



# Rapid parapatric speciation on holey adaptive landscapes

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A classical view of speciation is that reproductive isolation arises as a by-product of genetic divergence. Here, individual-based simulations are used to evaluate whether the mechanisms implied by this view may result in rapid speciation if the only source of genetic divergence are mutation and random genetic drift. Distinctive features of the simulations are the consideration of the complete process of speciation (from initiation until completion), and of a large number of loci, which was only one order of magnitude smaller than that of bacteria. It is demonstrated that rapid speciation on the time-scale of hundreds of generations is plausible without the need for extreme founder events, complete geographic isolation, the existence of distinct adaptive peaks or selection for local adaptation. The plausibility of speciation is enhanced by population subdivision. Simultaneous emergence of more than two new species from a subdivided population is highly probable. Numerical examples relevant to the theory of centrifugal speciation and to the conjectures about the fate of 'ring species' and 'sexual continuums' are presented.

**Keywords:** speciation; holey adaptive landscapes; mathematical models

## 1. INTRODUCTION

In spite of significant advances in both theoretical and experimental studies of evolution, understanding speciation still remains a major challenge (Mayr 1982; Coyne 1992). In recent years a view of speciation that can be traced to the classical Dobzhansky model (Dobzhansky 1937; Muller 1942) has become a point of renewed interest (Nei *et al.* 1983; Wagner *et al.* 1994; Orr 1995; Orr & Orr 1996; Gavrilets 1997*a,b*; Gavrilets & Hastings 1996; Gavrilets & Gravner 1997). Using the metaphor of 'adaptive landscapes' (Wright 1932), populations diverge genetically along the 'ridges' of highly fit genotypes and become reproductively isolated species when they come to be on opposite sides of a 'hole' in a 'holey' adaptive landscape (Gavrilets 1997*a*; Gavrilets & Gravner 1997).

Current renewal of interest in Dobzhansky-type models is coming from different sources. First, there is growing experimental support for the genetic architecture implied (reviewed in Orr (1995), Orr & Orr (1996) and Gavrilets (1997*a,b*)). On the theoretical side, there is a growing realization of serious problems with Sewall Wright's metaphor of 'rugged' adaptive landscapes (Whitlock *et al.* 1995; Gavrilets 1997*a*) and shifting balance theory (Gavrilets 1996; Coyne *et al.* 1997). Both have for a long time have been a focus of theoretical studies of evolution. On the other hand, it recently has been demonstrated that the existence of 'ridges' of highly fit genotypes, which is postulated in Dobzhansky-type models, is actually a general property of

multidimensional adaptive landscapes (Gavrilets & Gravner 1997; Reidys *et al.* 1997).

Earlier theoretical studies of speciation as a consequence of genetic divergence along 'ridges' in the adaptive landscape have shown it to be a distinct possibility. These studies involved various approximations such as small number of loci (Nei *et al.* 1983; Wagner *et al.* 1994; Gavrilets & Hastings 1996), linkage equilibrium (Nei *et al.* 1983), infinitely large number of highly mutable unlinked loci and preferential mating (Higgs & Derrida 1992; Manzo & Peliti 1994), or absence of within-population variability during divergence (Orr & Orr 1996). Here we extend the previous work and report results of individual-based simulations that did not involve any approximations typical in studying multi-locus systems. Using a linear algorithm for generating random numbers with a given distribution (Vose 1991) has allowed us to model hundreds of linked loci potentially influencing fitness. The number of considered loci, which is only one order of magnitude smaller than that of bacteria (Blattner *et al.* 1997), is a significant distinctive feature of our simulations. An analytical theory for the dynamic patterns observed will be published elsewhere (S. Gavrilets, unpublished).

## 2. MODEL

We model finite subdivided populations of sexual haploid individuals different with respect to  $L$  diallelic loci. Evolutionary factors included were mutation, recombination, migration, genetic drift and selection. To decrease the number of parameters, we used some symmetry assumptions. Mutation rates were equal for

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forward and backward mutations and across loci. Recombination rates between adjacent loci on the same chromosome were equal and recombination events took place independently of each other. The population was subdivided into subpopulations of equal size.

Without any loss of generality, each individual can be represented as a sequence of 0's and 1's. Let  $l^\alpha = (l_1^\alpha, \dots, l_L^\alpha)$  where  $l_i^\alpha$  is equal to 0 or 1, be such a sequence for an individual  $\alpha$ . We will be interested in the levels of genetic variability within subpopulations and genetic divergence between subpopulations. Both can be characterized in terms of genetic distance,  $d$ , defined as the number of loci at which two individuals are different. More formally, the genetic distance  $d^{\alpha\beta}$  between individuals  $\alpha$  and  $\beta$  is

$$d^{\alpha\beta} = \sum_{i=1}^L (l_i^\alpha - l_i^\beta)^2. \quad (1)$$

Genetic distance,  $d$ , is the standard Hamming distance. To characterize the levels of genetic variability within subpopulations and genetic divergence between subpopulations we used the average genetic distances (AGD) between individuals from the same subpopulation and from different subpopulations, respectively. To reflect the idea that reproductive isolation arises simultaneously with genetic divergence, we posit that an encounter of two individuals can result in mating and viable and fecund offspring only if the individuals are different in no more than  $K$  loci (cf. Higgs & Derrida 1992). Otherwise the individuals do not mate (pre-mating reproductive isolation) or their offspring is inviable or sterile (post-mating reproductive isolation). More formally, we assign 'fitness'  $w$  to each pair of individuals depending on the genetic distance  $d$  between them

$$w(d) = \begin{cases} 1 & \text{for } d \leq K, \\ 0 & \text{for } d > K. \end{cases} \quad (2)$$

In this formulation, any two genotypes different in more than  $K$  loci can be considered as sitting on opposite sides of a hole in a holey adaptive landscape. At the same time, a population can evolve to any reproductively isolated state by a chain of single-locus substitutions. The neutral case (no reproductive isolation) corresponds to  $K$  equal to the number of loci. In our simulations, individuals migrated before mating and pairing of individuals occurred randomly. There were 384 on a single chromosome, the rate of recombination between adjacent loci was 0.005, and the mutation rate per locus was  $10^{-4}$ . The  $K$  values used are 10, 20 and 30, which are within the range of estimates of the minimum number of genes involved in reproductive isolation (Singh 1990; Coyne & Orr 1998).

Our simulations started with all  $N$  individuals identical. During the first 1000 generations there were no restrictions on migration between subpopulations and the whole population evolved as a single, randomly mating unit. One thousand generations was sufficient for the population to reach a state of stochastic equilibrium between factors affecting its dynamics. This was apparent from the behaviour of AGD (see figures) as well as from the behaviour of the

number of segregating loci and the number of different genotypes (data not presented). Starting with generation 1000, restrictions on migration were introduced. We used both the island model (Wright 1932) and the one-dimensional stepping-stone model (Kimura & Weiss 1964). In the former case, with probability  $m$  an individual migrated to another subpopulation (with all subpopulations equally accessible). In the later case, the subpopulations were arranged along a line with migration only between neighbouring subpopulations (with rate  $m/2$ ). The simulations were continued until generation 3000. We have chosen this relatively short time span for two reasons. First, here we are interested in the plausibility of rapid speciation. Second, only during relatively short time intervals may one assume the constancy of abiotic and biotic environment implied in our model.

### 3. NUMERICAL RESULTS

Extensive simulations have revealed the existence of three different dynamical regimes. In the first regime, the AGD both between and within subpopulations reach (stochastic) equilibrium values below  $K$  (figure 1a). Between-subpopulations matings take place and are fecund. No further genetic divergence and speciation take place (at least until generation 3000). In the second regime, the AGD between subpopulations steadily increases after introduction of restrictions on migration (figure 1b). Subpopulations diverge, genetically accumulating different mutations. After some time, three effects take place simultaneously: (i) AGD between subpopulations significantly exceed AGD within them; (ii) encounters between individuals from different subpopulations do not result in viable and fertile offspring; and (iii) evolutionary changes in a subpopulation do not affect other subpopulations. Thus, subpopulations form separate genotypic clusters in genotype space, become reproductively isolated and undertake changes as evolutionary independent units. These dynamics are interpreted as speciation according to any of the species concepts common in the literature (e.g. Mallet 1995; Claridge *et al.* 1997). Here, speciation has occurred in the presence of gene flow and, thus, is parapatric. The third regime is a combination of the first two. After some transient time during which the AGD both within and between subpopulations have appeared to reach a new stochastic equilibrium, the AGD between subpopulations starts suddenly increasing (figure 1c). The system undergoes a stochastic transition resulting in speciation and further accumulation of genetic differences between subpopulations. After speciation has taken place, the genetic variability within (sub)populations decreases. (Note that instead of the three different dynamical regimes, one may choose to think of a single regime with a varying (from zero to infinity) time until the initiation of divergence.)

Dynamic behaviour depends on the intensity of different factors operating in the system. As expected, reduced migration and increased mutation both increase the plausibility of speciation (data not presented). Population size and the strength of selection play a double role. With strong selection (small  $K$ ),

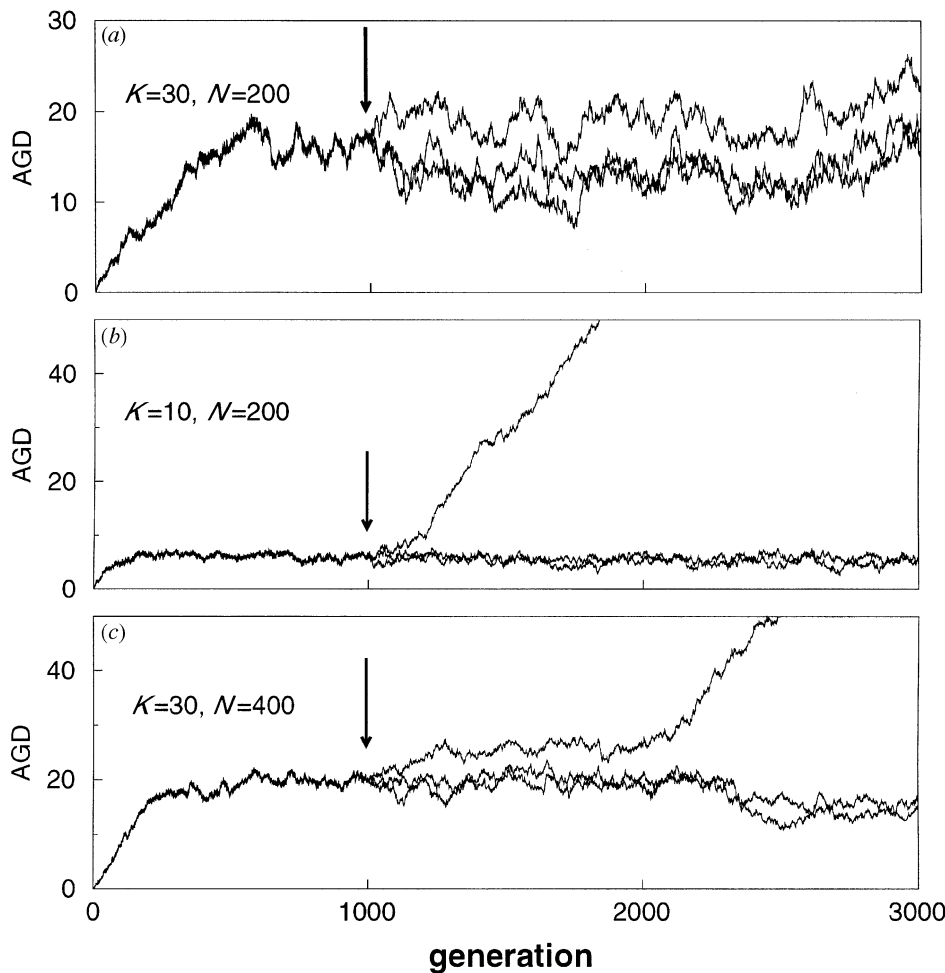


Figure 1. Three types of dynamics. The population is subdivided into two subpopulations. Of the three curves apparent after generation 1000, the upper curve gives the AGD between the subpopulations, whereas the two remaining curves give the AGD within each subpopulation. The total population size  $N$ , and  $K$  value, are given on the graphs. The arrows mark generation 1000 when restrictions on migration ( $m=0.01$ ) were introduced.

increased population size delays speciation (compare figure 2*a* and *b*). With weak selection (large  $K$ ), decreasing population size delays speciation (compare figure 2*c* and *d*). With smaller population sizes, decreasing the strength of selection delays speciation (compare figure 2*a* and *c*). With larger population size, increasing the strength of selection seems to delay speciation (compare figure 2*b* and *d*).

These effects can be explained in the following way. A necessary condition for genetic divergence and speciation is fixation of alternative alleles in different subpopulations. After the (sub)population becomes polymorphic at  $K$  loci, new mutations are selected against because individuals carrying them have a reduced probability of fecund mating. Genetic drift operating in small populations overcomes the effect of selection and allows for genetic divergence. Genetic divergence of very large, randomly mating subpopulations connected by migration will not occur. On the other hand, if (sub)populations are too small, they lack genetic variability necessary to initiate divergence. Genetic divergence of very small, randomly mating subpopulations connected by migration will not occur either. The dynamics of genetic divergence are not neutral. During the phases of stochastic equilibrium the AGD both within and between subpopulations are well below neutral expectations (which are given in Watterson (1975), Li (1976), Slatkin (1987) and Strobeck (1987)). After speciation has taken place, the rate of

between-population divergence is smaller than the neutral expectation (which is twice the expected number of mutations per generation,  $v$ ).

Increased population subdivision promotes speciation. For example, in a population with  $N=800$  subdivided into two subpopulations, no speciation has been observed (figure 3*a*). However, subdividing into four 'islands' immediately initiates divergence and emergence of four species (figure 3*b*). The migration rate in these simulations was small ( $m=0.01$ ). Speciation can also occur for higher migration rates with appropriate spatial subdivision. Figure 3*c* shows results for a single run of a stepping-stone model with eight subpopulations and  $m=0.06$  (that is there are six migrants per subpopulation per generation). Here, after some transient time, the population splits into two species. Splits have occurred in 70 runs (out of 92 performed), in 18 of which the population was split into three species. Figure 4*a* shows that the two peripheral populations have a reduced probability of separating from the whole system. Figure 4*b* suggests that this is so because peripheral populations on average have reduced genetic variability and are more similar to their neighbours relative to other populations. Figure 4*c* shows that, as expected, genetic distance increases with the geographic distance. The AGD between the first subpopulation and subpopulations 4–8 is above  $K$ , meaning that these pairs of subpopulations are reproductively isolated. However, they evolve together and have a common evolutionary trajectory.

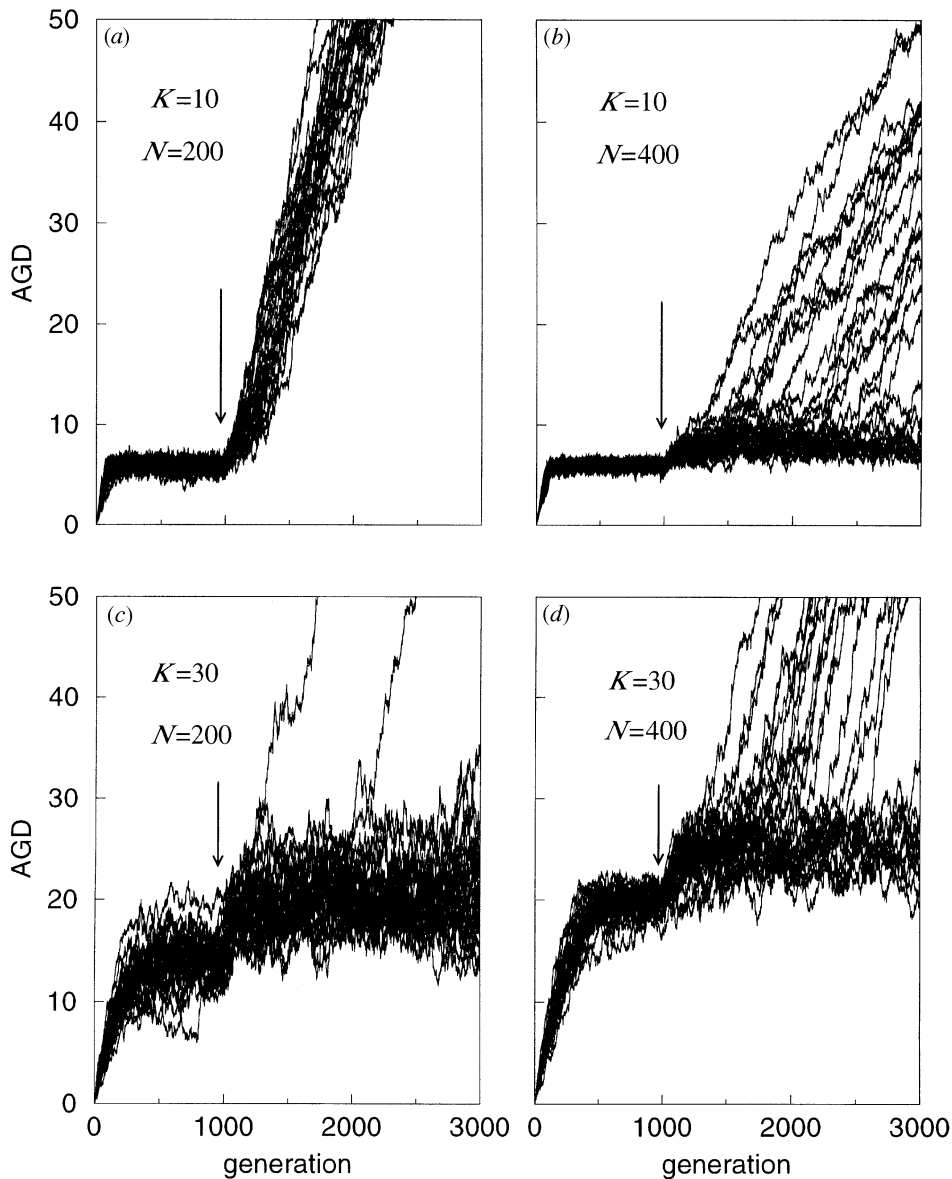


Figure 2. Effects of population size and the strength of selection on evolutionary divergence and speciation. The population is subdivided into two subpopulations. AGD between the subpopulations are shown (30 runs for each parameter configuration). (a) With  $K = 10$  and  $N = 200$ , subpopulations steadily diverged immediately after generation 1000 in all runs. (b) However, with  $N = 400$  the time until the initiation of divergence varied and divergence was not observed in 13 runs. Comparing the slopes of the curves representing AGD between subpopulations in (a) and (b) shows that increasing population size decreases the rate of divergence as well. (c) With  $K = 30$  and  $N = 200$ , speciation was observed in only two runs. (d) With  $N = 400$ , speciation took place in 18 runs. Other parameters are the same as in figure 1.

#### 4. DISCUSSION

Here, individual-based simulations were used to evaluate the plausibility of rapid speciation as a result of genetic divergence along the ridges of a holey adaptive landscape. Distinctive features of the simulations are the consideration of the complete process of speciation (from initiation until completion), and of a large number of loci, which was only one order of magnitude smaller than that of bacteria. Our numerical results have implications for several important evolutionary questions that have been extensively discussed in the literature but have not been approached using explicit mathematical models.

**(a) *Rapid speciation is plausible without the need for extreme founder events, complete geographic isolation, the existence of distinct adaptive peaks or selection for local adaptation***

In our simulations, speciation was observed when the migration rate was on the order of several individuals per

subpopulation per generation. The time-scale in the simulations was short, meaning that restrictions on migration should not be long-lasting. Several hundred generations might be sufficient for a significant divergence and evolution of reproductive isolation (figures 1–3). Restoring migration after that to higher levels will not return the system back to its initial state of free gene exchange between subpopulations. The rates of speciation observed here are much higher than in models of speciation via transitions between adaptive peaks across valleys of maladaptation (e.g. Barton & Rouhani 1993) and in earlier models of holey adaptive landscapes that considered only few loci (Nei *et al.* 1983; Wagner *et al.* 1994; Gavrillets & Hastings 1996). In our model, random genetic drift and mutations were the only source of genetic divergence and speciation. Here we tacitly assumed that the loci controlling reproductive isolation are different from those responsible for local adaptation. If this were not the case, or if there were close linkage between the two types of loci, selection for local adaptation might accelerate genetic divergence and speciation (e.g. Schluter 1996).

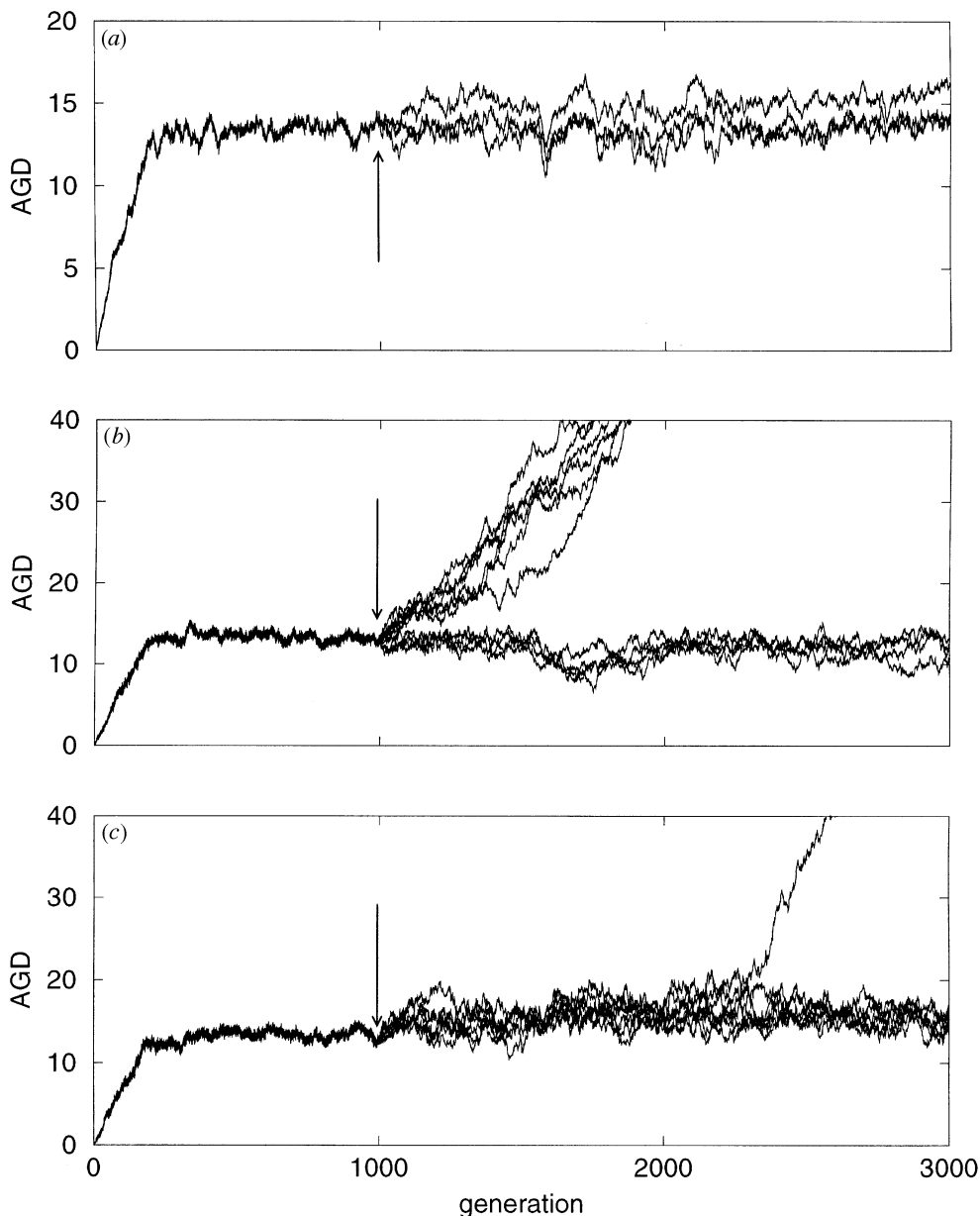


Figure 3. Effects of spatial subdivision ( $N = 800$ ,  $K = 20$ ; number of loci and the rates of recombination and mutation are the same as in figure 1). Figures (a) and (b) show AGD within and between subpopulations for a single run. Results for the 29 other runs are very similar. (a) The population is subdivided into two equal subpopulations with migration rate  $m = 0.01$ . No speciation is observed (cf. figure 1a). (b) The population is subdivided into four equal subpopulations; island model with  $m = 0.01$ . All AGD between subpopulations steadily increase after generation 1000, indicating emergence of four species (cf. figure 1b). (c) Corresponds to a stepping-stone model with eight local subpopulations with migration rate  $m/2 = 0.03$  between neighbouring subpopulations. AGD between neighbouring subpopulations for a single run resulting in the emergence of two species are shown. All distances remain below  $K$  (no reproductive isolation between neighbouring subpopulations), except between subpopulations 4 and 5 where AGD starts increasing around generation 2300 (cf. figure 1c) indicating the split into two species with four subpopulations each.

**(b) The plausibility of speciation is enhanced by population subdivision**

In our model, increasing the number of subpopulations makes speciation more plausible (figure 3). The number of subpopulations can be interpreted as a measure of the geographic range size of the population. Thus, our results show that populations with larger geographic range sizes have a greater probability of speciation (cf. Rosenzweig 1995). Our conclusion about the effect of population subdivision on the probability of speciation in Dobzhansky-type models differs from that of Orr & Orr (1996). They argued that the degree of population subdivision has no effect on the rate of speciation if speciation is caused by mutation and random drift. The problematic assumption of their analysis is that fixation of new mutations is a neutral process. However, the existence of holes in the adaptive landscape makes the process of substitution non-neutral and new mutations are selected against when rare (see

above). Such mutations are fixed more easily in smaller subpopulations (figure 2).

**(c) Simultaneous emergence of several new species from a subdivided population is highly probable**

Hoelzer & Melnick (1994) have emphasized that this possibility should be incorporated more explicitly in the contemporary methods for reconstructing phylogenies. Recently, several cases of rapid speciation have been described (Schluter & McPhail 1992; McCune 1996; Johnson *et al.* 1996). The most spectacular one is probably the origin of hundreds of species of Lake Victoria cichlids in 12 000 years (Johnson *et al.* 1996). Our simulations have provided examples of two, three and four new species emerging from a subdivided population during a short time interval. Numerical examples with hundreds of new species can be constructed by increasing the number of subpopulations. Overall our simulation model provides a justification for a verbal 'micro-allopatric' model of

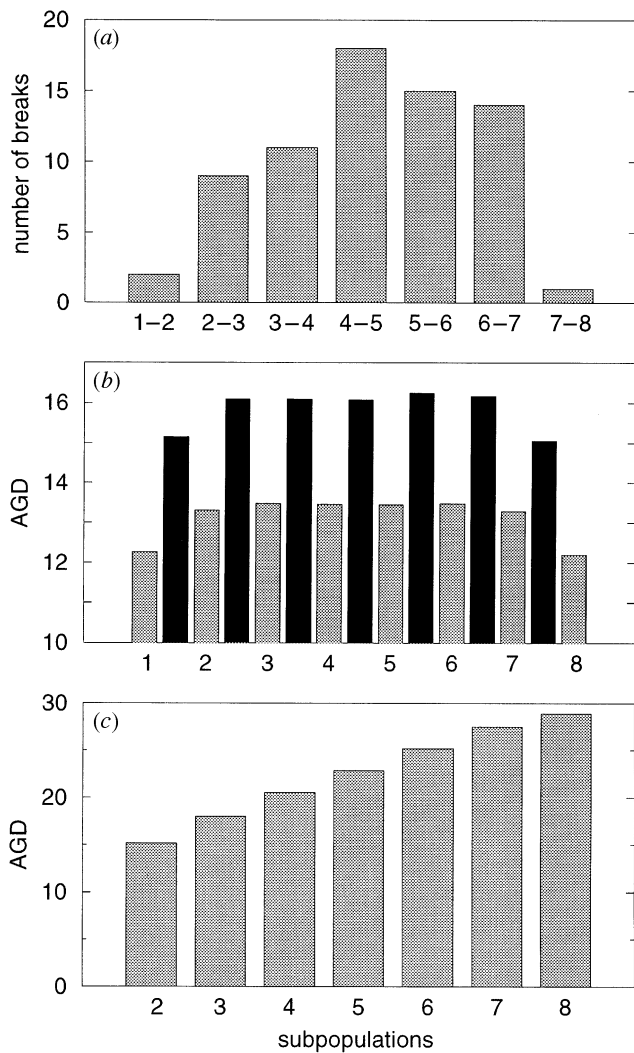


Figure 4. Splitting patterns in a stepping-stone system with eight local subpopulations. All parameters are the same as in figure 3c. (a) The observed distribution of the position of the first break using data from 70 runs (out of 92 total runs) that resulted in speciation. The abscissa gives the pair of subpopulations between which the split occurred. (b) Shown are the AGD within the subpopulations (the bars above the integers from 1 to 8) and between the subpopulations (the bars between the integers) calculated over generations 1500–3000 in 22 runs that did not result in speciation. (c) The AGD between the first subpopulation and other seven subpopulations using the same data as in (b).

speciation suggested for cichlid fishes (e.g. Reinthal & Meyer 1997).

#### (d) *Peripatric speciation versus centrifugal speciation*

Under appropriate conditions, a subdivided population will split into two or more distinct species. An interesting question concerns the likelihood of the split at different points along the geographic range of the species (e.g. Gaston 1998). Mayr's (1963) theory of peripatric speciation argues that peripheral populations are more likely to split off. Surprisingly, our simulations of a one-dimensional stepping-stone model show that the breaks resulting in the splitting of peripheral populations have the lowest probability (figure 4a). A reason for this is that

peripheral populations have lower genetic variability and are more similar to their neighbours than the 'inner' subpopulations (figure 4b). That genetic changes resulting in speciation are more probable in the middle of the species range was argued by Brown (1957) in his theory of centrifugal speciation. It would be interesting to see if the splitting pattern that we have observed stays the same in more complex models of spatial arrangement of subpopulations.

#### (e) *'Ring species' and the instability of the 'sexual continuum'*

About one-quarter of the runs of the stepping-stone model with eight subpopulations did not result in speciation within the time interval studied. In these runs, the neighbouring subpopulations were not reproductively isolated. At the same time, the AGD between peripheral populations significantly exceeded the threshold value  $K$  (figure 4c), meaning that if these populations somehow came into a direct contact they would be reproductively isolated. The situation observed here is analogous to that in 'ring species', which are traditionally considered as examples of incipient, but incomplete, speciation (e.g. Mayr 1942, 1963; Wake 1997). The population as a whole is characterized by the existence of reproductively isolated groups that exchange genes through a series of intermediate genotypes. Maynard Smith & Szathmáry (1995, pp. 163–167), who called such a population state 'sexual continuum', conjectured that 'sexual continuum' is unstable and would break up into distinct 'species'. Noest (1997) has proposed a model in which a uniform 'sexual continuum' was unstable to a range of perturbation. His analysis did not address whether the system will evolve to a non-uniform 'sexual continuum' or to a discontinuous state. Although the 'sexual continuum' observed in the runs described by figure 4c appears to be stable, continuing simulations for a longer period of time would almost definitely result in speciation in all runs. This provides a justification for Maynard Smith & Szathmáry's (1995) conjecture. Developing an analytical theory for predicting the persistence time of a 'sexual continuum' and 'ring species' is an important direction for future work.

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