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Spatial populations with seed-bank

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Summary

Imagine a meadow with red and purple poppies. You might wonder whether there will be a moment when there are only red poppies left or only purple poppies left, or whether there will always be both red and purple poppies. And if, after multiple generations, only one colour is left, then what is the probability that there are only red poppies left and what is the probability there are only purple poppies left?

The above questions concern the genetic evolution of a poppy population. If after a number of generations only one colour of poppies is left, then we say that the genetic diversity in the population is lost. In this thesis we study genetic evolution in populations in a broader setting. A mathematical model that describes the genetic evolution in a population is the Fisher-Wright model. Different evolutionary mechanisms can be incorporated into the Fisher-Wright model, for example, mutation of genes or selection of stronger genes. There also exists a model where individuals live in multiple colonies, each evolving according to the Fisher-Wright model, and individuals are allowed to migrate between different colonies.

A recent extension of the Fisher-Wright model is the addition of a seed-bank to the population. In a population with seed-bank, individuals can stop reproducing themselves for awhile. We then say that these individuals become dormant. The repository of the dormant individuals is called the seed-bank. After a number of generations individuals resuscitate and reprise reproduction. The poppy is a species that has a seed-bank. If a poppy seed drops on the soil, but due to a storm gets covered with a thick layer of sand, then it may happen that the seed does not germinate next spring, but only five springs later. The seed-bank phenomenon is also observed in bacteria. When environmental conditions are bad, for example, the nutrition level is low or the temperature is low, a bacteria can produce an endospore. An endospore can survive difficult conditions, but cannot reproduce itself. When the environmental conditions improve, the endospore can transform itself back into a bacteria and reprise reproduction.

In this thesis we study the Fisher-Wright model with seed-bank in which individuals carry one of two gene types, the individuals can migrate between different colonies, and can become dormant in a seed-bank for a certain amount of time. We assume that in each colony there are infinitely many individuals. The corresponding mathematical model is called the “multi-colony continuum Fisher-Wright model with seed-bank”. The goal of this thesis is to determine whether on the long term the genetic diversity will be maintained (in case of the poppies, there will always be both red and purple poppies) or whether genetic diversity is lost (there are after a long time only red or only purple poppies). In particular, we try to determine the effect of the seed-bank on the genetic diversity in the population.

We study this question in different geographical spaces. In the first part of the thesis the colonies in which individuals live are placed on a general geographical space.

The most important example of such a space is the lattice $\mathbb{Z}^d$. In the second part of the thesis the colonies are placed on the hierarchical group. Intuitively, the hierarchical group may be interpreted in the following way. Each colony is a house, a couple of houses together forms a street, a couple of streets together forms a city and a couple cities together form a province, and so on. Individuals move more often between the houses in the street, than between the different streets in the city. One level up, the individuals move more often between the streets in their own city than between the different cities in the province, and even less often between different provinces. In ecology for instance, this multi-layer structure is natural. The hierarchical group describes this structure in a mathematical way.

The thesis consists of two parts, preceded by an introduction to population genetics in Chapter 1. In part I of the thesis we consider three versions of “the multi-colony continuum Fisher-Wright model with seed-bank”. In each of these three versions individuals carry one of two gene types, denoted by type $\heartsuit$ and type $\diamondsuit$. In the first model the population in each colony consists of active and dormant individuals. The dormant individuals together form the seed-bank. The active individuals reproduce themselves, migrate between different colonies, and become dormant. The dormant individuals can only wake up: they do not reproduce themselves and also do not migrate. The second model is an extension of the first model in which the seed-bank has extra structure, which allows individuals become dormant in different ways, so that they can sleep shorter or longer. In the third model the seed-bank has the same structure as in the second model, but when an individual becomes dormant it is allowed to do so in a different colony than where it resides. In each of the three models the reproduction rate is dependent on the genetic diversity of the population.

In Chapter 2 we set up a system of stochastic differential equations for each of the three models. These systems describe the frequency of the gene type $\heartsuit$ in the population. We show that the processes described by these systems are well defined and have the Markov property. Due to the internal structure of the seed-bank in the second and third model, the time an individual spends in the seed-bank can be fat-tailed, while the Markov property of the system is maintained.

In Chapter 2 we also show that, in the special case where the diffusion function in the system of stochastic differential equations is the Fisher-Wright diffusion, there exists a dual. This dual enables us to describe the long-time behaviour of the system of stochastic differential equations.

Finally, in Chapter 2 we determine for each of the three models whether the genetic diversity is lost on the long term or not. It turns out that in the first model only the way in which the individuals migrate determines whether genetic diversity is preserved or lost. It turns out that in the second model if individuals are dormant long enough, then both the way in which the individuals migrate as well as the amount of time individuals are dormant determine whether genetic diversity is preserved or lost. The internal structure of the seed-bank can prevent the loss of genetic diversity. If in the second model individuals become dormant for a very long term, then the genetic diversity in the population is always preserved, independently of the way in which the individuals migrate. In the third model we find similar results as for the second model. Chapter 3 contains the proofs of the theorems stated in Chapter 2.

In part II of the thesis we consider the second model in the specific case where

the geographical space is the hierarchical group. The first goal of Part II is to apply the results obtained in Part I. The second goal is to analyse the genetic diversity in the so-called “hierarchical mean-field limit”. In Chapter 4 we formally describe the model on the hierarchical group, state the results that follow from Part I and describe the “hierarchical mean-field limit”. Chapters 5–10 contain the proofs of the theorems stated in Chapter 4. Again, it turns out that if individuals can become dormant for a long enough period, then the seed-bank can prevent the loss of genetic diversity within the population.