Disorder-induced genetic divergence: A Monte Carlo study

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We present a Monte Carlo simulation of a system composed of several populations, each living in a possibly different habitat. We show the influence of landscape disorder on the genetic pool of finite populations. We demonstrate that a strongly disordered environment generates an increase of the genetic distance between the populations on identical island. The distance becomes permanent for infinitely long times. On the contrary, landscapes with weak disorder offer only a temporarily allelic divergence which vanishes in the long time limit. Similarities between these phenomena and the well-known first-order phase transitions in the thermodynamics are analyzed.

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I. INTRODUCTION

Island problems play an important role in understanding biological evolution. Actually, various questions related to adaptation, reproduction, biological transmission, and natural selection can be studied using island concepts. Usually, one takes into account that an island is in contact with the mainland. The underlying dynamics of colonization, migration, and extinction lead to a biological equilibrium depending on various control parameters, e.g., the island size and the distance to the mainland [1–5]. The predictions of such models have been verified for a wide range of taxa including birds [6,7], insects [8], and plants [9]. The decisive contributions to the stabilization of the biological equilibrium arise from the interplay between colonization, migration, and extinction [10]. The importance of these dynamical factors has been confirmed in several experimental systems [11–14].

Obviously, the biological equilibrium is not a real equilibrium but a stationary state in the sense of a statistical interpretation. This can be verified by an artificial interruption of the colonization and migration currents. Such a change corresponds to a transition from a canonical system (which is in contact with a thermal bath, i.e., the mainland) to a microcanonical system (which is completely isolated). The dynamics of the evolution are different in the two cases, in contrast to an equilibrium system, where the dynamics are essentially the same with the exception of possible boundary effects. Also a partial change of the influx currents changes the evolution, e.g., in absence of further colonization, species diversity dynamics on islands are controlled only by extinction, as with mammals on Great Basin mountains [5]. Furthermore, the case of a complete isolation of the islands will lead to speciation between the island and the mainland [15] and also between islands in an archipelago [16].

Both island-island models and mainland-island models are used also for studies of premating isolation [17–19]. Here, the boundary conditions emerging from speciation by vicariance and peripheral isolation correspond to a symmetric and one way migration, respectively [20].

In this paper we shall discuss another question: what is the influence of the island landscape (i.e, living conditions) on the speciation? It can be assumed that the formation of new species is the result of a complicated interaction between the modification of the genotypes due to mutations and the natural selection. The appearance of mutations is a pure biological property, which is only weakly related to the local environment. On the other hand, the environment favors certain phenotypes which have a higher survival chance. Consider now a large territory which can be decomposed into several smaller ones, with possibly different living conditions. If the differences are small the subpopulations occupying the territories evolve in a coherent manner. Different territories may lead to different evolutionary patterns. A homogeneous environment leads to a systematic drift of the genetic composition, but the effects of a heterogeneous environment may be locally different. Hence, a heterogeneous landscape represents a further random quantity apart from the above mentioned mutations.

We analyze the evolution of populations on complete isolated islands, i.e., both the island-mainland and the island-island contacts will be interrupted after the initial colonization. A realistic example is the occupation of similar islands which are temporary within easy reach over landbridges. The immigrated populations are separated after sinking of the bridges. In consideration of the initial question we assume that all islands have identical random landscapes and the initial distributions of the islands are also identical. We shall study two problems. In one, the islands are identical but the genetic pools of the colonists are different and in the second one also the habitats are different.

We demonstrate, on the base of Monte Carlo (MC) simulation, that for strongly disordered environments an increase of the genetic distance between the populations on different islands occurs which becomes permanent also for infinite long times. Landscapes that do not differ much will generate only a temporarily allelic divergence which vanishes in the long time limit.

II. MODEL

How can we model the biological evolution of species in terms of a Monte Carlo simulation? The first problem is the definition of the habitat. The general shape of the island is irrelevant, but the area is important because it determines the

maximum number of inhabitants (the so-called carrying capacity of the environment). Each island consists of territories, and each territory can be occupied at the most by one animal of the population. Therefore, we map the islands on a square lattice of size L. Each lattice cell corresponds now to a territory and the total number of territories per island is $N=L^2$.

A. Numerical rules

The outward appearance of an animal is characterized by a set of properties which are defined by the animal's phenotype. The phenotype of an animal in the ith territory is described by a G dimensional vector $\Phi_i=\{\varphi_i^1,\varphi_i^2,\ldots,\varphi_i^G\}$. Each component of this vector corresponds to a property, which is either $\varphi_i^\alpha=T$ (true) or not $\varphi_i^\alpha=F$ (false). Furthermore, $\varphi_i^\alpha=T$ may correspond to an advantageous property. Such a property becomes dominant in the course of the biological transmission.

To quantify the reproduction of animals, a genotype is assigned to each individual. The genotype of an animal at position i consists of two sequences $R_{i,1}$ and $R_{i,2}$ each of length G. An element of a sequence can be either true (T) or false (F). The phenotype of the animal follows from both sequences using the logical OR operation $\varphi_i^\alpha=R_{i,1}^\alpha \vee R_{i,2}^\alpha$, i.e., φ_i^α is true if and only if at least one of $R_{i,1}^\alpha$ and $R_{i,2}^\alpha$ is true. This rule represents the dominance of $\varphi_i^\alpha=T$ against $\varphi_i^\alpha=F$. The reproduction and therefore the biological transmission takes place due to simplified genetic principles. In the first step two individuals at the positions i and j are chosen randomly. These animals are denoted as parents. The distance $|i-j|$ on the square lattice between both parents should not exceed the maximum distance $r_{\max}$. The genetic sequences of the parents must now be prepared for reproduction. Therefore, the genotype sequences are split into two subsequences of length m and $G-m$, respectively, i.e., we obtain $(R_{i,1}R_{i,2})\rightarrow([R_{i,1}^m R_{i,1}^{G-m}],[R_{i,2}^m R_{i,2}^{G-m}])$. Here the length m is chosen randomly between 0 and G. These subsequences are recombined to two new sequences (gametes) $\tilde{R}_{i,1}=[R_{i,1}^m R_{i,2}^{G-m}]$ and $\tilde{R}_{i,2}=[R_{i,2}^m R_{i,1}^{G-m}]$. One of these new sequences is chosen randomly and combined with a gamete prepared by a similar procedure on the base of the genotype of the other parent. These two gametes form the genotype of an offspring. This procedure is commonly called recombination. If more than one offspring is created, the whole procedure is repeated again. The maximum number of offspring is n_0, but we have to consider that a new animal has to find a vacant territory. Therefore, only if a vacancy exists in a region of radius $r_{\max}$ around the average parent position, the offspring has a chance of survival.

The natural selection of animals is determined by the phenotype. The local character of a territory i may be defined by the environment vector $S_i=\{\sigma_i^1,\sigma_i^2,\ldots,\sigma_i^G\}$ (with $\sigma_i^\alpha=T$ and $\sigma_i^\beta=F$, respectively), which defines the optimal properties for survival of the animal which has occupied this territory. The product of a component of the phenotype vector Φ_i with a component of the local environment vector S_i is defined using the logical procedure XOR. (This procedure does not have a mathematical standard symbol, but is sometimes denoted as $\underline{\vee}$.)

$$\langle \varphi_i^\alpha|\sigma_i^\alpha\rangle = f(\varphi_i^\alpha \underline{\vee} \sigma_i^\alpha),$$

$$\text{with} \quad f(T)=1 \quad \text{and} \quad f(F)=-1.$$

Therefore, the fitness of an animal is given by $A_i=(1+\langle\Phi_i|S_i\rangle)/2$ with the scalar product $\langle\Phi_i|S_i\rangle = G^{-1}\Sigma_{i=1}^G\langle\varphi_i^\alpha|\sigma_i^\alpha\rangle$. Obviously, the fitness is restricted by $0\leqslant A_i\leqslant 1$. Fitness and the actual life time τ_i of an animal determine the state of the animal. As in many biological models (see e.g., [21]) we assume that the rate of survival is given by an exponential distribution function, i.e., the chance of survival of an individual is defined by

$$P_i=\exp\left\{-\beta\frac{\tau_i}{A_i}\right\}.$$

β^{-1} can be interpreted as the averaged age of the animals. If an individual dies, the corresponding territory becomes vacant and can be occupied by a new animal.

B. Preparation of island landscapes and initial populations

Now we turn back to the original problem. We assume that the genetic pool of the initial colonists has been formed on the mainland by a certain phenotype, namely $\Phi^0=\{T,T,\ldots,T\}$. This phenotype corresponds to the best environment vector $S^0=\{T,T,\ldots,T\}$ which may be relevant for the mainland. Furthermore, we have to take into account that the islands are identical, but the landscapes of the islands deviate from the optimum environment vector S^0 by random perturbations. We consider two special cases. On one hand, we have spatially homogeneous landscapes, i.e., the property vectors of all territories are equivalent $S_1=S_2=\ldots S_N\neq S^0$. Therefore, we obtain $f(\sigma_i^\alpha)=\langle f(\sigma^\alpha)\rangle$, where the average is performed over all territories. The function f maps logical observables on numerical quantities, $f(T)=1$ and $f(F)=-1$, as explained above. On the other hand, we have to deal with completely heterogeneous landscapes, i.e., the territories characterized by different property vectors. Therefore, we use two parameters for characterizing the two types of disorder of the landscapes:

$$\Delta_0=\frac{1}{G}\sum_{\alpha=1}^{G}\langle[f(\sigma^\alpha)-\langle f(\sigma^\alpha)\rangle]^2\rangle \tag{1}$$

$$\text{and} \quad \overline{\Delta}=\frac{1}{G}\sum_{\alpha=1}^{G}\left[\langle f(\sigma^\alpha)\rangle-\frac{1}{G}\sum_{\alpha=1}^{G}\langle f(\sigma^\alpha)\rangle\right]^2. \tag{2}$$

We obtain $\Delta_0=0$ in the case of a pure homogenous disorder, whereas the second quantity converges asymptotically to zero for a pure heterogeneous disorder, $\lim_{N\rightarrow\infty}\overline{\Delta}=0$. For a parametrization of the disorder we use the following procedure. We start from the G-dimensional reference vector $S^0=\{T,T,\ldots,T\}$ and change randomly a fraction of μG components $T\rightarrow F$. The obtained vector S' is now used as pro-

visional property vector of each territory, i.e., $S_i' = S'$. Without further changes, the vector S_i' defines a completely homogeneous landscape. To obtain a heterogeneous landscape, we change again with the probability κ, each component of the vectors S_i', independently of the logical character of the components, i.e., $T \to F$ and $F \to T$. The result is a random set of property vectors S_i, which are used to describe the landscape of the islands. Hence, we obtain

$$\Delta_0 = 4\kappa(1-\kappa) \quad \text{and} \quad \overline{\Delta} = 4\mu(1-\mu)(1-2\kappa)^2.$$

The genetic structure of the population is characterized by the $2N$ genotypes $R_{i,1}$ and $R_{i,2}$. We require that the initial sequences of the colonists are completely randomly distributed, but the initial distributions of characteristics of all islands are identical.

C. Numerical simulations

In the MC simulations we compare the time evolution of 100 pairs of identical islands of size $N = 40 \times 40$. Each individual is characterized by its genotype of length $G = 20$, hence it has two gene sequences of 20 components. In general, these arbitrary settings differ from reality, but the main messages of the simulations are also valid for longer sequences and for a large number of territories. Furthermore we choose the radius $r_{\max} = 5$ and the maximum number of offspring $n_0 = 3$.

After generation of the initial distribution, the originally identical populations diverge due to the random effects in the biological transmission, the life time, and the occupation of vacant territories (genetic drift). The combination of biological transmission and natural selection emphasizes a certain phenotype. This phenotype is well defined in the case of vanishing disorder: individuals with $\Phi = \{T, T, \ldots, T\}$ have supplanted all other individuals after a sufficiently long evolution time. Thus, the divergence of the genetic distance shows a crossover to a convergence and at sufficiently long times we find a vanishingly small difference.

The situation becomes more complicated in the case of disordered island landscapes. Here, it can be expected that the divergence of the genetic distance becomes finite also at sufficiently long times, in spite of identical landscapes and identical initial distributions due to genetic drift and randomness introduced by genetic shuffling in th process of recombination.

We use the following quantity for the characterization of the difference between the phenotypes at both islands of a given island pair:

$$\vartheta_{ik}(t) = \frac{1}{G} \sum_{\alpha=1}^{G} [\langle f(\varphi^\alpha)(t)\rangle_{(i)} - \langle f(\varphi^\alpha)(t)\rangle_{(k)}]^2.$$

The indices i and k indicate the number of the island. Obviously, this quantity depends on the actual landscape of the islands. Therefore, we have to average over all possible realizations of the landscape disorder, defined by the above introduced parameters μ and κ. This ensemble average is marked by an overline. Thus we obtain the following measure for the mean square genetic distance between the populations on two islands with disordered landscapes:

$$\delta\Theta(t) = \frac{1}{G} \sum_{\alpha=1}^{G} \overline{[\langle f(\varphi^\alpha)(t)\rangle_{(1)} - \langle f(\varphi^\alpha)(t)\rangle_{(2)}]^2}. \quad (3)$$

Another quantity is the so-called overlap function

$$\Theta_{\text{overlap}}(t) = \frac{1}{G} \sum_{\alpha=1}^{G} \overline{\langle f(\varphi^\alpha)(t)\rangle_{(1)} \langle f(\varphi^\alpha)(t)\rangle_{(2)}}, \quad (4)$$

which describes similarity of the respective phenotypes. It should be remarked, that this quantity contains similar information as the Edwards–Anderson order parameter [22,23] which describes the thermodynamic similarity between nonergodic spin glass states [23]. Obviously, there is an interesting analogy between the biological evolution of isolated populations and the relaxation of spin glasses into a stable stationary state. This similarity will be analyzed in detail in the discussion.

Furthermore, we determine the mean misfit of adaptation

$$M^{(1)}(t) = \frac{1}{2G} \sum_{\alpha=1}^{G} \left[\sum_{k=1}^{2} \overline{\langle f(\varphi^\alpha)(t)\rangle_{(k)}} - 2\overline{\langle f(\sigma^\alpha)\rangle} \right]$$

$$= \frac{1}{2G} \sum_{\alpha=1}^{G} \sum_{k=1}^{2} \overline{\langle f(\varphi^\alpha)(t)\rangle_{(k)}} - (1-2\mu)(1-2\kappa) \quad (5)$$

and the mean square misfit of adaptation

$$M^{(2)}(t) = \frac{1}{2G} \left\{ \sum_{\alpha=1}^{G} [\overline{\langle f(\varphi^\alpha)(t)\rangle_{(1)}^2} + \overline{\langle f(\varphi^\alpha)(t)\rangle_{(2)}^2}] - 2\sum_{\alpha=1}^{G} \overline{\langle f(\sigma^\alpha)\rangle^2} \right\}, \quad (6)$$

which is related to (3) and (4) via

$$M^{(2)}(t) = \frac{1}{2}\delta\Theta(t) + \Theta_{\text{overlap}}(t) - (1-2\kappa)^2. \quad (7)$$

III. DISCUSSION

First, we analyze the adaptation of the populations to the landscape of the islands. Therefore, we study the quantities $M^{(1)}(t)$ and $M^{(2)}(t)$. The initial mean misfit of adaptation can be determined immediately, because $\overline{\langle f(\varphi^\alpha)(0)\rangle} = 1/2$ is valid for all populations. Hence, we obtain $M^{(1)}(0) = -1/2 + 2\mu + 2\kappa - 4\mu\kappa$. The mean misfit of adaptation $M^{(1)}(t)$ converges for long times to another asymptotic value, which depends also on the parameters κ and μ defining the disorder of the island landscape. The misfit vanishes in the case of a vanishing local disorder at the islands ($\kappa = 0$), i.e., the remaining phenotype shows an optimal adaptation to the island landscape. This phenomenon can be observed for globally disordered islands, i.e., for $\kappa = 0$ and $1 \geqslant \mu \geqslant 0$. It should be remarked, that this statement is also valid for $\kappa = 1$, because the above mentioned construction changes the character of

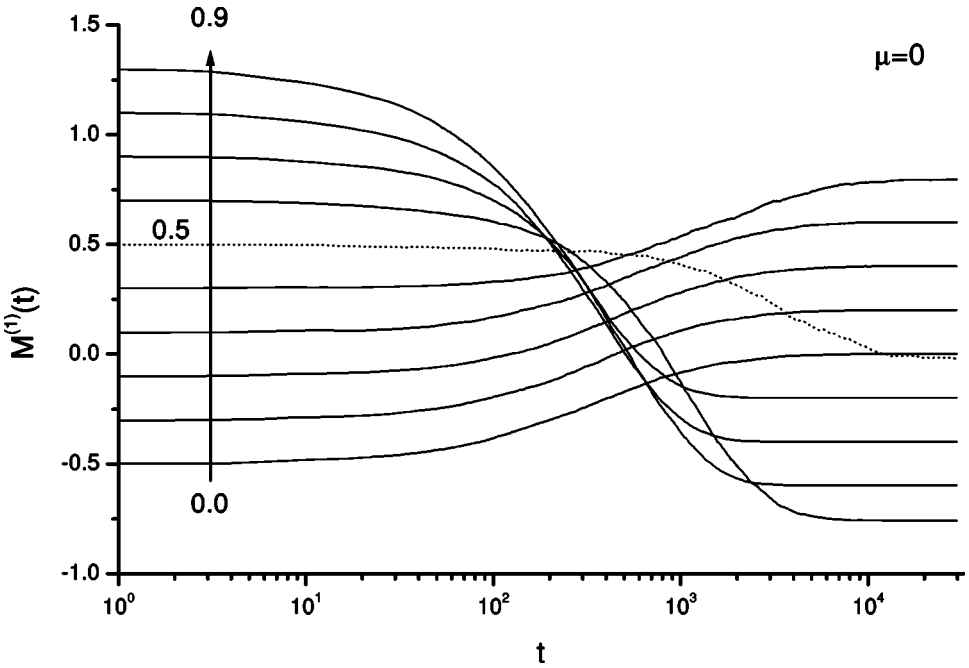

FIG. 1. $M^{(1)}(t)$ as a function of evolution time t for the global disorder parameter $\mu=0$ and various local disorder parameters $\kappa=0,0.1,0.2,\ldots,0.9$. The arrow shows in the direction of increasing κ. The dotted line corresponds to $\kappa=0.5$.

all properties in all territories. We may therefore say that a weak disorder is related to $\kappa\to 0$ and $\kappa\to 1$, whereas a strong disorder occurs for $\kappa=1/2$. Another is the situation for nonvanishing local disorder. Obviously, a finite misfit remains after an infinitely long evolution time also, which cannot be eliminated by the action of the natural selection, see Figs. [1,2]. The surprising result arises for $\kappa=1/2$. The final mean misfit of adaptation $M^{(1)}(\infty)$ increases with increasing κ for $\kappa<1/2$ and then follows an abrupt drop at $\kappa=1/2$, see Fig. 3. Finally, the misfit approaches again the value 0 for $\kappa\to 1$. The jump at $\kappa=1/2$ indicates a behavior similar to a first-order phase transition [24] induced by the static local disorder of the island landscape.

A characteristic slowing down of the relaxation from the initial value $M^{(1)}(0)$ to the final value occurs for $\kappa=1/2$. Here, we expect a decay from the initial value $M^{(1)}(0)=1/2$ to $M^{(1)}(\infty)=0$. This statement is correct if we realize the average, over all possible initial distributions of the genotypes and over all disordered landscapes corresponding to $\kappa=1/2$ and a fixed value of μ. But if we consider only one special landscape with $\kappa=1/2$ and fixed μ and one initial configuration then we arrive at a nonvanishing value for $M^{(1)}(\infty)$. If we repeat the numerical procedure with another landscape characterized again by the same disorder parameters $\kappa=1/2$ and μ or with another initial configuration, we obtain another value for $M^{(1)}(\infty)$. The quantity $M^{(1)}(\infty)$ approaches zero, not until we perform the average over a large set of landscapes and initial configurations. This is the rea-

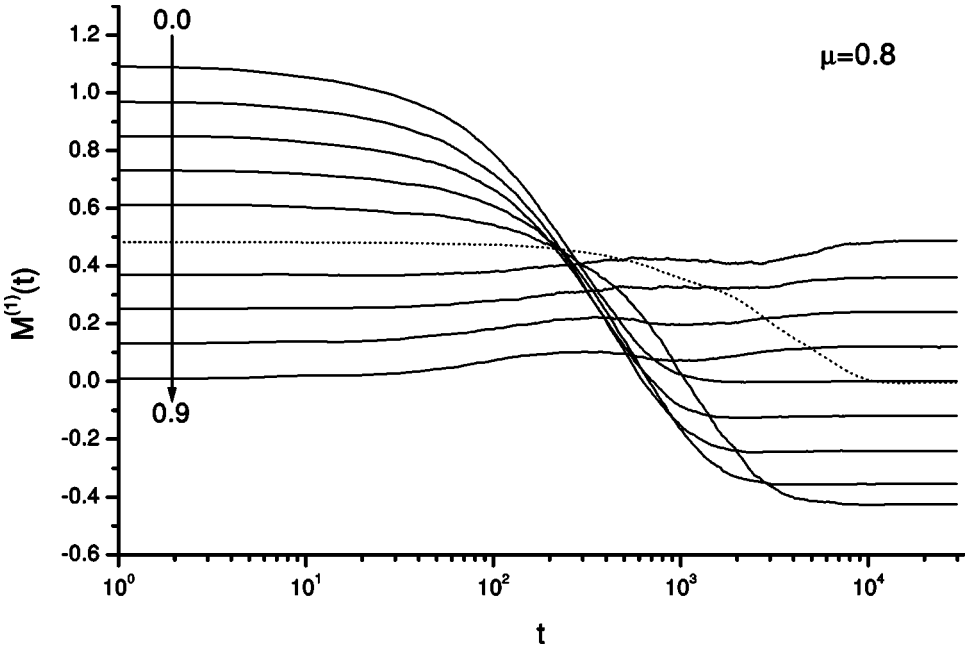

FIG. 2. $M^{(1)}(t)$ as a function of evolution time t for the global disorder parameter $\mu=0.8$ and various local disorder parameters $\kappa=0,0.1,0.2,\ldots,0.9$. The arrow shows in the direction of increasing κ. The dotted line corresponds to $\kappa=0.5$.

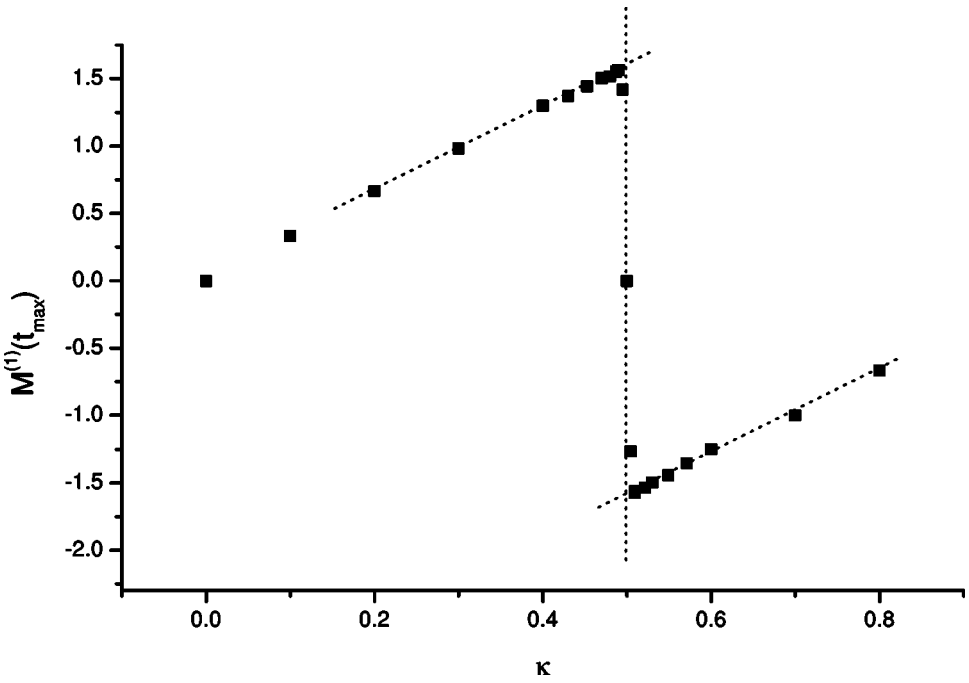

FIG. 3. $M^{(1)}(t_{\max})$ as a function of the local disorder parameter κ ($\mu=0$). The maximum simulation time $t_{\max}$ is sufficiently large, so that $M^{(1)}(t_{\max}) \simeq M^{(1)}(t \to \infty)$. The step at $\kappa=0.5$ indicates a phase transition.

son, that the numerically determined value of $M^{(1)}(t\to\infty)$ shows a small deviation from the expected result $M^{(1)}(\infty)=0$ due to the finite number of numerical realization. This mismatch disappears with increasing number of considered landscapes and initial distributions of genotypes. We conclude, that $M^{(1)}(\infty)$ is not a self-averaging quantity at least close to $\kappa=1/2$. Far from this region, each landscape with fixed κ and μ produces the same value of $M^{(1)}(\infty)$ apart from some very rare events.

We reduce the misfit of adaptation by mapping $[M^{(1)}(t)-M^{(1)}(t_{\max})]/[M^{(1)}(0)-M^{(1)}(t_{\max})] \to M^{(1)}(t)$ with the maximum simulation time $t_{\max}$. Figure 4 shows that the reduced quantity can be described very well by an exponential decay $\exp\{-t/\tau(\mu)\}$. The relaxation time $\tau(\mu)$ shows only a weak dependence on the disorder parameter μ.

The origin of the misfit of adaptation becomes more clear after a discussion of the mean square misfit $M^{(2)}(t)$. The initial value of this quantity is given by $M^{(2)}(0)=-3/4+4\kappa-4\kappa^2$, i.e., it is independent from the global disorder parameter μ. This behavior reflects also a symmetry defined by the construction of the disorder. Configurations related to the local, κ, and global, μ, disorder parameters are equivalent to configurations related to the pair $(1-\kappa,1-\mu)$. Because $M^{(2)}(0)$ is independent from μ, it must be invariant against a change $\kappa\to 1-\kappa$, see also Figs. [5, 6]. Also the final values $M^{(2)}(\infty)$ do not depend on μ. Obviously, one and only one phenotype dominates a given island after a sufficiently long evolution time. This means that the average

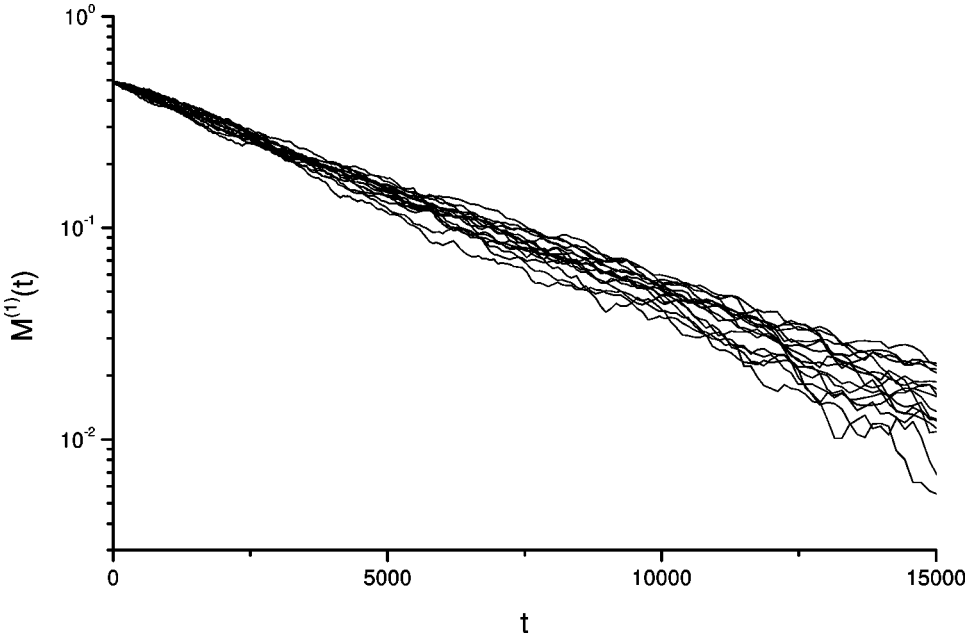

FIG. 4. Half logarithmic plot of the reduced misfit of adaption for $\kappa=0.5$ and various order parameters $\mu=0,0.05,0.1,\ldots,0.95,1.0$. The decay of all these functions shows an exponential behavior.

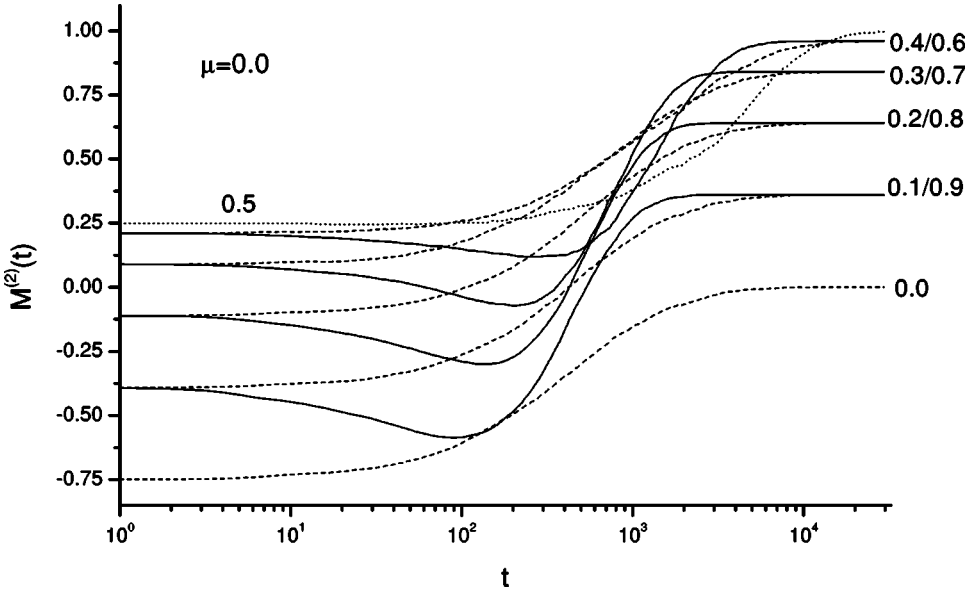

FIG. 5. $M^{(2)}(t)$ as a function of evolution time t for the global disorder parameter $\mu=0$ and various local disorder parameters $\kappa=0,0.1,0.2,\ldots,0.9$. The dashed curves correspond to $\kappa<0.5$, the full curves represent $\kappa>0.5$. The dotted line corresponds to $\kappa=0.5$.

of each property approaches the value $\langle f(\varphi^{\alpha})(\infty)\rangle=\pm 1$. Consequently, we obtain $M^{(2)}(\infty)=1-(1-2\kappa)^2=4\kappa(1-\kappa)$, see Fig. 7. It seems, that these properties φ^{α} of the phenotype become dominant, which are favored by the island landscape: if the majority of territories has a landscape property $S_i^{\alpha}=T$ (or F), then the corresponding phenotype property of all animals becomes $\varphi_i^{\alpha}=T$ (or F) in the long time limit. The only critical situation occurs for $\kappa=1/2$, i.e., for the case when half of the territories have the property $S_i^{\alpha}=T$ and the other half has $S_i^{\alpha}=F$. Here, the future evolution is open and a behavior similar to a phase transition can be expected again.

We analyze now the order parameter $\delta\Theta(t)$ and $\Theta_{\text{overlap}}(t)$ for a better understanding of the biological evolution at a strong disorder, especially for the case $\kappa=1/2$. Both order parameters compare the evolution at two identical islands and they are modifications of similar parameters describing the behavior of spin glasses. These glasses are thermodynamic systems, which have no equilibrium below a critical temperature. In other words, a spin glass shows more than one thermodynamic ground state in opposition to a usual thermodynamic system which has only one ground state. After cooling down of a spin glass, the influence of the random thermodynamic fluctuations and the initial conditions determines the final ground state. But if the system has reached one of these ground states, a change to another ground state is forbidden below the critical temperature and for a macroscopic (infinite large) system. The thermodynamic behavior of a spin glass can be characterized by the Edwards-Anderson order parameter, which compares two replicas, i.e., two identical thermodynamical systems. If both replicas are in the same ground state, the order parameter becomes 1, otherwise it has a smaller value. This situation is comparable with the biological evolution at two identical islands. If the order parameter $\Theta_{\text{overlap}}(t\rightarrow\infty)$ becomes 1, the phenotypes at both island are identical. In other words,

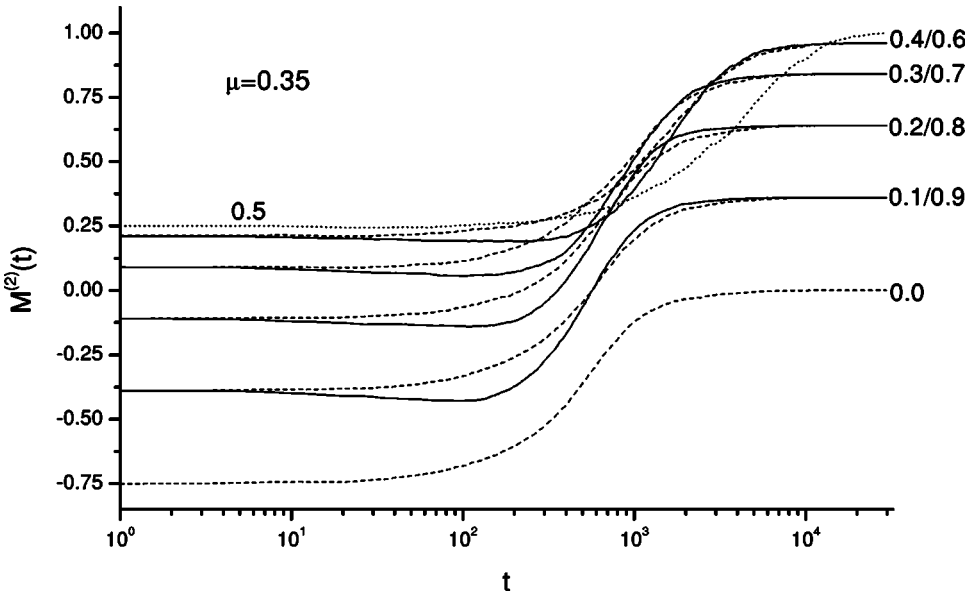

FIG. 6. $M^{(2)}(t)$ as a function of evolution time t for the global disorder parameter $\mu=0.35$ and various local disorder parameters $\kappa=0,0.1,0.2,\ldots,0.9$. The dashed curves correspond to $\kappa<0.5$, the full curves represent $\kappa>0.5$. The dotted line corresponds to $\kappa=0.5$.

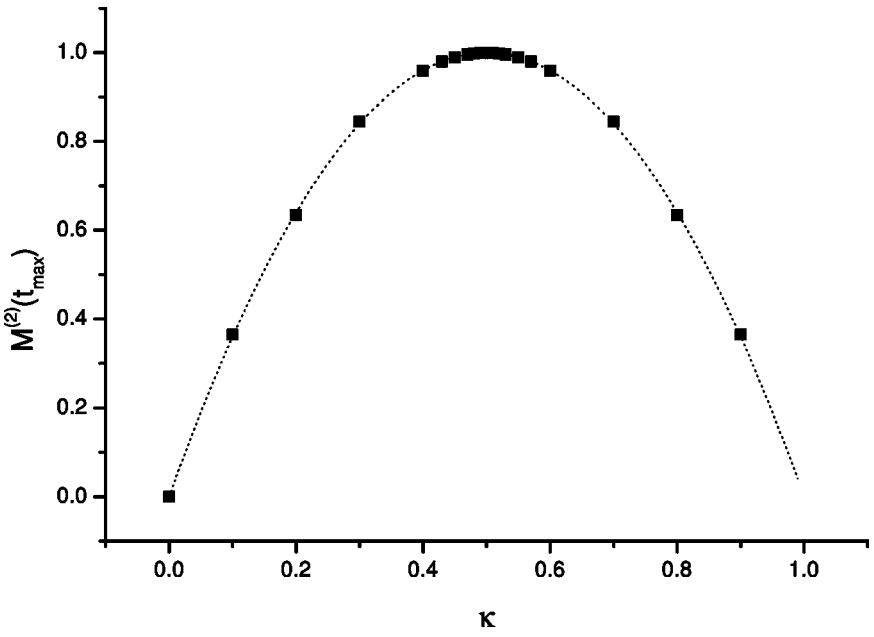

FIG. 7. $M^{(2)}(t_{\max})$ as a function of the local disorder parameter κ ($\mu=0$). The maximum simulation time $t_{\max}$ is sufficiently large, so that $M^{(2)}(t_{\max}) \simeq M^{(2)}(t \to \infty)$.

there is a complete overlap between the populations at both islands. In case of an incomplete overlap $\Theta_{\text{overlap}}(t\to\infty) < 1$, the final populations are different. An analogous behavior shows the order parameter $\delta\Theta(t)$, which vanishes for a complete overlap, whereas a finite value indicates a difference between the phenotypes of the island populations. A similar function, measuring the overlap of a given and stored patterns, has been introduced in the theory of neural networks, see e.g., Ref. [26].

Figure 8 shows the time evolution of $\Theta_{\text{overlap}}(t)$ for $\mu=0$. The order parameter approaches 1 for weak disorder, i.e., for small values as well as for large values of κ. Deviations can be observed only for a small interval close to $\kappa \approx 0.5$ with a maximum for $\kappa=1/2$, i.e. for the strong disorder regime. The existence of an incomplete overlap not only for $\kappa=1/2$ is a finite size effect [25]. Note, that with increasing island size the interval with $\Theta_{\text{overlap}}(t\to\infty)\neq 1$ decreases and it remains only a singularity at $\kappa=1/2$ for infinite large islands.

A similar behavior shows the order parameter $\delta\Theta(t)$ which vanishes for weak disorder in the long time limit $t\to\infty$. A relatively sharp peak $\delta\Theta(t\to\infty)\neq 0$ occurs only for $\kappa\approx 1/2$, see Fig. 9. Hence, a weak disorder is related to a biological identity of the populations at different islands. But we observe a splitting of the biological evolution for $\kappa=1/2$ (and in case of a finite size effect also for a small interval around $\kappa=1/2$). This allelic divergence is a typical feature of the speciation induced by the disorder

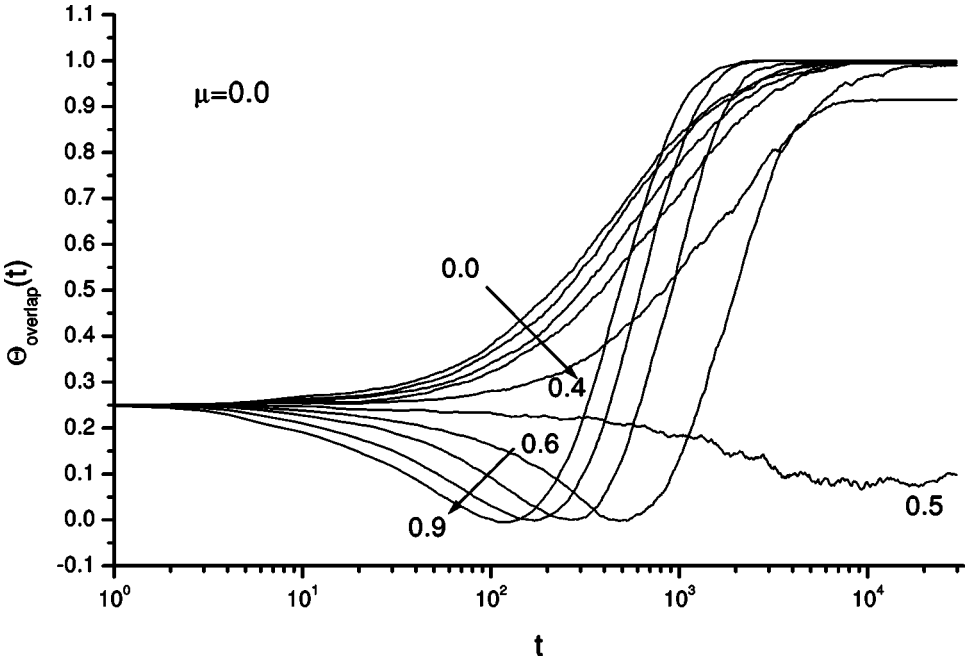

FIG. 8. $\Theta_{\text{overlap}}(t)$ as a function of evolution time t for the global disorder parameter $\mu=0$ and various local disorder parameters $\kappa=0,0.1,0.2,\ldots,0.9$. The arrows show in the direction of increasing κ. A serious deviation of $\Theta_{\text{overlap}}(\infty)\simeq\Theta_{\text{overlap}}(t_{\max})$ from the value 1 occurs only for $\kappa=0.5$. The smaller deviations for $\kappa=0.4$ and 0.6 seems to be finite size effects.

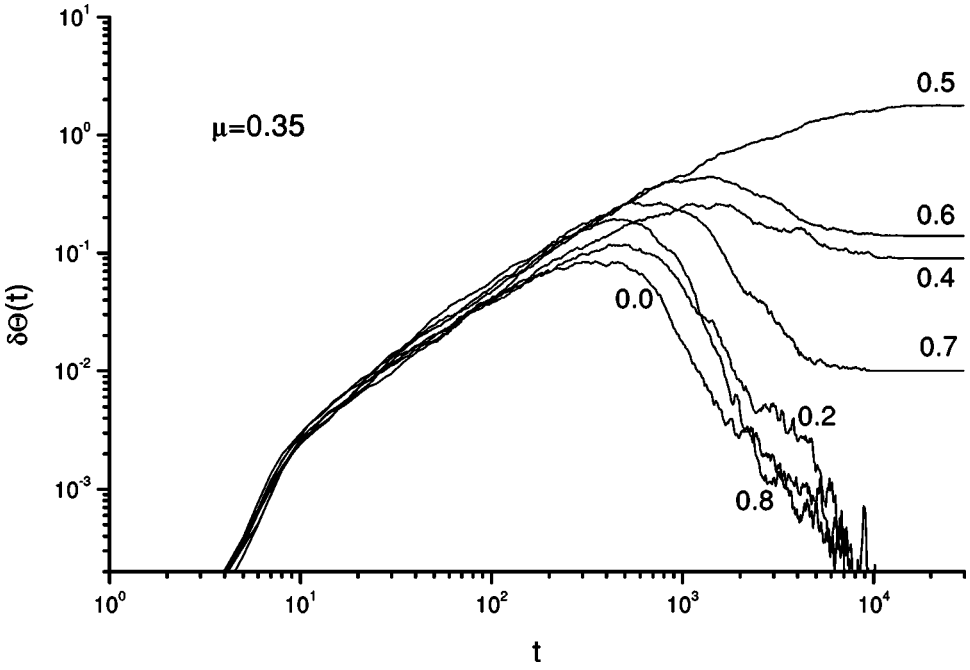

FIG. 9. $\delta\Theta(t)$ as a function of evolution time t for the global disorder parameter $\mu=0.35$ and various local disorder parameters $\kappa=0,0.2,\ldots,0.8$ and 0.5. A finite value of $\delta\Theta(\infty)\simeq\delta\Theta(t_{\max})$ can be obtained only for $\kappa=0.5\pm0.2$. It can be assumed again, that all finite values of $\delta\Theta(t_{\max})$, except the value for $\kappa=0.5$, are finite size effects. The linear behavior between $t=10^1$ and $t=10^3$ indicates a intermediate algebraic law in the time evolution of $\delta\Theta(t)$.

of the landscape. The singularities at $\kappa=1/2$ in both order parameters suggest again a behavior similar to a first-order phase transition.

Finally, we present a phase diagram which reflects the above discussed behavior, see Fig. 10. Only a small strip along the $\kappa=1/2$ line offers a considerable finite value of $\delta\Theta(t\rightarrow\infty)$. The finite width of the strip is related to the above mentioned finite size effect.

The presented numerical Monte Carlo study demonstrates the influence of disordered landscapes on the genetic divergence of species. Obviously, the disorder becomes relevant if the whole system island-population shows undecided configurations, i.e., the future evolution and the final population are determined by small random events. This situation takes place for $\kappa=1/2$. Here, the initial population can reach at least two different global phenotypes. The question, which final population will be realized, is controlled by a random

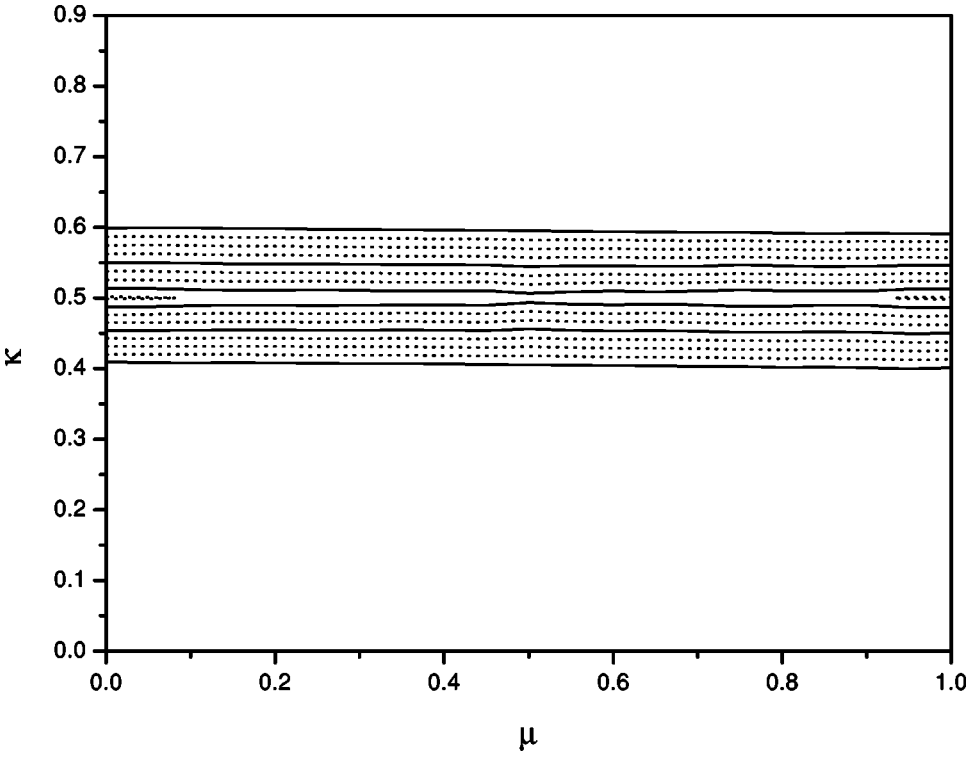

FIG. 10. Phase diagram for the dependence of the final order parameter $\delta\Theta(t_{\max})$ on the disorder parameters κ and μ. The small strip along the $0.4<\kappa<0.6$ represents values $\delta\Theta(t_{\max})>0.25$.

procedure and cannot be defined by a deterministic law.

However, this global analysis generates new questions, which should be analyzed in subsequent studies. Especially, we assume that in the first step the dominance of some possible final phenotypes can be observed in small regions of the island. These regions increase during the biological evolution and at the cost of other regions. Finally, only one of the possible phenotypes dominates the whole island. This behavior is similar to the dynamics of a first-order phase transition. Small domains of a new phase increase in competition with other phases. Finally, only one phase, the so called macrophase, occupies the whole system. Hence, we arrive at the question, whether this aspect of biological evolution can be described by the same well-known theories for thermodynamic systems (spinodal separation, nucleation, and growth) or not.

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