Physica A 421 (2015) 54–68

Contents lists available at ScienceDirect

Physica A

journal homepage: www.elsevier.com/locate/physa

A dynamical analysis of allele frequencies in populations evolving under assortative mating and mutations

David M. Schneider [a,*], Eduardo do Carmo [b], Marcus A.M. de Aguiar [a]

[a] Instituto de Física 'Gleb Wataghin', Universidade Estadual de Campinas, Unicamp, 13083-859, Campinas, SP, Brazil

[b] Universidade Federal da Integração Latino Americana, 85867-970, Foz do Iguaçu, PR, Brazil

HIGHLIGHTS

- A resolution of the dynamics of a population of two biallelic loci individuals evolving under assortative mating and mutations is provided.
- A bifurcation diagram is constructed to describe the dynamics in a qualitative way.
- The fate of initial conditions is obtained by the employment of a constant of motion.
- A trade-off between assortativity and the effect of mutations is discussed.

ARTICLE INFO

Article history:
Received 11 June 2014
Received in revised form 29 October 2014
Available online 15 November 2014

Keywords:
Population genetics
Modes of speciation
Assortativity
Bifurcation analysis

ABSTRACT

We study the evolution of allele frequencies for infinitely large populations subjected to mutations and assortative mating. Haploid individuals are described by two biallelic genes, and assortativity is introduced by preventing mating between individuals whose alleles differ at both loci. In the absence of mutations, evolution leads to the disappearance of one of the alleles. However, a particular combination of the allele frequencies at the two loci is maintained constant. We show that this combination remains constant even when mutations are present, revealing the robustness of the epistatic correlation introduced by the non-random mating mechanism. We obtain the equilibrium solutions for arbitrary values of the mutation rate and provide a description of the dynamics on the basis of a bifurcation analysis.

1. Introduction

The concept of species is deeply rooted in the idea of reproductive isolation: groups of individuals form separate species if individuals belonging to different groups are unable to generate fertile offspring through mating [1–3]. Such isolation prevents genetic modifications occurring in one group to spread to other groups, causing their evolution to follow relatively independent paths. Understanding the genetic and ecological mechanisms that lead to the emergence of reproductive isolation is, therefore, a fundamental quest of evolutionary theory.

In a series of recent papers [4–6] it has been shown that speciation may occur spontaneously in spatially extended populations where individuals are allowed to mate only if they are close enough and not too different genetically. Mating restriction by genetic similarity, also termed assortative mating, can be modeled by attributing haploid genomes with B

---

[*] Corresponding author. Tel.: +55 19 3521 5463.
E-mail address: schneide@ifi.unicamp.br (D.M. Schneider).

http://dx.doi.org/10.1016/j.physa.2014.11.030

biallelic loci to individuals and allowing them to mate only if the genomes differ in no more than G loci [7–9,4,5]. This rule is supported by the idea that individuals have limited tolerance to differences when choosing a mate, so that if the other individual is too different, it will not be considered as a mating option [10].

The model proposed in Ref. [4] considers finite populations, includes mutations and is not panmictic, since mating occurs only between spatially close and genetically similar individuals. Speciation occurs because of the combined effects of isolation by spatial distance [11] and isolation by genetic distance. Individuals are initially identical and differentiation occurs only by mutation and drift. However, as the population diversity increases the genetic constraint aids differentiation by disruptive selection. If G, the maximum allowed genetic distance, is much smaller than B, the total number of genes, mutations may lead to incompatible haplotypes. Analytical expressions indicating when speciation is possible under these conditions were recently obtained [12,13], but the contribution of the genetic mating restriction to the process was included as an ansatz based on numerical simulations. The dynamical equations describing the evolution of haplotype frequencies in the general case of B loci and arbitrary G were recently derived and their solutions were obtained in the absence of mutations [14].

In a previous paper [15] we have analyzed in detail the dynamics of allele frequencies for infinitely large populations of haploid individuals not subjected to mutations. We considered the simplest case of two loci, $B = 2$, and $G = 1$, so that individuals whose alleles differ at both loci are considered incompatible and mating does not happen. In this case there are only four haplotypes, AB, Ab, aB and ab, AB—ab and Ab—aB being the incompatible pairs. We derived the evolution equations for the haplotype frequencies $p_{u'u''}$ (with $u' = A, a$ and $u'' = B, b$), and found that the coupling between the loci introduced by the restricted mating leads to a strong correlation between the allele frequencies. For $\tilde{p}_A = p_{AB} + p_{Ab}$ the frequency of the allele A and $\tilde{p}_B = p_{aB} + p_{AB}$ the frequency of the allele B, the quantity $T = (\tilde{p}_A - 1/2)/(\tilde{p}_B - 1/2)$ remains constant during the evolution, although $\tilde{p}_A$ and $\tilde{p}_B$ do change. Using this conserved quantity we were able to solve the dynamical equations and show that one of the alleles always disappears from the population.

Models with one or two loci and two alleles have been extensively studied in the past, but focused mostly on selection and not on assortativity [16–21]. A comprehensive review of recent models of assortative mating can be found in Ref. [22]. One-locus diploid models where individuals have equal mating success usually lead to a decrease in the proportion of heterozygotes, going to zero for complete assortativity, where each type mates only with itself [23–25]. One locus models where mating success is frequency dependent have also been considered [26–28] but have also been shown to lead to the extinction of heterozygotes if assortativity is complete. The model considered here is similar to the two-allele two-locus version of the Moore model [22]. In that case, however, the heterozygotes Ab and aB correspond to the same phenotype, which lead to particularly simple and symmetric equilibria. Finally we mention the Higgs–Derrida model [29,30] where loci are unlinked (Ab and aB map to different phenotypes) but which considers the limit of infinitely many loci.

In this paper we extend the results obtained in Ref. [15] to include the effects of mutations. We show that, surprisingly, the function T remains constant for arbitrary values of the mutation rate. We obtain all the equilibrium solutions analytically and find that, contrary to the equilibrium solutions in the absence of mutations, they do not imply the lost of an allele. Instead, they are characterized by the fact that one of the four alleles ends up with a very small frequency, which is given as a function of μ and T (Fig. 3). As μ goes to zero, this allele vanishes and the result of Ref. [15] is recovered. In addition, we find that equilibrium solutions merge at a critical mutation rate. This value of the mutation rate is associated to a stability change and to a biologically meaningful bifurcation. Another bifurcation takes place for negative mutation rates. Not being relevant from a biological point of view, this second bifurcation is illustrative to describe, in addition to the former, the global structure of the phase space.

The paper is organized as follows: in Section 2 we describe the reproductive mechanism in the presence of mutations and derive the haplotype frequencies evolution equations for very general mating schemes. In Section 3 we briefly discuss the random mating scenario. The dynamical implications of the combination of assortativeness and mutations are studied in Section 4. Section 5 presents a qualitative description of the dynamics based on a bifurcation analysis, and Section 6 is devoted to discuss the results and to expose the main conclusions. Complementary technical calculations are added in separated appendices.

2. Reproductive mechanism

Consider a population of hermaphrodite individuals with two biallelic loci. Let A and a denote the alleles at one locus, and B and b the alleles at the other, so that the haplotypes are AB, Ab, aB, and ab. The number of individuals of each type in the generation t is given by N^t_{AB}, N^t_{Ab}, N^t_{aB} and N^t_{ab}, with $N^t_{AB} + N^t_{Ab} + N^t_{aB} + N^t_{ab} = N^t$, the total size of the population. Encounters between the members of this generation may succeed or not in producing offspring for the generation $t + 1$, depending on the probabilities $w_{h_1:h_2}$ (h_1 and h_2 being the parental haplotypes). The rates $w_{h_1:h_2}$ (see Table 1) incorporate both the effects of the compatibility between the parents (sexual selection) and the viability of the newly formed zygote (viability selection). In our model the viability selection is the same for all individuals, and takes place once the zygote was formed through the inheritance of a recombinated chromosome (at a recombination rate r). Assortativeness, represented by the sexual selection component, is described by the compatibility between the parents and acts at a prezygotic level. The reason for adding a postzygotic factor to the compound fitness $w_{h_1:h_2}$, from now on the compatibility–viability selection rate, has the only purpose of keeping the total number of individuals constant across generations, and represents an implicit