

Genetic tradeoff as a model for parapatric speciation

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ABSTRACT

This paper uses an individual-based modelling approach to explore the effects of genetic tradeoff across a spatial gradient. Tradeoff is represented by the ability of an individual to live at higher environmental values - individuals that can live at high values can also live at low values, but the cost for this generalised ability is an increased time to breeding maturity. This paper shows that for very low tradeoff gradients significant zones still occur across the environment, with a pronounced set of heterozygotic bands. It is proposed that these bands represent hybrid zones, and that the model demonstrates that weak tradeoff across an environmental gradient can produce isolated genetic individuals. This model therefore shows one mechanism leading to parapatric speciation.

Keywords and phrases: Genetic tradeoff, environmental gradient, parapatric speciation, individual-based model.

1 Introduction

One of the most important questions in evolutionary science relates to the mechanisms involved in speciation. Many different approaches that lead to speciation have been proposed in the literature, such as complete geographic isolation, assortative mating, and genetic tradeoff due to behavioural strategies. Genetic tradeoffs occur when organisms need to partition resources between different processes or activities. This leads to the benefit in one trait causing a reduction in fitness of another trait of the individual. This paper will deal with the response by a population to a simple genetic tradeoff to a linear environmental gradient across space.

There are many examples of genetic tradeoff between longevity and early fecundity found in the literature. For example, this response has been thoroughly investigated for *Drosophila melanogaster* (e.g. (Leroi, Chippindale & Rose 1994)). Here the selection for late-life reproductive success in populations has resulted in an increase in longevity and a correlated diminution of early fecundity (Rose, Corey, Coyle & Service 1984, Luckinbill, Arking, Clare, Cirocco & Buck 1984). Genetic tradeoff has also been observed for the seed beetle, *Stator limbatus* (Czesak & Fox 2002), where offspring differ in egg size and number between different environments. A final example of a spatially related tradeoff is seen in mangroves. Mangrove species make a tradeoff between growth rate and salt tolerance. Although (Ball 1988) found that all species grow fastest in 10% seawater, they differ in the upper limit of seawater that can be tolerated. Species with greater tolerance have slower growth rates and are out-competed by species with lower salt tolerance, but faster growth rate. The result is that salt marshes often display sharp zones, dominated by different species. In each case, species dominate zones that are at the extreme upper limits of their tolerance range. In this study we will use a simple tradeoff model that has many similarities to the Mangrove example. Individuals will be able to live at some extreme location of an environmental gradient, based on their genotype, but with a subsequent tradeoff of a higher age before reaching breeding maturity.

Most scenarios of speciation highlight the creation and maintenance of geographic variations as a necessary step. One possible mechanism leading to speciation is described by parapatric speciation, which is speciation with some gene flow between neighbouring subpopulations (S.Gavrilets, Li & Vose 2000). Many researchers have suggested that rapid and extensive speciation is possible without complete geographic isolation (Endler 1977, W & E 1993). This paper will show how the strength of a simple tradeoff response can influence the splitting of a population into subpopulations in a landscape with an imposed environmental gradient. The results demonstrate

how such a tradeoff affects the variation and distribution of alleles and the degree of heterozygosity in a stable population.

2 Materials and methods

In this study a spatially-explicit and individual-based modelling approach is used. The artificial landscape is described by grid of 160 x 100 cells. The upper and lower edges of the grid are wrapped around, forming a cylinder with a circumference of one hundred cells. However the left and right edges are discontinuous, representing the boundaries of the environment. The grid is divided into sixteen parts, 10 x 100 cells each, representing the ranges of an environmental gradient (e.g. pH-value, salt concentration, temperature, etc.). Each section of the environment is described by a increasing integer value between zero (at the left) and fifteen (righthand side of the environment). Each grid cell can be occupied by one individual, although whether an individual can live at a particular cell depends on the phenotype of the individual and the environmental value. The phenotype of the individual must be at least as large as the environmental value to allow the individual to survive. Hence an individual with a phenotype of 15 can live anywhere in the environment, whereas an individual with a phenotype of 0 can only live in the first 100 cells of the environment from the left. Each individual is considered to be monoecious and diploid, hence an individual can mate with itself and every locus is represented by two alleles. The alleles code for the phenotype and are interpreted as a value between zero and fifteen, with a similar interpretation as for the gradient ranges. The trait coded by the locus follows a dominant-recessive Mendelian inheritance. Hence, the highest of both allele values define the maximum range where the individual can live.

An individual is characterized by the two behaviours: the age when it reaches maturity (related to the expressed phenotype) and its age of death. The age at which each individual dies is drawn from a Gaussian distribution $N(80,5)$. The age to maturity depends on the value of the highest allele. There is a trade-off between the ability to live at a higher environmental value and the time when an individual can start to breed. As the range of environmental gradients viable for an individual increases, there is a subsequent tradeoff in terms of the time till fecundity. The tradeoff is represented by a linear relationship between the allele value v and the age before breeding $B(v)$:

$$B(v) = slope \cdot v + 30 \quad (1)$$

The degree of the slope determines the strength of the tradeoff (see Fig. 1). The age of an individual before breeding was then derived from a Gaussian distribution ($B(v),2$).

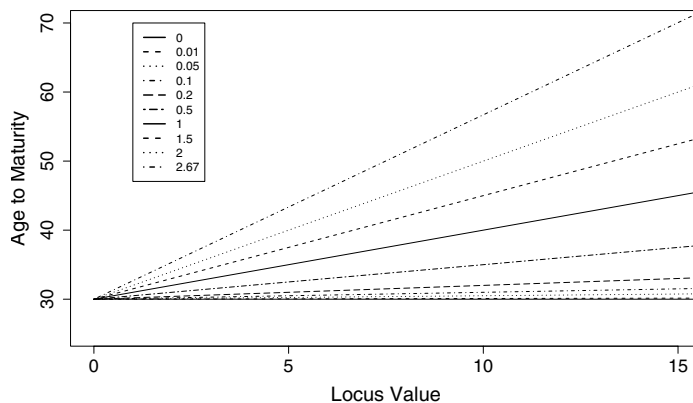


Figure 1: Age to maturity as locus response to gradient increase.

Given an empty cell a new individual is produced by considering a sub-population composed of all individuals living in the von Neumann neighbourhood (von Neumann 1966) of this cell *that have reached breeding maturity*. From this sub-population, two are randomly chosen with replacement and bred following standard Mendelian breeding to produce a child. For each allele the probability of mutation was set to 0.00001, which was applied independently to each allele. When mutation was activated the allele value was changed randomly to a value between zero and fifteen.

For each slope shown in Fig. 1, ten simulation runs over 1 million time steps were conducted. For each run the frequency of each allele, the degree of heterozygosity, the number of alleles changes during all time steps, the time since the last change in the phenotype and the final composition after 1 million time steps were measured.

3 Results

This section describes the main pattern for the results of ten simulation runs for each strength of trade-off. These results are based on the means of one column of one hundred cells representing the same environmental value. Note that in particular for lower trade-off slopes there is a large variation in behaviour due to the stochastic nature of the evolution.

The results were tested for three different initial population structures: a grid filled with individuals with allele values of five, ten and fifteen. Note that very similar patterns were observed independent of the initial population structure. Hence the observed pattern after many timesteps did not depend on the starting point of a simulation.

For the case of no tradeoff between the ability of living on a high environmental value and the date of maturity (i.e. a tradeoff slope of zero) we have only a few different alleles (Fig. 2 left), with the majority of alleles having the highest possible value (Fig. 2 right).

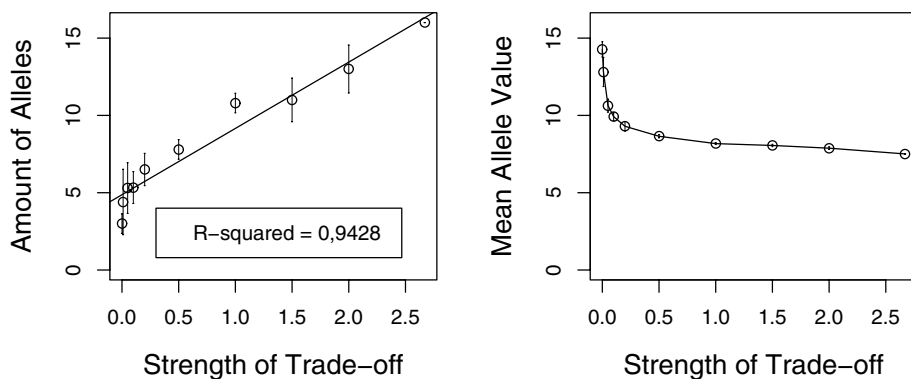


Figure 2: The number of alleles and the mean allele value based on strength of trade-off.

Sometimes a fixation of the highest allele value (15) could be observed after just a few time steps, but normally such a fixation occurred only in the upper region of environmental values after one million timesteps. If the trade-off is low, there is no selection against high allele values, however there is still a selection against low allele values at grid locations with high environmental values. Thus a directional drift for the benefit of high locus values accrue. As the trade-off slope increases selection against individuals with high locus values at locations with small environmental values becomes more pronounced (see Fig. 2).

With increasing slope of trade-off the number of different alleles increases (Fig. 2 left), whilst the mean allele value (Fig. 2 right) and the frequency of a single alleles decreases (Fig. 4 col.1). If there is a medium trade-off, there is often a lag over a few values in the existing alleles. Because of the very similar age of maturity of two individuals with adjacent allele values the higher one could easily displace the lower one by drift. In the case of a high trade-off nearly all alleles occur at the grid with a similar frequency. This implies that there is a large pressure on each phenotype, which forces it to the border of the dispersal range by phenotypes with earlier ages of maturity.

For low trade-offs the degree of heterozygosity is high over a large range of environmental values and there is a more or less equal number of phenotype changes for large parts of the grid (see Fig. 5). Again the fixation occurs only in the upper part of the environmental values and the variation after a million timesteps is high over a large part of the grid. Hence a low trade-off creates a very heterogeneous population. As trade-off slope increases larger fluctuations in the degree of heterozygosity, as well as in the number of value changes over the columns of the grid, can be observed. In addition, it is possible to distinguish regions of the grid with a constant allele value and low variation from ranges with an increasing allele value and large variation, resulting in a fixation of a phenotype at one grid location being more frequent.

The width of the hybrid zones, indicated by the percentage of heterozygotes, reduces with increasing trade off, however their number increases because of the increasing number of different alleles existing on the grid. The location of these hybrid zones are correlated with the intersection of two adjacent alleles. In the case of very high trade-offs they are located exactly at the borders of the gradient values.

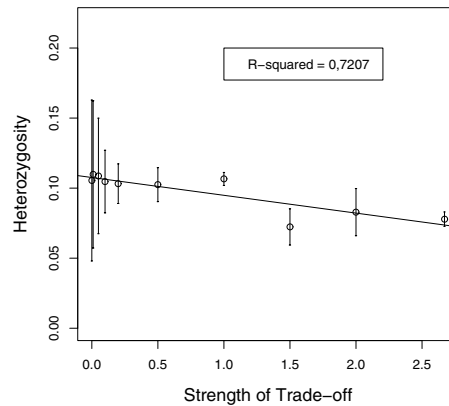


Figure 3: Degree of Heterozygosity shown for different trade-off strengths after one million timesteps.

The rate of heterozygotes decreases slightly with increasing trade-off (Fig. 3). This is in contrast to a Hardy-Weinberg population, where an increase of heterozygotes would be expected by increasing the number of alleles with equal allele frequency. Hence the existence of an environmental gradient and a high trade-off results in a large number of homozygotic phenotypes. As shown previously there are clustered bands across the grid. In these more or less uniform bands there is low genetic exchange between bands which may lead to the origin of subspecies across the gradient.

4 Discussion and Conclusion

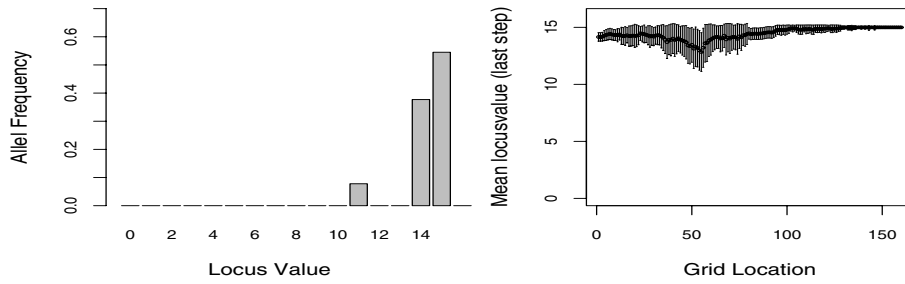
Genetic isolation is required as a first step towards speciation. Of course this isolation can be achieved by geographic separation, but there are other possible mechanisms that can affect genetic isolation within a population. In this study we have described a simple trade-off that could lead to distinct clusters of homogeneous individuals, and have shown that the existence of these clusters and the gene flow between them depends on the strength of the trade-off.

To summarize our results we could note: as the strength of trade-off increases, a larger number of different allele values occurs and a smaller number of hybrid zones between neighbouring allele clusters results. Alternatively, a low trade-off results in a lower genetic diversity, but also produces a high mixture of genotypes, while the population affected by a strong trade-off is highly diverse, but is deficient in heterozygotes. Hence a strong trade-off results in a higher degree of spatial isolation, which in turn could lead to parapatric speciation, however there are clear hybrid zones forming with even very weak tradeoff levels.

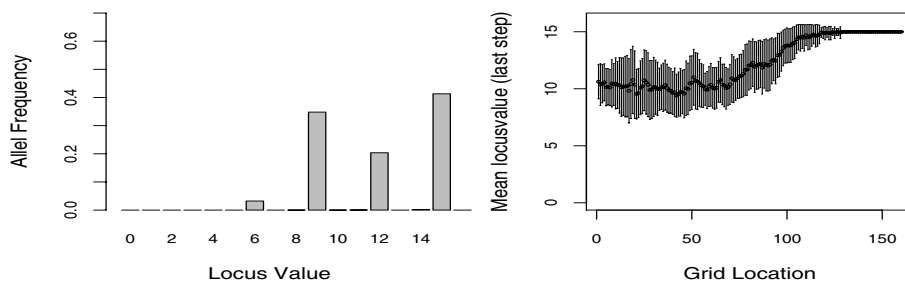
Additionally a type of founder effect could be observed, in particular for the case of low trade-off strengths. For this situation the alleles have an advantage that accrue early in time, when there is still a large amount of resources on the grid to be occupied. When the whole habitat is occupied, then it is much more difficult for a new genotype to establish, even if the new genotype has some advantage over the alleles that already exist.

This work has supported a better understanding of the influence of different intensities of a trade-off to the genetic composition of a population, however there are still many details that need to be analysed. For example, the influence of the width of the gradient should be tested for a high trade-off. As this width increases the space occupied by one gradient value will increase and therefore should be able to support the uniform allele clusters of homozygote individuals of these values in the habitat. In comparison to this cluster, the question that needs to be addressed is whether the hybrid zone will reduce with increasing width of the gradient. Hence a larger degree of heterozygotes could be suggested with a stronger trade-off under these situations.

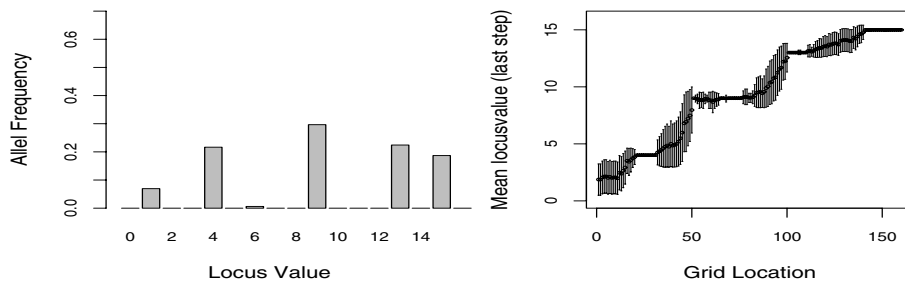
A final point is that many natural gradients run not in stages but instead are continuous between two extreme values. Hence in further studies we need to examine these compounding zones. Based on the results presented here we would expect, that in case of a large trade-offs, the behaviour for the hybrid zones would change.



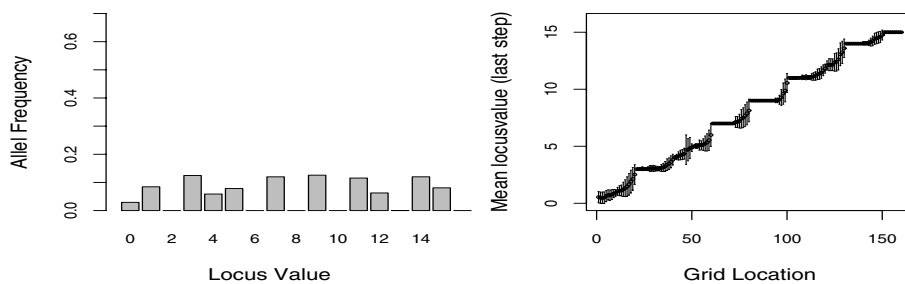
(a) Slope of trade-off = 0.0



(b) Slope of trade-off = 0.01



(c) Slope of trade-off = 0.20

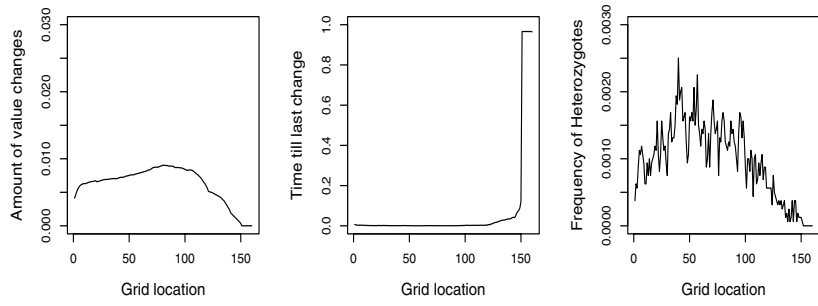


(d) Slope of trade-off = 2.0

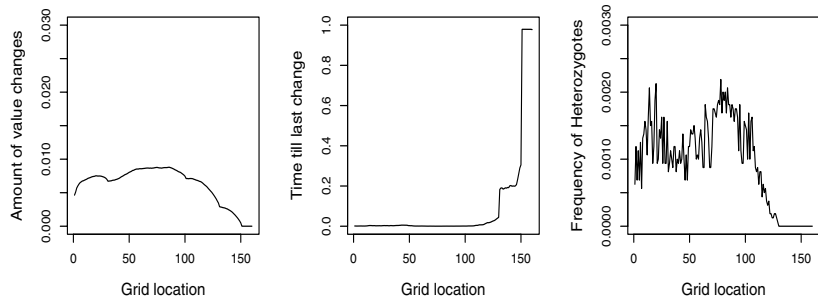
Figure 4: Four examples for different strength of trade-off. The left column shows allele frequency and right the mean and std. dev. locus value of each column after 1 million time steps.

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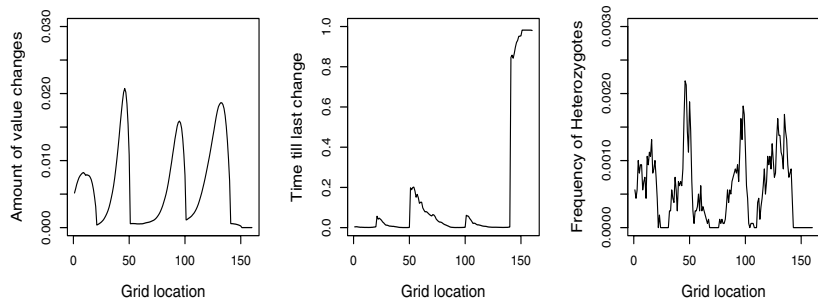
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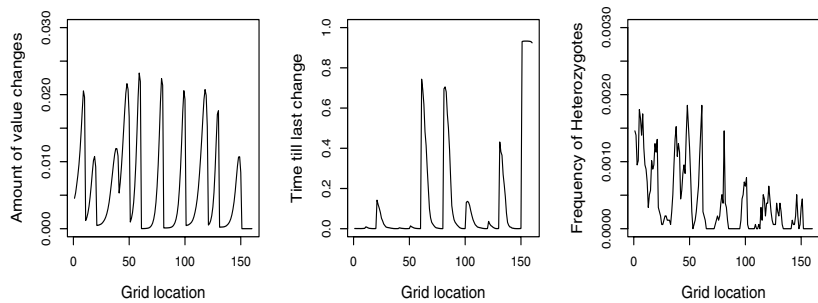
(a) Slope of trade-off = 0.0



(b) Slope of trade-off = 0.01



(c) Slope of trade-off = 0.20



(d) Slope of trade-off = 2.0

Figure 5: The left column describes the amount of change at every grid column during all time steps, the middle column shows the mean time till the last value change of all cells in a column, and the right shows the frequency of heterozygotes.