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## Conditions for neutral speciation via isolation by distance

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## HIGHLIGHTS

- We extend the analytical results on speciation of hermaphroditic populations to sex-separated ones.
- We provide detailed comparisons between the analytical and numerical results for both cases.
- We show that the analytical formulas match the simulations.

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## ABSTRACT

The branching of new species from an ancestral population requires the evolution of reproductive isolation between groups of individuals. Geographic separation of sub-populations by natural barriers, if sustained for sufficiently long times, may lead to the accumulation of independent genetic changes in each group and to mating incompatibilities (Mayr, 2001; Fitzpatrick et al., 2009). A similar phenomenon may occur in the absence of barriers via *isolation by distance* if the population is distributed over large areas (de Aguiar et al., 2009; Etienne and Haegeman, 2011; Gavrillets et al., 2000). The first demonstration of this process was based on computer simulations employing agent-based models. Recently, analytical results were derived combining network theory, to model the spatial structure of the population, and an ansatz that accounts for the effect of forbidding mating between individuals that are too different genetically (de Aguiar and Bar-Yam, 2011). The main result obtained with this approach is an expression that indicates when speciation is possible as a function of the parameters describing the population. The aim of this work is to test this analytical result by comparing it with numerical simulations for a hermaphroditic population (de Aguiar et al., 2009) and for a population whose individuals are explicitly separated into males and females (Baptestini et al., 2013). We show that the analytical formula is indeed a very good overall description of the simulations and that the exponents describing dependence of the critical threshold of speciation with the parameters are in good agreement with the simulations.

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## 1. Introduction

A central problem in genetics is to understand how allele frequencies change over time, resulting in a diversity of organisms. The resulting population structure may lead to speciation events, separating into multiple genetically incompatible groups (Mayr, 2001; Fitzpatrick et al., 2009). In real populations the problem involves a large number of variables that cannot usually be monitored or controlled, such as mutation rate, selection, number of genes involved, genetic incompatibilities, variable population size and area where the population lives (Baptestini et al., 2013; Lande and Kirkpatrick, 1988; Gavrillets, 2006). Here we compare

simulations and analytical results on speciation in spatially extended populations. Our results quantify the increase of speciation with decreasing population density, increasing mutation rate and genome size, more restrictive mating in space and genetic variation. All dependencies are incorporated in a single scaling function analysis of the threshold conditions for speciation through spontaneous segregation of interbreeding spatial populations.

One of the simplest theoretical formulations of the dynamics of population diversity was proposed by Moran, who described the neutral evolution of a single gene with two alleles in a population of haploid individuals subjected to mutations. An important feature of the Moran model is the overlapping of generations, meaning that only one individual is replaced at each time step, as opposed to the synchronous update of the entire population, as in the model proposed by Wright and Fisher (Ewens, 1979; Moran, 1971; Wakeley, 2009). The Wright–Fisher model describes, for instance, annual plants, whereas the Moran model is appropriate for perennial plants.

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The dynamics of the Moran model are as follows: consider a gene with alleles  $A_0$  and  $A_1$  in a population with fixed number  $N$  of haploid individuals. At each step one individual,  $k$ , is randomly selected to reproduce and die, being replaced by the resulting offspring. The offspring is generated by the mating of  $k$  with another random individual  $k'$  and it may keep the allele of either parent, and be subsequently altered by mutation. The population is said to be *panmictic*, or fully mixed, since any individual can mate with any other. The probability  $P_t(m)$  that the population has  $m$  alleles  $A_0$  at time  $t$  satisfies a linear equation, which can be solved for the case of zero (Watterson, 1961; Gladstein, 1978) and non-zero (Cannings, 1974; Gillespie, 2004; de Aguiar and Bar-Yam, 2011) mutations. Complete results for non-zero mutations were derived only recently by mapping the Moran model into a dynamical problem on fully connected networks where each node represents an individual (de Aguiar and Bar-Yam, 2011).

In equilibrium, the average genetic distance between two individuals in the population, the heterozygosity, is given approximately by

$$\langle d \rangle = \frac{2\mu N}{1 + 4\mu N} \quad (1)$$

where  $\mu$  is the mutation rate per gene. In de Aguiar and Bar-Yam (2011) the Moran dynamics were extended to include multiple genes, spatially extended populations and a condition of genetic incompatibility that allows the development of reproductive isolation. With these generalizations the model can be used to describe the evolution of neutral speciation. For individuals with  $B$  independent genes, Eq. (1) becomes

$$\langle d \rangle_B = B \langle d \rangle = \frac{B}{2} \left( \frac{4\mu N}{1 + 4\mu N} \right). \quad (2)$$

Here the genetic distance between individuals is measured by the number of genes bearing different alleles, the so-called Hamming distance.

The Moran model dynamics can be combined with network theory, where the network topology describes the set of possible mating events, enabling an analysis of the genetic dynamics of structured populations. Panmictic populations are mapped into fully connected networks (Chinellato et al., 2007). A particularly important case arises when the population is spread over a square region of size  $L \times L$  and mating is allowed only between individuals that are closer than a critical spatial distance  $S < L$ . This corresponds to a locally connected homogeneous spatial network with  $\rho\pi S^2$  connections per node, where  $\rho = N/L^2$  is the average population density. It can be shown (de Aguiar and Bar-Yam, 2011) that the dynamics of such a population are closely equivalent to the panmictic case, but with an effective mutation rate given approximately by

$$\mu_{ef} = \frac{\mu f}{1 + 2\mu f} \quad (3)$$

where  $f = L^2/\pi S^2$  is the ratio of the number of potential mates in the panmictic case to the number of potential mates in the structured population.

The multi-gene spatial version of the Moran model can describe speciation if a condition for genetic incompatibility is introduced, namely, that mating is possible only between individuals that are sufficiently similar genetically. This condition couples the genes and Eq. (2) becomes no longer exact. It is still a good approximation if the individuals are not too different genetically. When the genetic restriction is added, speciation via 'isolation by distance', or topopatric speciation becomes possible (de Aguiar et al., 2009) and understanding the conditions for its occurrence is of importance to evolutionary biology and biodiversity. Including the effects of restricting mating by genetic

proximity in the Moran dynamics is, however, more difficult and requires understanding the role of several variables in speciation.

In de Aguiar et al. (2009), de Aguiar and Bar-Yam (2011) and Baptistini et al. (2013) it was shown that the occurrence of speciation is sensitive to variation in the parameters describing the population, increasing with decreasing population density and with increasing mutation rate and number of genes. Taking these effects into account, the condition of genetic incompatibility can be included as an ansatz that can be understood as follows.

For a panmictic population, restricting mating by genetic proximity decreases the genetic diversity of the population by 'forcing' the individuals to be all genetically similar. If the maximum allowed genetic distance for mating is  $G$ , then, in equilibrium,  $\langle d \rangle_B \approx G$ . According to Eq. (2), and if  $4\mu N \geq 1$ , this can be interpreted as reducing the genome size  $B$  to an effective size  $B_{ef} = 2G$ . However, if mating is also constrained by the spatial distance  $S$ , the effective mutation rate increases as  $S$  decreases. This, in turn, increases the average genetic distance between individuals and, therefore, the size of the effective genome. The conflict between these two effects,  $G$  contracting the genetic diversity and  $S$  increasing it via mutations, is resolved by speciation. Indeed, when  $\langle d \rangle_B$  becomes larger than about  $2G$  the population becomes unstable and splits into smaller groups (species) where the average genetic distance is restored to values close to  $G$  and whose size is compatible with  $S$ . Writing

$$B_{ef} = 2G + (B - 2G)\mathcal{P} \quad (4)$$

the question becomes to estimate the fraction  $\mathcal{P}$  of genes added to the effective genome due to the spatial restriction  $S$  for a given total genome size  $B$ , mutation rate  $\mu$  and population density  $\rho = N/L^2$ . As discussed above, increasing  $B$  and  $\mu$  or decreasing  $\rho$  facilitates speciation. In de Aguiar and Bar-Yam (2011) it was proposed that  $\mathcal{P}$  could be written as

$$\mathcal{P} = \exp \left\{ - \left[ \frac{\pi(S - S_{min})^2 \rho}{\gamma^2 B \mu} \right]^2 \right\} \quad (5)$$

where  $\gamma$  is a fit parameter and

$$S_{min} = \sqrt{P/\pi\rho} \quad (6)$$

is the size of a neighborhood containing  $P$  individuals (see next section for comparison with the numerical model). The functional Gaussian form was suggested by simulations.

The condition for speciation is that

$$\langle d \rangle_B = \frac{B_{ef}}{2} \left( \frac{4\mu_{ef} N}{1 + 4\mu_{ef} N} \right) \gtrsim \beta G \quad (7)$$

where  $\beta$  represents the maximum average genetic distance between individuals that can be supported by a cohesive species and was originally estimated as  $\beta = 2$ . If  $4\mu_{ef} N \geq 1$ , which is the case in our simulations, Eq. (7) leads to

$$S \leq S_{min} + S_M \equiv S_c. \quad (8)$$

where

$$S_M = \gamma \sqrt{\frac{B\mu}{\pi\rho} \left[ \ln \left( \frac{B - \beta G}{\beta G} \right) \right]^{1/4}} \quad (9)$$

is the maximum spatial distance for speciation measured from  $S_{min}$ .

This expression describes the conditions for speciation as a function of the parameters of the problem, such as mutation rate, spatial and genetic restrictions, genome size and population density (de Aguiar and Bar-Yam, 2011). In this paper we compare this theoretical result with an agent-based model that simulates the neutral evolution of a population subjected to spatial and genetic mating restrictions and whose individuals are either

hermaphroditic (de Aguiar et al., 2009) or separated into males and females (Baptistini et al., 2013). We describe these simulations in more detail in the next section and show the comparisons in Section 3. In Section 4 we discuss our results and their implications.

## 2. Topopatric speciation

A population that is spatially extended can undergo speciation without the need for geographic isolation or even selection. If mating occurs only between close neighbors that are genetically similar, gene flow through the population is slow and the genomes of individuals that are geographically far apart can become very different (de Aguiar et al., 2009; Kopp, 2010; Hubbell, 2001; Etienne et al., 2007; Rosenzweig, 1995). This mechanism of *isolation by distance* (Wright, 1943; Martins et al., 2013) can, in turn, lead to speciation if the conditions are right (Wake, 2009; Irwin et al., 2005, 2001a, 2001b; Ashlock et al., 2010). These results were demonstrated in de Aguiar et al. (2009) using agent-based simulations. Because the numerical model has a large number of parameters, testing all the conditions that result in speciation becomes very hard and theoretical predictions based on explicit formulas are of fundamental importance.

In order to test the theory proposed in de Aguiar and Bar-Yam (2011) we simulated the dynamics of a population with  $N$  individuals homogeneously distributed in space and evolving according to the mating rules proposed in de Aguiar et al. (2009). Each individual is assigned a spatial position  $(x, y)$ ,  $1 \leq x, y \leq L$  and a haploid genome with  $B$  biallelic genes, which are labeled 0 or 1. The individuals, initially identical, accumulate differences over time due to mutation (at rate  $\mu$ ) and recombination. Sexual reproduction is constrained by two critical mating distances (de Aguiar et al., 2009). In physical space, an individual can mate only with others located in a certain neighborhood of its position, determined by the spatial mating distance  $S$ . Space has periodic boundary conditions to avoid the appearance of borders and corners. In genetic space, mating is allowed only between individuals that are sufficiently similar, i.e., if the number of distinct genes is no more than  $G$ , the maximum genetic mating distance (Etienne and Haegeman, 2011; Gavrillets, 2000; Gavrillets, 2004; Hoelzer et al., 2008; Higgs and Derrida, 1991, 1992; Manzo and Peliti, 1994). We consider two versions of the model, one in which the population consists of individuals that are hermaphroditic and one in which it is separated into males and females. In the first case any two individuals respecting the spatial and genetic constraints can mate. In the second case, we refer to as *sex-separated*, only individuals of opposite sex can do so. Depending on the values of the model parameters, the population may spontaneously break up into reproductively isolated groups (de Aguiar et al., 2009; Baptistini et al., 2013; Hoelzer et al., 2008).

The main result obtained in de Aguiar and Bar-Yam (2011) is the critical line in the  $S$  versus  $G$  plane below which speciation occurs. For hermaphroditic populations it is given by Eq. (8). The parameter  $P$  (minimum number of potential mates) was introduced in de Aguiar et al. (2009) to avoid the situation where the number of available mates is very small: given  $S$  and  $G$ , if the number of mates available to the reproducing individual is smaller than  $P$ , the spatial constraint is relaxed by making  $S \rightarrow S + 1$  until at least  $P$  mates are available. Other important properties can be derived, such as the number of species that arises from speciation, the average number of individuals in a species and the average radius of a species (de Aguiar et al., 2009; Baptistini et al., 2013).

Eq. (8) was derived for hermaphroditic populations. In this case each individual is mapped into a node of the network and links are established between potential mates—individuals that are genetically and spatially compatible. For sex-separated populations the

nature of the network changes considerably, since nodes representing females link only with nodes representing males, and vice-versa. The structure is that of a bipartite network.

In the sex-separated case it is useful to define a female *reduced network*, where two individuals are connected if they can mate with a common male, and a similar male network. Each of these networks has approximately half the nodes of the hermaphroditic network, so the average spatial density of individuals is  $\rho/2$ . Also, if the spatial mating restriction between males and females is  $S$ , the maximum separation between connected individuals of the same sex in the reduced network is  $2S$ . Moreover, gene flow in the female network is at least a two-step process, since it takes the mating of a first female with a male and the mating of the male offspring with a second female to combine the female's genes. Therefore, the time scale of crossover events slows down by a factor of two. Still, the analytic discussion continues to apply to the female or male network so the form of the analytic expressions should still be valid. We show below that Eq. (8) can indeed be applied to the sexual model if we change  $\rho$  to  $\rho/2$ ,  $S_{min}$  to  $\sqrt{2}S_{min}$  and  $S$  to  $2S$ . In order to obtain good qualitative fits we also need to change  $\gamma$  into  $\tilde{\gamma}$ . Therefore, Eq. (8) should also work for the sex-separated case with the changes

$$S^{sex} \leq S_{min}^{sex} + S_M^{sex} \equiv S_c^{sex} \quad (10)$$

where

$$S_M^{sex} = \tilde{\gamma} \sqrt{\frac{B\mu}{\pi\rho}} \left[ \ln \left( \frac{B-\beta G}{\beta G} \right) \right]^{1/4}, \quad (11)$$

$S_{min}^{sex} = \sqrt{2}S_{min}$  and the factor  $1/2$  in  $\rho/2$  is absorbed in  $\tilde{\gamma}$ .

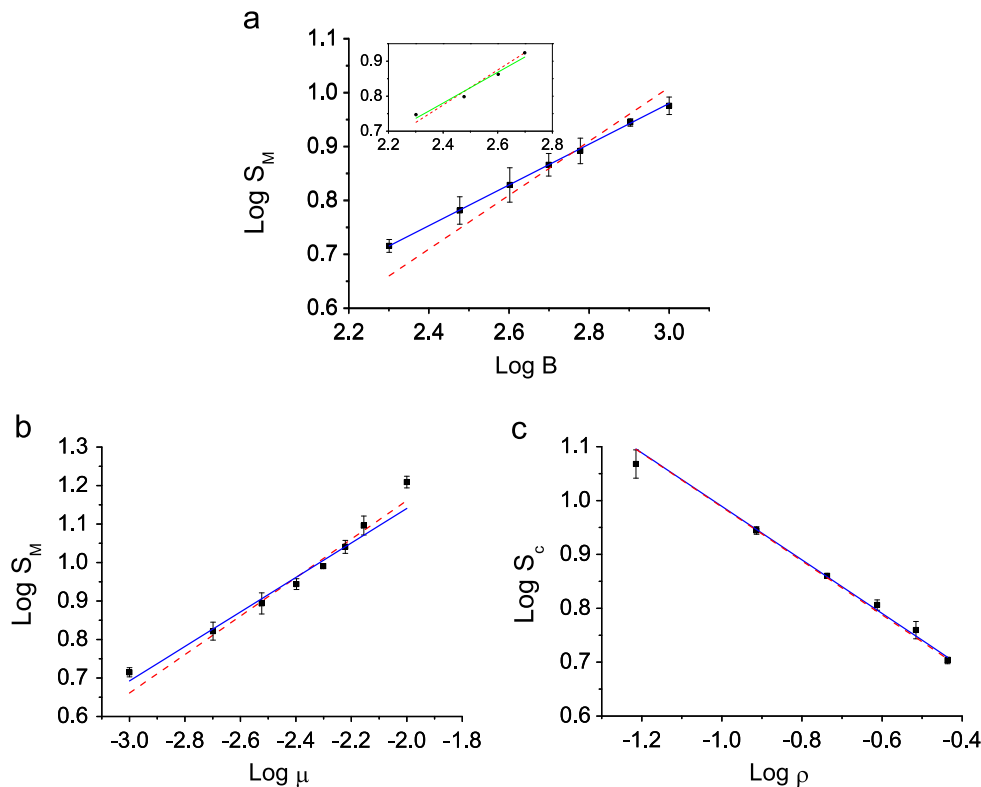
Eqs. (8) and (10) identify the combination of parameters that makes speciation possible. For example, low mutation rates, which hinder speciation, can be compensated by a large number of participant genes or by low population density.

## 3. Comparing theory and simulations

Eqs. (8) and (10) give an estimate of the multidimensional parameter region where speciation is possible. The results incorporate cutoffs at  $G = B/\beta$  and at  $S = S_{min}$ , which are in agreement with numerical simulations (de Aguiar et al., 2009). Here we found that  $\beta = 1.5$  gives a better fit to the numerical results than the original estimate  $\beta = 2$  and we used this value in all cases shown in this section. Eqs. (8) and (10) also predict speciation at large values of  $S$  if  $B$  is sufficiently large even if the ratio  $G/B$  is kept constant. This is in agreement with the previous results that have described speciation in well mixed populations with infinitely large genomes (Higgs and Derrida, 1991, 1992; Melian et al., 2012).

We performed simulations varying one parameter at a time and plotted the results on logarithmic scale, so that several exponents could be calculated and compared with the theoretical expressions. In all the plots the solid blue line is a linear fit through the data points (black squares) and the dashed red line is the theoretical prediction. For each parameter that was varied, the threshold value between speciation and non-speciation was numerically computed five independent times and from these values the mean and standard deviation were calculated. All simulations were ran for 4000 generations on a  $128 \times 128$  square lattice, except for the inset in Fig. 1(a) where  $L = 256$ .

Fig. 1 displays the results for the hermaphroditic case. In panels (a) and (b) we show  $S_M$  as a function of genome size  $B$  and mutation rate  $\mu$ . In panel (c) we show  $dS_c$  as a function of the population density  $\rho$  (notice that  $S_{min}$  also depends on  $\rho$ ). The parameter  $\gamma$  was adjusted to  $\gamma = 7.5$  for Fig. 1(a) and (b) and to  $\gamma = 8.5$  for Fig. 1(c). The inset in Fig. 1(a) shows the calculation on a



**Fig. 1.** Comparison between analytical (red dashed lines) and numerical (points with error bars) results for the hermaphroditic model. The solid blue lines show a linear fit to the numerical results. (a)  $\text{Log } S_M \times \text{Log } B$  with  $\rho = 0.122$ ,  $\mu = 0.001$ ,  $\gamma = 7.5$  and  $R^2 = 0.999$  (The inset shows results for a larger spatial grid, with  $L=256$  and  $\gamma = 8.7$ ); (b)  $\text{Log } S_M \times \text{Log }(\mu)$  with  $\rho = 0.122$ ,  $B=200$ ,  $\gamma = 7.5$  and  $R^2 = 0.953$ ; (c)  $\text{Log } S_c \times \text{Log } \rho$  with  $B=200$ ,  $\mu = 0.001$ ,  $\gamma = 8.5$  and  $R^2 = 0.994$ . Fixed parameters:  $G/B=0.25$ ,  $t=4,000$ . (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

**Table 1**  
Theoretical and simulated exponents for hermaphroditic model.

Plot	Value of exponent		
	Theoretical	Simulation fit	$R^2$
$\text{Log } S_M \times \text{Log } B$	0.5	$0.38 \pm 0.01$	0.999
$\text{Log } S_M \times \text{Log } \mu$	0.5	$0.45 \pm 0.04$	0.953
$\text{Log } S_c \times \text{Log } \rho$	-0.5	$-0.5 \pm 0.02$	0.994

larger spatial lattice with  $L=256$  and  $\gamma = 8.7$ . Table 1 summarizes the expected and simulated exponents.

Results for the sex-separated model are displayed in Fig. 2 for the same set of parameters used in Fig. 1, but are now compared with Eq. (10). In this case we show  $S_M^{\text{sex}}$  and we used  $\tilde{\gamma} = 4.0$  for panel (a),  $\tilde{\gamma} = 6.0$  for (b) and (c). Table 2 shows the expected and simulated exponents.

#### 4. Discussion

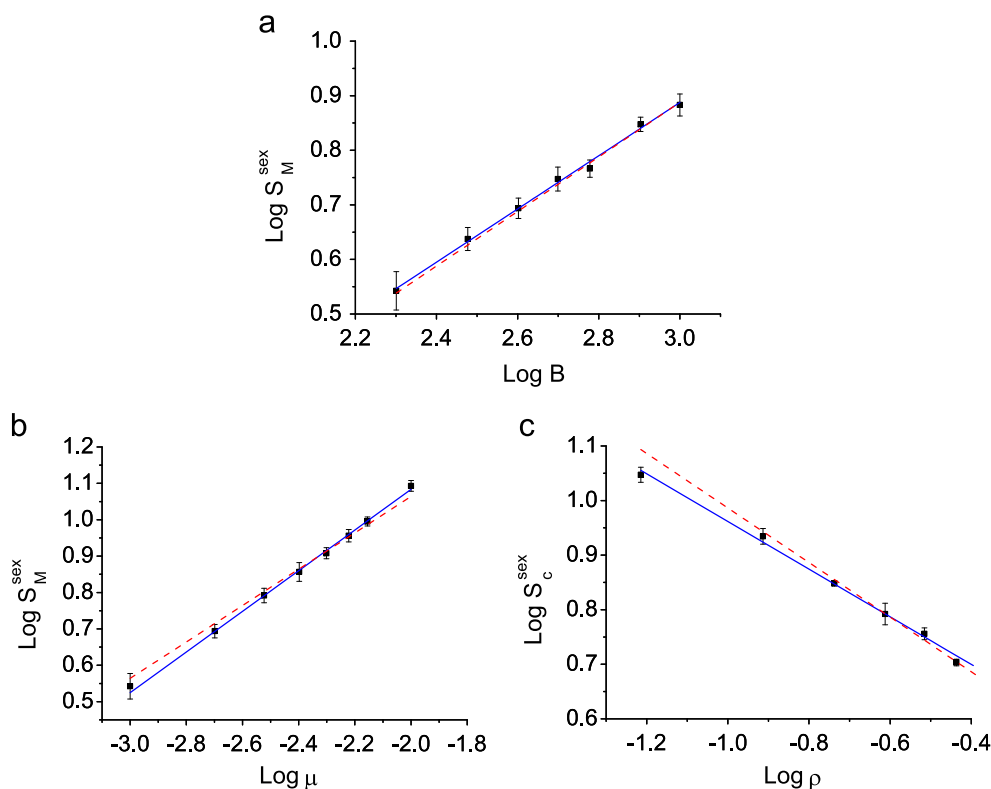
Spatially extended populations can break up spontaneously into species when subjected to mutations and to spatial and genetic mating restrictions, even in the absence of natural selection (de Aguiar et al., 2009). Numerical simulations have shown that this mechanism, termed topopatric speciation, occurs for a restricted range of parameters that include population density  $\rho$ , mutation rate  $\mu$  and the parameters  $S$  and  $G$  controlling the spatial and genetic mating restrictions. Because of this large number of independent parameters, exploring the system's phase space becomes computationally costly and theoretical predictions are essential. Moreover, having explicit formulas allow for a better

understanding of the role of each specific population characteristic in the speciation process.

In this paper we have shown that the analytical result obtained in de Aguiar and Bar-Yam (2011) provides a good description of neutral speciation for both the hermaphroditic case and the sex-separated case. For the sex-separated model the equations have to be adapted to incorporate features of the corresponding network that are not present in the hermaphroditic case.

The dependence of the critical spatial distance for speciation  $S_c$  on the genome size  $B$  (with fixed ratio  $G/tB$ ), mutation rate  $\mu$  and population density  $\rho$  follows closely the proposed power law with exponents 0.5 for  $B$  and  $\mu$  and  $-0.5$  for  $\rho$ . The largest deviation was found in the exponent of  $B$  for the hermaphroditic case,  $0.38 \pm 0.01$ . For the sex separated case, on the other hand, the numerical value  $0.49 \pm 0.01$  was very close to the theoretical prediction. The best fit numerical coefficients  $\gamma$  or  $\tilde{\gamma}$  varied in Fig. 1 between 7.5 in (a) and (b) and 8.5 in (c), and in Fig. 2 from 4.0 in (a) to 6.0 in (b) and (c). Among the possible reasons for these variations is the lattice granularity ( $128 \times 128$ ) and the small population (2000 individuals for panels (a) and (b) of both figures). We tested this conjecture by running simulations on a  $256 \times 256$  lattice with  $N=8000$  individuals, as shown in the inset of Fig. 1(a). Not only did the hermaphroditic scaling exponent increase to  $0.44 \pm 0.06$  but we also obtained  $\gamma = 8.7$ , which is very close to the value  $\gamma = 8.5$  in panels (b) and (c). This provides increased confidence that even the deviations that were observed are due to finite size effects in the simulated populations.

The overall agreement between the analytical formula and the simulations is quite strong. The precise results suggest that our ansatz about the role of spatial restriction in increasing the effective genetic variation as embodied in Eqs. (4) and (5) (de Aguiar and Bar-Yam, 2011) provides a useful way to characterize the dynamics of speciation in spatial populations.



**Fig. 2.** Comparison between analytical (red dashed lines) and numerical (points with error bars) results for the sex-separated model. The solid blue lines show a linear fit of the numerical results. (a)  $\text{Log } S_M^{\text{sex}} \times \text{Log } B$  with  $\rho = 0.122$ ,  $\mu = 0.001$ ,  $\bar{\gamma} = 4.0$  and  $R^2 = 0.991$ ; (b)  $\text{Log } S_M^{\text{sex}} \times \text{Log } \mu$  with  $\rho = 0.122$ ,  $B = 200$ ,  $\bar{\gamma} = 6.0$  and  $R^2 = 0.998$ ; (c)  $\text{Log } S_C^{\text{sex}} \times \text{Log } \rho$  with  $B = 200$ ,  $\mu = 0.001$ ,  $\bar{\gamma} = 6.0$  and  $R^2 = 0.992$ . Fixed parameters:  $G/B = 0.25$ ,  $t = 4,000$ . (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

**Table 2**

Summary of theoretical and simulated values of the exponents for sex-separated model.

Plot	Value of exponent		
	Theoretical	Simulation fit	$R^2$
$\text{Log } S_M^{\text{sex}} \times \text{Log } B$	0.5	$0.49 \pm 0.01$	0.991
$\text{Log } S_M^{\text{sex}} \times \text{Log } \mu$	0.5	$0.56 \pm 0.01$	0.998
$\text{Log } S_C^{\text{sex}} \times \text{Log } \rho$	-0.5	$-0.44 \pm 0.02$	0.992

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## References

- Ashlock, D., Clare, E.L., von Königslöw, T.E., Ashlock, W., 2010. Evolution and instability in ring species complexes: an in silico approach to the study of speciation. *J. Theor. Biol.* 264, 1202–1213.
- Baptistini, E.M., de Aguiar, M.A.M., Bar-Yam, Y., 2013. The role of sex separation in neutral speciation. *J. Theor. Ecol.*, <http://dx.doi.org/10.1007/s12080-012-0172-2>.
- Cannings, C., 1974. The latent roots of certain Markov chains arising in genetics: a new approach, I. Haploid models. *Adv. Appl. Probab.* 6, 260–290.
- Chinellato, D.D., de Aguiar, M.A.M., Epstein, I.R., Braha, D., Bar-Yam, Y., 2007. Dynamical Response of Networks Under External Perturbations: Exact Results. [arXiv:0705.4607v2](http://arxiv.org/abs/0705.4607v2) [nlin.SI].
- de Aguiar, M.A.M., Bar-Yam, Y., 2011. Moran model as a dynamical process on networks and its implications for neutral speciation. *Phys. Rev. E* 84, 031901.
- de Aguiar, M.A.M., Baranger, M., Baptistini, E.M., Kaufman, L., Bar-Yam, Y., 2009. Global patterns of speciation and diversity. *Nature* 460, 384–387.

- Etienne, R.S., Haegeman, B., 2011. The neutral theory of biodiversity with random fission speciation. *Theor. Ecol.* 4, 87–109.
- Etienne, R.S., Alonso, D., McKane, A.J., 2007. The zero-sum assumption in neutral biodiversity theory. *J. Theor. Biol.* 248, 522–536.
- Ewens, W.J., 1979. *Mathematical Population Genetics I. Theoretical Introduction*, Series: Biomathematics, vol. 9. Springer Verlag, New York.
- Fitzpatrick, B.M., Fordyce, J.A., Gavrillets, S., 2009. Pattern, process and geographic modes of speciation. *J. Evol. Biol.* 22, 2342–2347.
- Gavrillets, S., 2004. *Fitness Landscapes and the Origin of Species*. Princeton University Press.
- Gavrillets, S., 2006. The Maynard Smith model of sympatric speciation. *J. Theor. Biol.* 239, 172–182.
- Gavrillets, S., Arnqvist, G., Friberg, U., 2000. The evolution of female mate choice by sexual conflict. *Proc. R. Soc. B* 268, 531–539.
- Gillespie, J.H., 2004. *Population Genetics: a Concise Guide*. The Johns Hopkins University Press.
- Gladstein, K., 1978. The characteristic values and vectors for a class of stochastic matrices arising in genetics. *SIAM J. Appl. Math.* 34, 630–642.
- Higgs, P.G., Derrida, B., 1991. Stochastic models for species formation in evolving populations. *J. Phys. A: Math. Gen.* 24, L985.
- Higgs, P.G., Derrida, B., 1992. Genetic distance and species formation in evolving populations. *J. Mol. Evol.* 35, 454–465.
- Hoelzer, G.A., Drewes, R., Meier, J., Doursat, R., 2008. Isolation-by-distance and outbreeding depression are sufficient to drive parapatric speciation in the absence of environmental influences. *PLoS Comput. Biol.* 4, e1000126.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, New Jersey.
- Irwin, D.E., Bensch, S., Price, T.D., 2001a. Speciation in a ring. *Nature* 409, 333–337.
- Irwin, D.E., Irwin, J.H., Price, T.D., 2001b. Ring species as bridges between microevolution and speciation. *Genetica* 112–113, 223–243.
- Irwin, D.E., Bensch, S., Irwin, J.H., Price, T.D., 2005. Speciation by distance in a ring species. *Science* 307, 414–416.
- Kopp, M., 2010. Speciation and the neutral theory of biodiversity. *BioEssays* 32, 564–570.
- Lande, R., Kirkpatrick, M., 1988. Ecological speciation by sexual selection. *J. Theor. Biol.* 133, 85–98.
- Manzo, F., Peliti, L., 1994. Geographic speciation in the Derrida–Higgs model of species formation. *J. Phys. A: Math. Gen.* 27, 7079.
- Martins, A.B., de Aguiar, M.A.M., Bar-Yam, Y., 2013. Evolution and stability of ring species. *Proc. Nat. Acad. Sci. USA* 110.
- Mayr, E., 2001. *What Evolution is*. Basic Books.

- Melian, C.J., Alonso, D., Allesina, S., Condit, R.S., Etienne, R.S., 2012. Does sex speed up evolutionary rate and increase biodiversity? *PLoS Comput. Biol.* 8, e1002414.
- Moran, P.A.P., 1971. Maximum-likelihood estimation in non-standard conditions. *Math. Proc. Cambridge Philos. Soc.* 70, 441–450.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press.
- Wake, D.B., 2009. What salamanders have taught us about evolution. *Annu. Rev. Ecol. Evol. Syst.* 40, 333–352.
- Wakeley, J., 2009. *Coalescent Theory*. Roberts and Company Publishers.
- Watterson, G.A., 1961. Markov chains with absorbing states: a genetic example. *Ann. Math. Stat.* 32, 716–729.
- Wright, S., 1943. Isolation by distance. *Genetics* 28, 114–138.