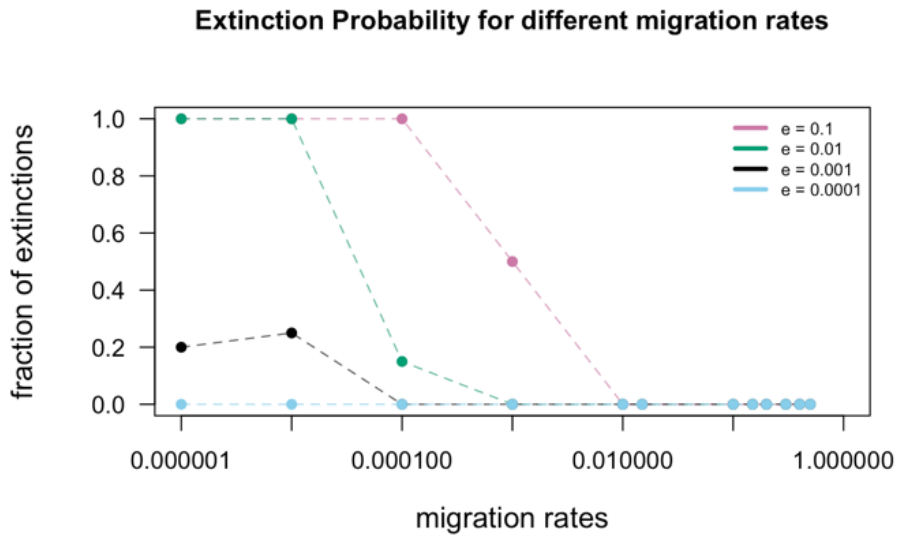

Figure 2: This graph shows the extinction probability of a metapopulation depending on different migration rates. The x Axis shows the different migration rates on a logarithmic scale and the y Axis the fraction of simulations which ended in extinction. The five colours represent the different extinction rates which we used for different runs of our model. The data points are represented as coloured points, connected with a dashed line.

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 evidently 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:

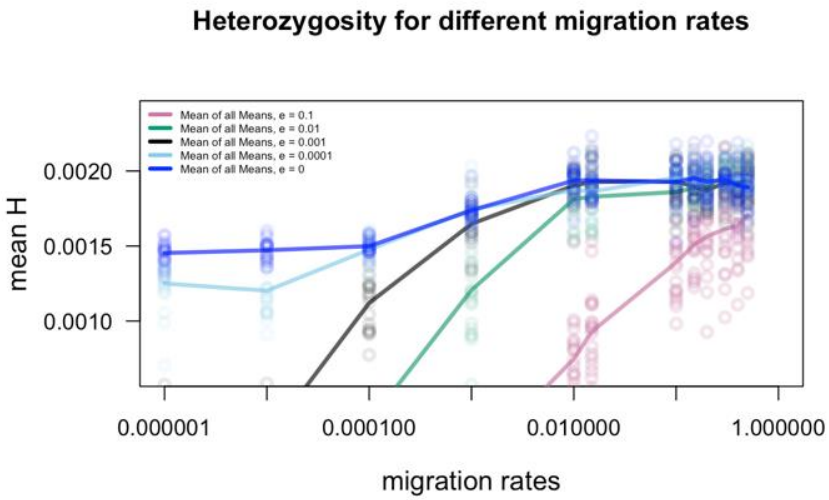

Figure 3: The x axis shows the different migration rates on a logarithmic scale and the y axis the genome wide mean heterozygosity of the different simulations. The output of different extinction rates is visible in different colours, as mentioned in the legend. The points show the mean Heterozygosity of every simulation, while the line indicates the mean of those means.

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.[6]

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.

So as summary, our analysis reveals, that higher amount of migration within a metapopulation leads to a higher genetic variation within the different subpopulations, decreasing their probability of extinction.

Implications

If we could choose how to build a reserve, one large habitat would be best. But if this is not possible, multiple small ones would also work but there must be a certain amount of migration to prevent extinction, as implemented by our model. Our study also 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.

If you know the extinction rate of an endangered species, you could assess the amount of migration needed for rescue with the help of our model. 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.

Limitations

The model assumes a neutral mutation and the same amount of migration between all the demes. The demes are connected with each other and migration is possible from every deme to all the other demes. Additionally, all the demes had the same carrying capacity, implementing same size. We did not calculate different measures of diversity, such as heterozygosity between the subpopulations, but it would be a nice extension of the model. For example, it would be practical to calculate the F_{ST}, since this is a metric, many researchers use, and which would help to compare our results to other studies.

According to Hedrick & Gilpin 1997[2], 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.

Future Prospects

The model computed is a good null model, from where one can manipulate different variables that might be of interest. For example, one could calculate the heterozygosity between the subpopulations, showing how different they are to each other. As mentioned in the limitation part, to compare our results to other studies one could

calculate the F_{ST} or a similar widespread measure. One could also incorporate the fact, that demes have different carrying capacities. This would be especially interesting regarding the question of what the best option is for reserve planning. Furthermore, our model assumes that migration is the same for every possible path. This might not be very realistic, and it would be interesting to incorporate various migration barriers by adding a probability into our model, such that individuals do not always reach the deme they want to migrate to.

In our model, we only look at one mutation type which is neutral. If one is interested in how different mutation types with variable selection coefficients change the dynamic in a metapopulation, this might be a great basis model for doing so.

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.

References

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Author Contributions

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

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