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Journal of Theoretical Biology

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

Smallness of the number of incompatibility loci can facilitate parapatric speciation

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HIGHLIGHTS

- We study waiting time to parapatric speciation of a species on two islands.
- The model includes mutation, migration, and mixing processes.
- Finiteness of the number of loci makes the waiting time shorter.
- An intermediate migration rate realizes the fastest rate of species creation.
- Smaller number of loci makes species creation rate faster.

ARTICLE INFO

Article history:

Received 9 June 2015

Received in revised form

14 October 2015

Accepted 22 October 2015

Available online 12 November 2015

Keywords:

Genetic drift

Neutral loci

Recurrent migration

Speciation rate

Stochastic model

ABSTRACT

We studied the time to speciation by geographic isolation for a species living on two islands connected by infrequent migration. Assumptions were that incompatibility was controlled by a finite number of quantitative loci, and individuals differing in loci of more than some threshold fraction do not mix genetically with each other. We also assumed sexual haploid species, each population being nearly monomorphic, and free recombination between loci for within-population processes. The genetic distance (defined as the fraction of loci differing between populations) followed stochastic processes, which were analyzed by means of stochastic differential equations, diffusion equations, and individual-based simulations. The distance increases by the accumulation of novel mutations but decreases by migration and hybridization. It may converge to a quasi-equilibrium around which it fluctuates thereafter. If the threshold fraction of speciation is controlled, the smallness of the number of incompatibility loci enhanced the magnitude of fluctuation around the quasi-equilibrium and shortened the time to speciation considerably. Novel species were created by mutation accumulation and repeated infrequent migration, and the rate of species creation was the fastest for an intermediate rate of migration. A smaller number of loci increased the optimal migration rate and the species creation rate.

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1. Introduction

Speciation by geographic isolation is an important means by which new species are created (Mayr, 1942, 1963; Coyne and Orr, 2004). If a species is subdivided into a number of subpopulations, the local populations accumulate novel mutations independently of the others, and, after many generations, will become very different from each other. When individuals from different populations mix, they may no longer be able to engage in sexual

reproduction. The two populations can then be regarded as different species, produced via allopatric speciation.

The classical framework proposed by Dobzhansky (1937) and Muller (1942) was a simple two-locus, two-allele diploid model of the appearance of genetic incompatibility between two populations. The initial genotype *aabb* in both populations was replaced by *AAbb* in one population in a neutral evolution because *aabb*, *Aabb*, and *AAbb* are equal in fitness. In the other population, the original population was replaced by *aaBB* by a neutral evolution, because there is no reproductive isolation among genotypes *aabb*, *aaBb*, and *aaBB*. In contrast, the two populations did not cross because the offspring of *AAbb* and *aaBB* were *AaBb*, which was non-viable. An even simpler model of allopatric speciation considering a single locus with multiple alleles has also been

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developed (Nei et al., 1983; Wu, 1985). Some theoretical works on allopatric speciation have examined various extensions of these models (cf. Higgs and Derrida, 1992; Manzo and Peliti, 1994; Gavrillets and Gravner, 1997; Gavrillets et al., 2000b), and discussed how the waiting time to speciation is affected by population size (Orr and Orr, 1996) or by the founder effect (Gavrillets and Hastings, 1996).

In these theoretical studies, no migration was assumed to occur among populations in calculating the time to speciation. However, empirical studies suggest that the most common mode of speciation is parapatric: different populations are indeed isolated, but not absolutely so (Endler, 1977). The geographical structures of most species are consistent meta-populations, composed of many local populations that are connected by infrequent migration (Avice, 2000; Gavrillets et al., 2000a). Gavrillets (2000) studied a model of parapatric speciation incorporating recurrent migration between two populations. Gavrillets considered the case in which incompatibility was controlled by a number of loci. Assuming that each population is monomorphic, the two populations become separate species when the number of incompatibility-controlling loci that differ between them exceeds some threshold value. According to the analysis of the birth-and-death process, the waiting time to speciation increased with the migration rate between populations.

However, in the perfect absence of recurrent migration, no new species would be produced after populations on two islands become separate species. In contrast, the number of species can increase further if recurrent migration occurs between the two populations at a positive (but very small) rate. Suppose that there are two islands (say, 1 and 2), initially occupied by the same species. The two populations accumulate different incompatibility genes, and finally become two separate species (say, species A and species B on islands 1 and 2, respectively). Then, subsequent migration of species A to island 2 will result in a population of species A on island 2 that does not mix with species B. Further accumulation of incompatibility loci will make species A on island 2 become a species different from species A on island 1. Then, we have three species on two islands. In this manner, recurrent migration between two islands that occurs at a very slow rate provides a simple mechanism to maintain generation of novel species.

There may exist an intermediate optimal rate of migration that realizes the fastest rate of species generation, consistent with recent empirical studies in various taxa (Agnarsson and Kuntner, 2012; Claramunt et al., 2012). This theoretical prediction was investigated in a previous paper of ours (Yamaguchi and Iwasa, 2013). We studied a stochastic process to calculate the time to speciation in two populations connected by infrequent migration. Genetic distance between the two populations, defined as the number of different incompatibility-controlling loci, increases via replacement of alleles occurring independently in the two populations (Orr, 1995), but decreases after a successful migration event that is followed by genetic mixing of migrants and residents (cf. Slatkin, 1987). Speciation occurred when the genetic distance exceeded a particular threshold (e.g., Turelli and Orr, 1995; Gavrillets, 2000). An intermediate optimal rate of migration was observed, which attained the maximal rate of species creation via recurrent invasion and diversification.

To simplify the analysis, Yamaguchi and Iwasa (2013) focused on the case in which only the stochasticity caused by the random timing of migration was considered, but the stochasticities accompanied by the accumulation of novel mutations and also by the fraction of loci at which migrant allele became fixed after each migration event were neglected, which they called a “population-based model.” This was a good approximation if the number of incompatibility loci was very large. However, when the number of

relevant incompatibility loci was not very large, neglecting two sources of stochasticity underestimates the variance in genetic distance dynamics, as shown by comparison with an individual-based model.

In the present study, we examined a stochastic model incorporating the two additional sources of stochasticity neglected in the analysis of Yamaguchi and Iwasa (2013). This is, in effect, to analyze the effect of the finiteness of the number of loci controlling incompatibility. We developed formulae obtained by the integration of forward and backward equation (diffusion equations), a stochastic differential equation (SDE), and performed direct computer simulations of an individual-based model (IBM), and show that all yielded consistent predictions. The finiteness of the number of loci inflates the magnitude of fluctuation around the quasi-equilibrium and may reduce the time to speciation greatly.

2. The model

We consider two populations of a sexually haploid species with discrete non-overlapping generations. The populations are isolated geographically, each with a population size N . The organisms can disperse to meet the other population after sexual maturation. Successful migration events occur only infrequently. Most migration attempts fail. However, when an attempt is successful, a number of individuals from one population can arrive at the other population and participate in reproduction processes (see Yamaguchi and Iwasa, 2013).

We assume that mating compatibility between individuals is controlled by a set of l autosomal loci. Specifically, the possibility of successful mating between immigrants and residents is determined by the fraction of loci differing between them. We denote this value by z , and call it the “incompatibility genetic distance” or simply the “genetic distance.” Two individuals cannot result in viable and fecund offspring if z exceeds a threshold value z_c . In contrast, if z is less than z_c , individuals can mate and produce fully viable offspring. The threshold value may vary between species (Coyne and Orr, 1998).

We posit that the size of each population N is much smaller than the inverse of the overall mutation rate u of the incompatibility-controlling loci ($1/u \gg N$). This assumption renders island populations monomorphic most of the time, except for brief periods of allelic replacement and migration events (Kimura and Ohta, 1969a; Maruyama, 1970, 1983; Slatkin, 1976, 1981; Lande, 1979, 1985; Tachida and Iizuka, 1991; Barton, 1993; Rieseberg, 2001; Whitlock, 2003; Patwa and Wahl, 2008). This allows us to discuss the incompatibility genetic distance between populations as the distance between two individuals from different populations. If a population is polymorphic with respect to these loci, we may use the average genetic distance to represent the incompatibility genetic distance between the two populations (Gavrillets et al., 1998).

2.1. Accumulation of novel mutations

As two populations accumulate different mutations, the incompatibility genetic distance between them increases. We adopt an infinite allele model (Kimura and Crow, 1964): a newly formed mutant is novel and different from all existing alleles. Two populations accumulate different mutations, and their genetic distance increases over time. We also assume that these mutations are neutral in the process of accumulation because a one-step difference does not cause any significant effect on incompatibility. Two populations accumulate mutations independently of each other at the total rate $2ul$. The genetic distance increases by allele

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