Eur. Phys. J. B (2006)
DOI: 10.1140/epjb/e2006-00251-5

THE EUROPEAN PHYSICAL JOURNAL B

Monte Carlo simulations of parapatric speciation

V. Schwämmle[1,2,a], A.O. Sousa[2], and S.M. de Oliveira[1]

[1] Instituto de Física, Universidade Federal Fluminense, Av. Litorânea, s/n, Boa Viagem, Niterói 24210-340, RJ - Brazil
[2] Institute for Computer Physics, University of Stuttgart, Pfaffenwaldring 27, 70569 Stuttgart, Germany

Received 13 January 2006 / Received in final form 25 April 2006
Published online 22 June 2006 –

Abstract. Parapatric speciation is studied using an individual-based model with sexual reproduction. We combine the theory of mutation accumulation for biological ageing with an environmental selection pressure that varies according to the individuals geographical positions and phenotypic traits. Fluctuations and genetic diversity of large populations are crucial ingredients to model the features of evolutionary branching and are intrinsic properties of the model. Its implementation on a spatial lattice gives interesting insights into the population dynamics of speciation on a geographical landscape and the disruptive selection that leads to the divergence of phenotypes. Our results suggest that assortative mating is not an obligatory ingredient to obtain speciation in large populations at low gene flow.

PACS. 87.10.+e General theory and mathematical aspects – 87.23.-n Ecology and evolution – 87.23.Cc Population dynamics and ecological pattern formation – 87.23.Kg Dynamics of evolution

1 Introduction

Several types of speciation are found in the literature, and the existence of some of them is still controversial. The two most discussed ones are the sympatric and the allopatric speciations. The widely accepted mechanism of allopatric speciation is the appearance of a geographical barrier between two populations of the same species. Due to genetic drift and natural selection along several generations, these populations develop so many differences that they become reproductively isolated, that is, even if the barrier is removed the populations can no longer interbreed. In fact, speciation in allopatry is known to be a slow process [1]. The other form of speciation, the by far more complex sympatric speciation where there is no physical barrier to prevent gene flow, is supposed to be a fast process [2]. Assortative mating (non-random mating) and competition for different niches seem to be its essential ingredients [2–10], although some authors claim that assortative mating alone is enough to produce reproductive isolation followed by sympatric speciation [11]. On the other side, the model of [12] suggests that a small gene flux between different populations does not prevent speciation if the hybrids present a low viability.

There have been great achievements to explain the processes of speciation in the last decade. The combination of laboratory experiments [13], measurements [14–16] and numerical models [2–9,12,17] gave enormous insights, especially into the theory of sympatric speciation and the processes driving it. However, less numerical research has been done focusing on parapatric speciation, a mixture of speciating in sympatry and in allopatry (for a review see [18,19]). The population occupies a spatially continuous habitat and adaptation evolves from a gradient, such as an increasing altitude or a continuous change of food resources [20–22], which may or not result in speciation [3,23,24].

Speciation in parapatry is hardly controversial because even weak disruptive selection can cause sharp divergence [21,25,26]. The interesting feature demonstrated by Doebeli and Dieckmann [27] was that discrete clusters emerge, even when the optimal trait value changes linearly. They explained the evolution of the clusters as a consequence of a narrow frequency-dependent competition, similarly to the sympatric model of Dieckmann and Doebeli [8]. However, Polechova and Barton [28] have argued that the clustering in Doebeli and Dieckmann cannot be due to competition, because it occurs even in the limit of no competition. Rather, they propose that it arises because the densities of similar phenotypes are only weakly coupled so that large differences can be generated by weak perturbations–in this case, due to edge effects. The same explanation was independently presented by Gavrilets [18]. Very recently, Brigatti and collaborators (`q-bio.PE/0505017`) have obtained speciation using a strategy similar to that of Doebeli and Dieckmann, and there they present an analysis of the controversy just mentioned.

Here we modify the Penna model [29–31], which is based on the mutation accumulation hypothesis for biological ageing, in order to include an environmental

[a] e-mail: `veit@ical.uni-stuttgart.de`

selection pressure that, besides acting according to individuals phenotypes, also varies according to their positions on a spatial lattice. Using this strategy we study under which conditions parapatric speciation happens and observe that it depends strongly on the fluctuations of the system, as already obtained in previous simulations of sympatric speciation [9,17]. The connection of the individual deaths with their phenotypic traits and lattice positions through a simple function is shown to produce a complex behaviour of the whole population, that may or may not yield speciation.

Our implementation of the sexual Penna model with a phenotypic trait on a spatial lattice is based on [32] and [9]. We succeed in reproducing qualitatively the results of [33], although there speciation is obtained just with a mechanism of assortative mating, while in our case speciation is obtained with the implementation of an environment where the optimal trait value varies linearly in space, and assortative mating is not necessary.

In the next section we explain our model, and in Section 3 we present the results. In Section 4 we discuss some relevant aspects of the model and Section 5 contains the conclusions.

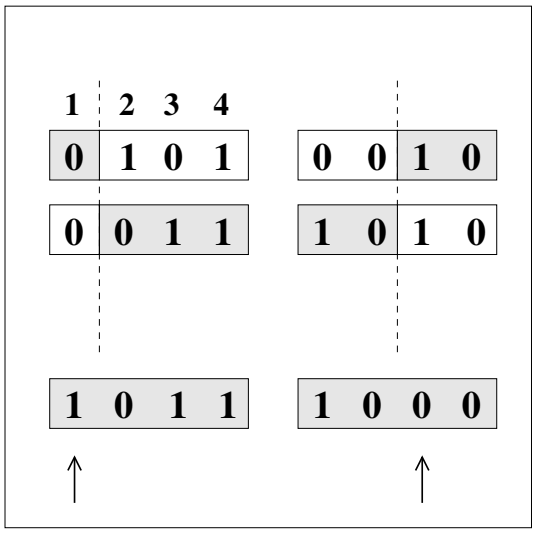

Fig. 1. Reproduction process. Each pair of bit-strings is cut at a random position and two complementary pieces are recombined to form a gamete. Mutations are then introduced at random positions in both parts (arrows). For the age-structured part (left part), only bad mutations are allowed, while for the non-structured part (right part), both back and forward mutations can randomly occur. The union of the male and female gametes forms the offspring genome.

2 Model

We consider sexual reproduction where individuals are *diploids* and half of the population is male and half is female. Their genomes are represented by two pairs of bit-strings, each string with 32 bits; each pair is read in parallel. The first pair of bit-strings corresponds to the "chronological genome" of the Penna model and presents an age-structure. The second pair is non-structured and codes for a given phenotypic trait, like the individual's size or colour. Both pairs are subjected to crossing and recombination, in the moment of reproduction (Fig. 1), but these two pairs are related to different genetic characteristics and work in a completely independent way. Let us describe now the role of each pair, separately.

2.1 The age-structured part of the genomes

Each one of the 32 possible bit-positions of this pair (the first one in Fig. 1) represents a period in each individual's life, which means that each individual can live at most for 32 periods. If we consider each period as one year, ages vary between $0 \leq \text{age} \leq 32$ years. Bits 1 correspond to a harmful recessive allele. If an individual carries two bits 1 at the same bit-position (homozygous), say position (or age) i, it means that the individual will start to suffer the effects of a genetic disease from its ith year of life on. In dominant positions one bit set to one is enough to switch on a disease. At the beginning of the simulation we choose randomly 5 bit-positions to be the dominant ones. They are the same for all individuals and remain fixed during the whole simulation. At the beginning of every iteration a new bit-position of each individual's chronological genome is read and its age is increased by one; then the actual number of accumulated diseases is computed: if this number reaches a threshold T, the individual dies due to the accumulation of inherited mutations.

At every iteration, females with age $\geq R$, the minimum reproductive age, search for a partner also with age $\geq R$ to breed, and produce offspring with a birth rate b. As already mentioned, the offspring genome is constructed by crossing, recombining and mutating each parent's genome. The whole process is illustrated in Figure 1. First the chronological genome of the mother is cut at a random position and two random complementary pieces are joined to form a female gamete. Deleterious mutations ($0 \rightarrow 1$) at random positions are then introduced, with a mutation rate m. The same process occurs with the father's chronological genome and the union of the two gametes completes the offspring genome. In this part of the genome only deleterious mutations ($0 \rightarrow 1$) may appear, since they are 100 times more frequent than the backward mutations [34]. In this case, if the randomly chosen bit of the parent genome is already one, it remains one in the offspring genome (no mutation occurs). On the other hand, if the chosen bit is zero, it is set to one in the offspring genome.

2.2 The phenotypic trait

The second pair of bit-strings of each genome is translated into some phenotypic characteristic of the individual [17], related to its ability in surviving in a given environment (ecology). This non-structured pair also suffers crossing, recombination and mutations, (Fig. 1), at the same time

it occurs for the age-structured pair, that is, at the moment of reproduction. However, for this pair both forward ($0 \rightarrow 1$) and backward ($1 \rightarrow 0$) mutations are allowed, with a rate m_p. Moreover, 16 of the 32 bit-positions are randomly chosen to be the dominant ones, and the remaining 16 to be the recessive ones. The effective number of bits 1, taking into account the dominance, corresponds to a given phenotypic characteristic. This number, which we call the phenotype number n, is an integer between zero and 32. For example, we may consider that small values of n correspond to small sized individuals, while large values of n denote big ones. Observe that in principle a particular value of n has nothing to do with the individual's fitness. That is why we allow for mutations in both directions in this part of the genome. A given value of n will be advantageous or not depending on the environment, that is, the selective character of the phenotype will be expressed according to the ecology, which is introduced as follows.

2.3 Spatial lattice and ecology

The individuals are distributed on a two dimensional square lattice. They move at every iteration, with a rate m_m, to a randomly chosen less or equally populated nearest neighbouring site. Movements can be carried out more than one time per iteration ($m_m > 1$). If all nearest neighbours sites are more populated than the current individual's site, the movement is not carried out. This strategy guarantees a fast and balanced distribution of individuals over the whole landscape. The boundary conditions in this model are reflective.

The reproductive females select their mating partners randomly from the reproductive males localised at the same or at a nearest neighbour site. Reproduction between different phenotypes is not forbidden. Offspring are distributed into empty nearest neighbouring sites. If there is no empty site, the offspring is not produced. In this way the population size is controlled by the size of the lattice [35], and there is no need to use the random killing Verhulst factor, present in the traditional version of the Penna model to avoid unlimited population growth.

The interaction between phenotypic trait and geographical position on a square lattice of linear size L is given by:

$$E(x,n) = S \cdot \left(1 - \left|g(x) - \frac{n}{32}\right|\right), \qquad (1)$$

which we call the ecological function. It gives the probability of an individual dying, at every iteration, depending only on its own x-position and phenotype number. This function is independent of the y-position of the individual and there is no direct competition, neither with individuals on neighbouring sites nor with individuals having similar phenotypes. In this way, edge effects for extreme phenotypes should not play any role in our approach. The parameter S is the strength of the interaction and varies between zero and one. The larger the value of S is, the stronger the selection pressure acting on the individuals. The coordinate function is given by $g(x) = \frac{x}{L-1}$, where the coordinate x is an integer between zero and $L-1$. For extreme phenotypes with $n = 0$, the perfect region in which to live corresponds to $x = L-1$ where $E(L-1,0) = 0$, while for extreme phenotypes with $n = 32$ the perfect region corresponds to $x = 0$. Individuals with intermediate phenotypes also live better at the extremes of the lattice, but are less fitted than those with extreme phenotypes living in the correct extreme of the lattice. Figure 2 illustrates the ecological function behaviour for three different values of n.

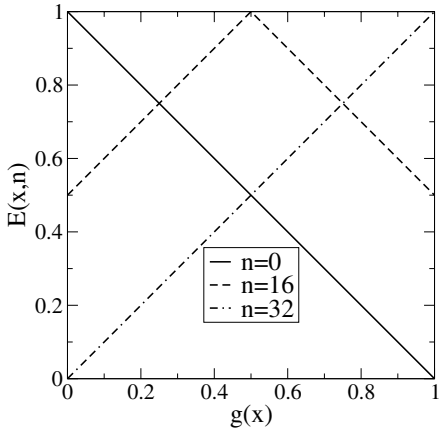

Fig. 2. Behaviour of the ecological function (or probability to die according to x-position and phenotype) $E(x,n)$. Individuals with high or low n survive better on opposite sides of the lattice whereas the ones with intermediate phenotype numbers have a higher death probability at intermediate values of x.

3 Results

In this section we describe the relevant features of speciation found with our simulations, that is, we focus on the interaction between phenotypic trait and the lattice. We want to make it clear that simulations without ageing also give speciation as a possible outcome. That is, we have also run the program considering the mutation rate $m = 0$, which means that all chronological genomes remain only with zeroes and individuals that are not killed due to their phenotypes can survive up to the age 32. These simulations give qualitatively the same results. However, ageing not only makes the model more realistic, but also directly illustrates the hybrids' viability, since it allows us to check if they live enough to produce offspring or not.

The fixed parameters that we adopt in the simulations are:

i) threshold number of genetic diseases $T = 3$;
ii) minimum reproductive age $R = 8$;
iii) birth rate $b = 4$;
iv) rate of bad mutations in the chronological genome $m = 1$;
v) number of dominant positions in the chronological genome $D = 5$;
vi) mutation rate of the phenotypic trait $m_p = 0.15$ or $m_p = 0.2$;

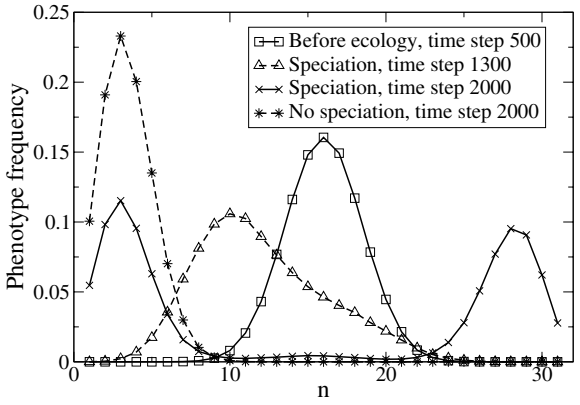

Fig. 3. The evolution of phenotypic frequency (given by the second pair of bit-strings) versus time. The same set of parameters may or not yield speciation for different random seeds. The central curve (solid line, squares) correspond to the distribution of phenotype numbers before switching on the ecological function ($t = 1000$ time-steps). The final distribution when speciation occurs is given by the double-peaked distribution (solid line, crosses). The dashed line with stars corresponds to the final distribution for a case where speciation has not occurred; the dashed line with triangles shows the intermediary distribution in the course of speciation. The parameters: $S = 0.24$, $m_m = 0.99$ and $m_p = 0.2$ on a 500×500 lattice with around 400 000 individuals.

vii) number of dominant positions in the phenotypic trait $D_p = 16$.

The relevant parameters for speciation are the movement rate m_m, the lattice size L and the strength S of the environmental pressure.

We start the simulations with all the genomes randomly filled with zeroes and ones, and all individuals randomly distributed on the lattice. In order to reach a genetically stable initial population, we run the simulations without any ecological function for 1000 iterations. During this period the dynamics of the population is neither affected by the phenotype numbers nor by the lattice positions of the individuals. The initial distribution of the phenotype numbers is regulated solely by the mutations, and shows a Gaussian behaviour (central curve of Fig. 3).

After these transient steps, the ecology is abruptly changed by setting the ecological function as an additional death probability. Disruptive selection driven by the ecology leads to a better survival of individuals with high and low phenotype numbers, depending on their current positions on the lattice. Three different situations, described below, can be observed, where the environmental pressure and the movement rate are the crucial parameters.

i) At low selection pressures (S small), and independently of the movement rate, the distribution of the phenotype numbers remains unaltered (Gaussian). The population decreases slightly at intermediate positions on the x-direction, but during the entire simulation individuals stay in contact over the whole lattice. Gene flow prevents disruptive selection from dividing the system into two subpopulations.

ii) For intermediate selection pressures and for movement rates around one movement per iteration ($m_m \sim 1.0$), shortly after turning disruptive selection on, the system reaches an extremely dynamical state where fluctuations may or may not drive the system to divergence. In the cases where speciation does not occur, the adaptation of individuals on one of the lattice sides is faster than the other, and due to gene flow their corresponding phenotypes finally dominate the whole lattice (dashed-line with stars in Fig. 3).

When phenotypic adaption is balanced, the distribution of phenotype numbers bifurcates. Figure 3 shows that even in the case of speciation, the phenotypic distribution usually drifts away from symmetry before bifurcating, but the final and stable state corresponds to two populations with different phenotypes. We emphasise that during the speciation process the whole population stays in contact and gene flow can not be neglected as in allopatric speciation.

Speciation events are likely to occur with around 50% probability in the interval $S = [0.2, 0.27]$. Below $S = 0.15$ and above $S = 0.32$ speciation nearly does not occur. Unfortunately, the long computational time needed for each run make it difficult to obtain a good statistics of speciation events for different values of S.

Figure 4 shows the typical spatial distributions of the phenotypes at four different moments of the simulations. Initially, the population is homogeneously distributed over the whole lattice. As soon as the new ecology is turned on, almost all individuals occupying the central x-positions of the lattice die, and the population becomes temporarily divided into two similar groups, with weak contact between them. When the adaptation process of the extreme phenotypes starts, offspring with intermediate phenotype numbers continue to be produced. As the adaptation proceeds, competition with the more fitted extreme phenotypes makes the intermediate ones disappear. Finally, when speciation occurs, each half of the lattice becomes mostly occupied by one of the two extreme phenotypes, respectively. The number of iterations needed to reach the final distribution is about 5000, which corresponds to 625 generations. However, we would like to emphasise that we have run our simulations for up to 100 000 time-steps, to be sure we were obtaining stable distributions.

The final result of a simulation where no speciation occurred, using the same parameters as in Figure 4 but with another initial random seed, is illustrated in Figure 5. In this case only one of the extreme phenotypes remains.

iii) Low movement rates or very high selection pressures prevent speciation events. In both cases a great part of the population dies out at the time when the ecological function is set. Fluctuations dominate divergent adaptation and the initial Gaussian distribution of phenotypes moves to one of the extremes.

It is important to say that for small population sizes fluctuations seem to always prevent speciation, independently of the movement rate: no speciation events have been obtained for lattice sizes smaller than $L = 150$, which

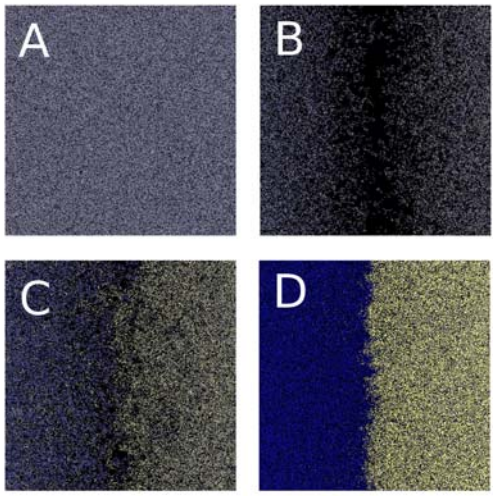

Fig. 4. Illustration of the phenotype distribution on a 500 × 500 lattice. The parameters are $m_m = 0.9$, $S = 0.25$ and $m_p = 0.1$. Black sites are empty. The colours indicate the average value of the phenotype numbers (between yellow and blue). Without disruptive selection, the initial population is homogeneously distributed over the whole lattice (A). When the ecological function is turned on the population is divided into two regions with weak contact (B). Selection prefers different phenotypes with respect to the horizontal location of the individuals and adaptation proceeds (C). Fluctuations decide if the final result is speciation or if it is a single population with phenotypically similar individuals. In case of speciation, two phenotypically different populations can be easily distinguished, each one occupying one side of the lattice (D).

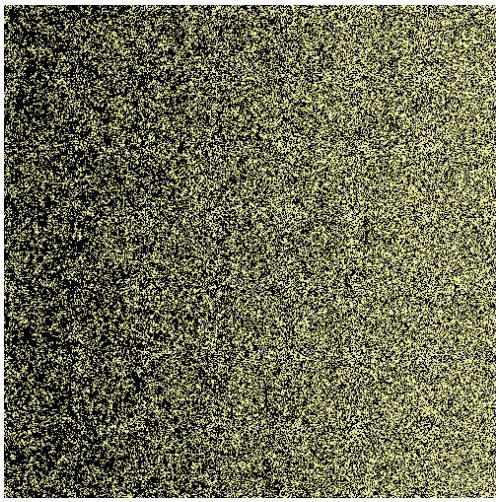

Fig. 5. Another random seed has driven the system to the case of no speciation. One of the two sub-populations randomly dominates and finally occupies the whole lattice. In this case, the worst region of the lattice for the winning extreme phenotype to survive (left side in this figure) remains less populated than the rest of the lattice, that is, the occupation is not uniform. The parameters are the same as in Figure 4.

leads to a population of around 40 000 individuals. Lattice sizes above 300×300 apparently do not increase the probability to obtain speciation. Concerning the selection pressure, it was also found by Doebeli [27] that very high values of S prevent speciation.

In order to study the effect of assortative mating in our simulations, we introduce the strategy used in [33] to prevent the mating of extreme phenotypes (prezygotic isolation). We measure the absolute difference of the phenotype numbers of both male and female, before mating. If the difference is larger than d, they can not reproduce. If there is no appropriate male among the nearest neighbours, no offspring is produced. Figure 6 shows the final phenotype distributions for different strengths S of the ecological function, in cases where speciation occurred. We compare different results using random mating to one where assortative mating is used, with $d = 10$. It can be seen that assortative mating completely prevents the production of hybrids with phenotype numbers around 16. Additionally, the occurrence of speciation is controlled by the parameter d, as in [33]. Very small values of d ($d < 8$) prevent speciation due to the lack of genetic diversity, which is an important ingredient for the distribution of phenotype numbers to bifurcate. Assortative mating alone is not sufficient to generate speciation. We carried out simulations with $S = 0$ for different values of d, and no speciation event occurred.

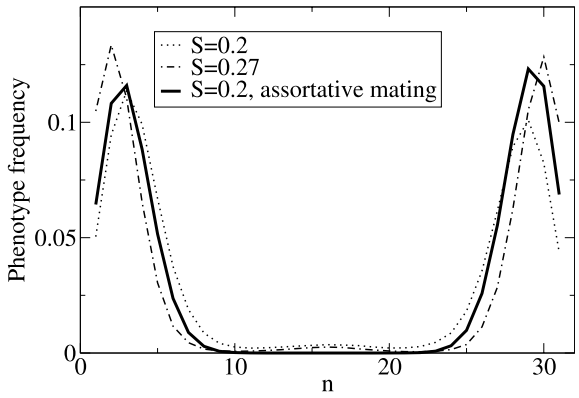

Fig. 6. Comparison of the final states of the phenotype distributions for different values of the parameter S. The stronger the ecology is, the less frequent are the hybrids. Assortative mating leads to the non-existence of hybrids, depicted by the thick curve where $d = 10$. The movement rate $m_m = 0.9$ and the mutation rate related to the phenotype is $m_p = 0.15$. The lattice size is 500×500 and the population fluctuates around 400 000 individuals.

In order to know more about the gene flow between different extreme phenotypes in case of random mating, Figure 7 shows the histogram of the fraction of the population that dies at a given age, for different phenotype numbers. The majority of the hybrids die at low ages and do not generate offspring. This low viability of the hybrids characterises a speciation process [12] in the presence of random mating.

A cline is defined as a gradient in a measurable character. Relative to the dispersal rate of a species, the slope of a cline between regions is indicative of the extent to which the inhabitants have differentiated. A steep cline means

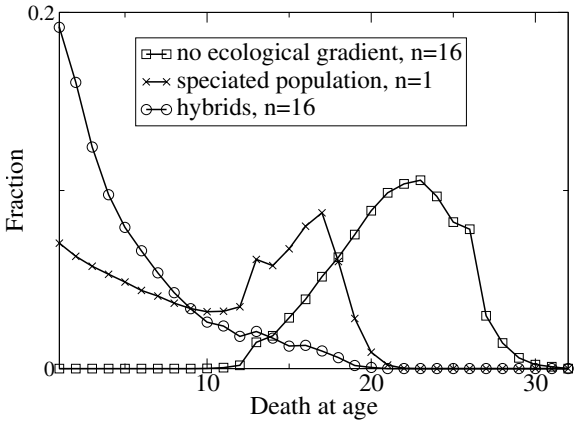

Fig. 7. Life span for different phenotype numbers. Most of the hybrids die at early ages, before reproduction. The parameters are the same as in Figure 4.

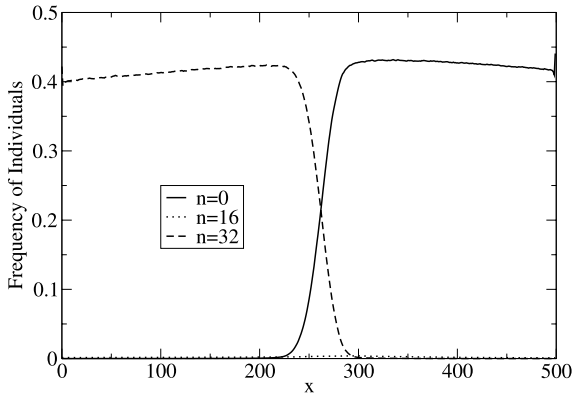

Fig. 8. Frequency of individuals with phenotype numbers $n = 0, 16$ and 32 for each position x of the lattice, averaged over the last 10 000 time steps. The frequency of individuals with $n = 16$ is almost zero for any position of the lattice, and so the dotted line is barely visible in the plot. The parameters are the same as in Figure 4.

sharp differentiation while a gentle cline means indistinct divergence between areas [21]. In our case we choose the phenotype number, n, as the measurable character. Figure 8 shows the fraction of individuals with $n = 0$, $n = 16$ and $n = 32$ at each position x of the lattice. A steep cline can be observed for the $n = 0$ and $n = 32$ populations, as well as the almost disappearance of the hybrids with $n = 16$ in spite of the random mating.

A common outcome in Nature consists of phenotypically distinguishable forms at geographic extreme regions and inter-grading hybrid forms in between. Populations separated by hybrid zones may differ greatly, or sometimes a few genes seem to be involved; for example, the races of the mimetic butterfly *Heliconius erato* that hybridise in South America, differ by between one and six major genes affecting wing pattern. A central tenet of evolutionary biology has been that the gene flow strongly impedes divergence, so that species can only form in geographical isolation. But the existence of sharp, stable clines and hybrid zones shows that gene flow need not destroy spatial divergence [36,37].

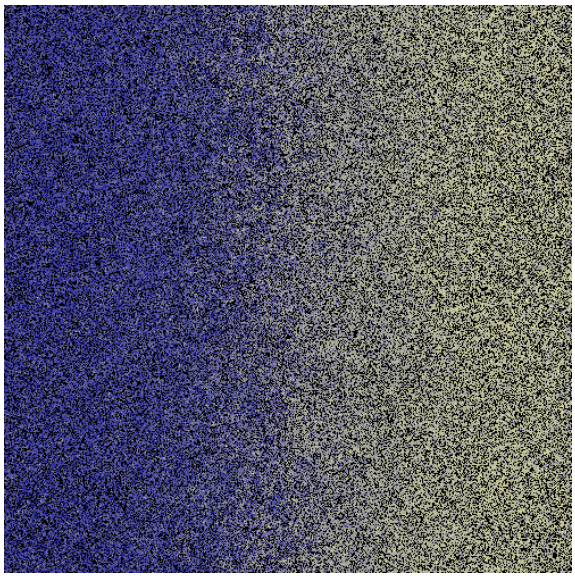

Fig. 9. Final state of the simulation without disruptive selection. No speciation occurs. The parameters are $m_m = 0.9$, $m_p = 0.01$, $S = 0.2$ on a 500×500 lattice with random mating.

In our case disruptive selection due to the ecological function in equation (1) prevents hybrid forms. However, using the following ecological function:

$$E(x, n) = S \cdot \left| g(x) - \frac{n}{32} \right|, \qquad (2)$$

hybrids are now favoured and so do not disappear, that is, there is no speciation as shown in Figures 9 and 10. From Figure 9 we can observe that the mean value of the phenotypes changes continuously with the geographic position x and there is no sharp separation between the two extreme regions. It is important to say that in using equation (2) speciation is not obtained even if assortative mating is included (Fig. 10).

4 Discussion

As reported by Gavrilets [33] the dynamics of parapatric speciation is very fast (less than 10 000 generations) and is independent of the mutations rate m_p of the phenotypic trait. We have made some simulations with smaller mutation rates and the time needed to reach a steady state did not increase for $m_p > 0.0001$.

In our model the ecological function must be disruptive, i.e. individuals with intermediate phenotypes have to be discriminated. In a non-disruptive ecology individuals of all phenotypes can adapt to their local environments and hybrids evolve easily at intermediate x-positions. At the end of the simulations individuals of all phenotypes populate the lattice. If the selection against individuals with intermediate phenotype numbers is not strong enough, only an unstable polymorphism appears: the two

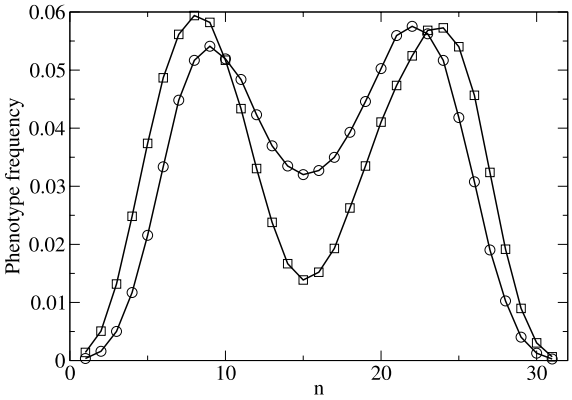

Fig. 10. Final phenotype distribution for simulations with the ecology function equation (2). The circles display the result for a run with random mating. Even for a simulation with assortative mating (squares) gene flux prevents speciation. The parameters are the same as in Figure 9.

subpopulations coexist with large gene flux between them until one of them completely dominates and uniformly occupies the whole lattice.

Different from other speciation models, ours allows fluctuations of all quantities, which hinders adaptation and the division of the system into two different phenotypic populations, even for intermediate values of the selection pressure. This could explain the not so frequent occurrence of speciation in Nature, where many environmental factors act on the different population quantities, like the phenotypic distribution, and where fluctuations of these quantities are ubiquitous. Even if the conditions are optimal, speciation remains a statistical event (that is, for ten different initial random seeds, about five result in speciation and the other five result in an unimodal phenotypic distribution). Speciation is observed frequently for large lattices, where the phenotype distributions fluctuate less. Our results suggest that parapatric speciation occurs preferably in cases where a large population undergoes a sudden disruptive selection over large geographical distances compared to the range of individuals movements.

We have studied the effect of assortative mating in our model, but the final results obtained were nearly the same as those using random mating, although the rule of [33] increases the probability of speciation occurring. Even without assortative mating, only a very small number of hybrids is born (less than 1% of the total population) due to the small range of the mating region (only between nearest neighbours individuals). Moreover, Figure 7 shows that these hybrids die mainly at low ages and do not produce offspring, which can be interpreted as a form of postzygotic reproductive isolation. In this way a small gene flow does not prevent speciation in this parapatric scenery, even without assortative mating.

5 Conclusions

We present an individual-based model for parapatric speciation, where individuals with different phenotypes are distributed on a spatial lattice. Individuals may die due to genetic diseases or due to a competition for resources that depends on their phenotypes and on their geographical positions. Mating occurs only between next nearest neighbours. Surprisingly, even when considering random mating, fluctuations due to a disruptive selection may drive the system to speciation. On the other hand, under very strong disruptive selection, fluctuations prevent speciation.

In fact, the importance of our approach is that it allows fluctuations in nearly all quantities. Physicists are very conscious about the importance of fluctuations in physical systems, mainly when they present a phase transition, which can be regarded as a process of bifurcation, like the speciation process, from a single phase (for instance, gas) into a state where two different phases coexist (liquid and vapour). The simplest, naive strategy to deal with such a phenomenon is the mean-field approach, in which the influences of the many units of the system over a particular one are replaced by an average influence or an "average unity", disregarding completely all possible fluctuations. However, this kind of treatment always gives wrong values for the critical exponents and sometimes signals the existence of a phase transition when it does not exist, since the fluctuations that would prevent the transition are omitted [38]. Concerning the speciation process, such an approach can predict a speciation event when in fact it does not occur.

V. Schwämmle is funded by the DAAD (Deutscher Akademischer Austauschdienst); S. Moss de Oliveira is partially supported by the Brazilian Agencies CNPq and FAPERJ. We thank D. Stauffer, P.M.C. de Oliveira and J. S. Sá Martins for a critical reading of the manuscript.

References

1. E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, 1963)
2. S. Gavrilets, Nature **403**, 886 (2000)
3. R. Lande, Evolution **36**, 213 (1982)
4. F. Turner, G.M. Burrows, Proc. R. Soc. Lond. B **260**, 287 (1995)
5. G. van Doorn, A. Noewst, P. Hogeweg, Proc. R. Soc. Lond. B **265**, 1915 (1998)
6. M. Higashi, G. Takimoto, N. Yamamura, Nature **402**, 523 (1999)
7. A. Kondrashov, F. Kondrashov, Nature **400**, 351 (1999)
8. U. Dieckmann, M. Doebeli, Nature **400**, 354 (1999)
9. K. Luz-Burgoa, S. Moss de Oliveira, J.S. Sá Martins, D. Stauffer, A.O. Sousa, Braz. J. Phys. **33**, 623 (2003)
10. M.E. Arnegard, A.S. Kondrashov, Evolution **58**, 222 (2004)
11. C.R. Almeida, F.V. de Abreu, Evol. Ecol. Res. **5**, 730 (2003)
12. A.H. Porter, N.A. Johnson, Evolution **56**, 2103 (2002)
13. W.R. Rice, E.E. Hostert, Evolution **47**, 1637 (1993)
14. U.K. Schliewen, D. Tautz, S. Pääbo, Nature **368**, 629 (1994)
15. D. Schluter, Science **3266**, 798 (1994)

16. S. Via, Trends Ecol. Evol. **16**, 381 (2001)
17. J.S. Sá Martins, S. Moss de Oliveira, G.A. de Medeiros, Phys. Rev. E **64**, 021906 (2001)
18. S. Gavrilets, *Fitness landscapes and the origin of species* (Princeton University Press, 2004)
19. J. Coyne, H. Orr, *Speciation* (Sinauer Associates, 2004)
20. M. Slatkin, Genetics **75**, 733 (1973)
21. J.A. Endler, Science **179**, 243 (1973)
22. M. Kirkpatrick, N.H. Barton, Am. Nat. **150**, 1 (1997)
23. N. Sanderson, Evolution **43**, 1223 (1989)
24. T. Day, Evolution **54**, 715 (2000)
25. J.B.S. Haldane, J. Genet. **48**, 277 (1948)
26. M. Caisse, J. Antonovics, Heredity **40**, 371 (1978)
27. M. Doebeli, U. Dieckmann, Nature **421**, 259 (2003)
28. J. Polechova, N.H. Barton, Evolution **59**, 1194 (2005)
29. T.J.P. Penna, J. Stat. Phys. **78**, 1629 (1995)
30. S. Moss de Oliveira, P.M.C. de Oliveira, D. Stauffer, *Evolution, Money, War and Computers* (Teubner, 1999)
31. D. Stauffer, P.M.C. de Oliveira, S. Moss de Oliveira, T.J.P. Penna, J.S. Sá Martins, An. Acad. Bras. Ci. **731**, 15 (2001)
32. A.O. Sousa, Eur. Phys. J. B **39**, 521 (2004)
33. S. Gavrilets, H. Li, M. Vose, Proc. R. Soc. Land. B **265**, 1483 (1998)
34. P. Pamilo, M. Nei, W.H. Li, Genet. Res. **49**, 135 (1987)
35. D. Makowiec, Physica A **289**, 208 (2001)
36. N. Barton, G.M. Hewitt, Nature **341**, 497 (1989)
37. M. Turelli, N.H. Barton, J.A. Coyne, Trends in Ecol. Evol. **16**, 330 (2001)
38. R. Baxter, *Exactly Solvable Models in Statistical Mechanics* (Academic Press, 1982)