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Spontaneously Broken Neutral Symmetry in an Ecological System

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Spontaneous symmetry breaking plays a fundamental role in many areas of condensed matter and particle physics. A fundamental problem in ecology is the elucidation of the mechanisms responsible for biodiversity and stability. Neutral theory, which makes the simplifying assumption that all individuals (such as trees in a tropical forest)—regardless of the species they belong to—have the same prospect of reproduction, death, etc., yields gross patterns that are in accord with empirical data. We explore the possibility of birth and death rates that depend on the population density of species, treating the dynamics in a species-symmetric manner. We demonstrate that dynamical evolution can lead to a stationary state characterized simultaneously by both biodiversity and spontaneously broken neutral symmetry.

Neutral models have been proposed to capture the statistical structure of tropical forests [1]. Even though the approach is highly debated [2], the neutral hypothesis has led to a general and fundamental framework to study both the statics [3] and the dynamics [4] of ecosystems using general tools borrowed from stochastic processes and nonequilibrium statistical mechanics. The fundamental assumption of neutral theory [1] is that within a trophic level any individual or organism behaves independently of the species it belongs to. In other words, the dynamics of the system is unaffected by interchanging or permuting species labels of individuals. By using this extremely simplifying hypothesis, many empirically measured statistical patterns can be well reproduced [3–5]. Going one step further, a model can be symmetric—but, strictly speaking, nonneutral—a generalization of neutrality, where the dynamics may depend, for instance, on the local or global density of individuals in a community, but no change occurs on the behavior of a population and on its effects on others in the community upon switching two arbitrary species' labels [3]. In this Letter, we address the following issues: (i) Within a generalized neutral framework—allowing for intraspecific density-dependent demographic rates [6]—are species able to coexist in a stable way up to the temporal scale of speciation that eventually averts monodominance and extinction? (ii) Can this generalized neutral symmetry be spontaneously broken so that non-neutral behavior of species can emerge from an underlying symmetric dynamics?

In order to illustrate this, we consider a simple stochastic model, a variant of the (multispecies) voter model [7,8], defined as follows: at every vertex of a regular lattice of linear size L in d dimensions reside a fixed number M of individuals belonging to one of S species. At every time step, an individual is picked at random and killed, and its

place is filled by copying one of its neighbors, selected according to a probabilistic rule to be defined in detail below. For illustration, let us consider a generic system of $S = 4$ species and global dispersal where the neutral symmetry is not broken [see Fig. 1(a)]. The fraction of each species' population fluctuates around the same average, $1/4$, and is statistically indistinguishable from the others. Also, at stationarity, the four probabilities $P_i(n)$ to find the ith species with population n are identical within statistical errors. In this case, the dynamics of the ecosystem is not changed by any permutation of species' labels; however, if each species has its own specific parameters for birth, death, dispersal, etc., the dynamics is no longer symmetric. This explicitly broken symmetry makes the previous system of $S = 4$ species behave in a completely different way [see Fig. 1(b)]. For instance, if a given species and the remaining ones are identified by distinct sets of parameters, the population fraction of one species fluctuates around a given average, $2/5$ in this case, whereas the other ones fluctuate around a different average, $1/5$. Even the probabilities P_i's have distinct behaviors: three of them are identical and the fourth is different, as shown in the left inset of Fig. 1(b). Notice that the probability to find a species with n individuals, $P(n)$, irrespective of the species identity, has a two-peak structure in the nonsymmetric case. Unlike the symmetric case, a nonsymmetric model is necessarily characterized by a much larger set of parameters, which make the approach unsuitable for understanding emergent phenomena (such as biodiversity). However, we will show in the present study that it is possible to define a symmetric theory from which the behavior of non-neutral species emerge naturally on appropriate temporal scales. This enables us to describe species-rich ecosystems with a parsimonious set of parameters that allows species to coexist without the overall
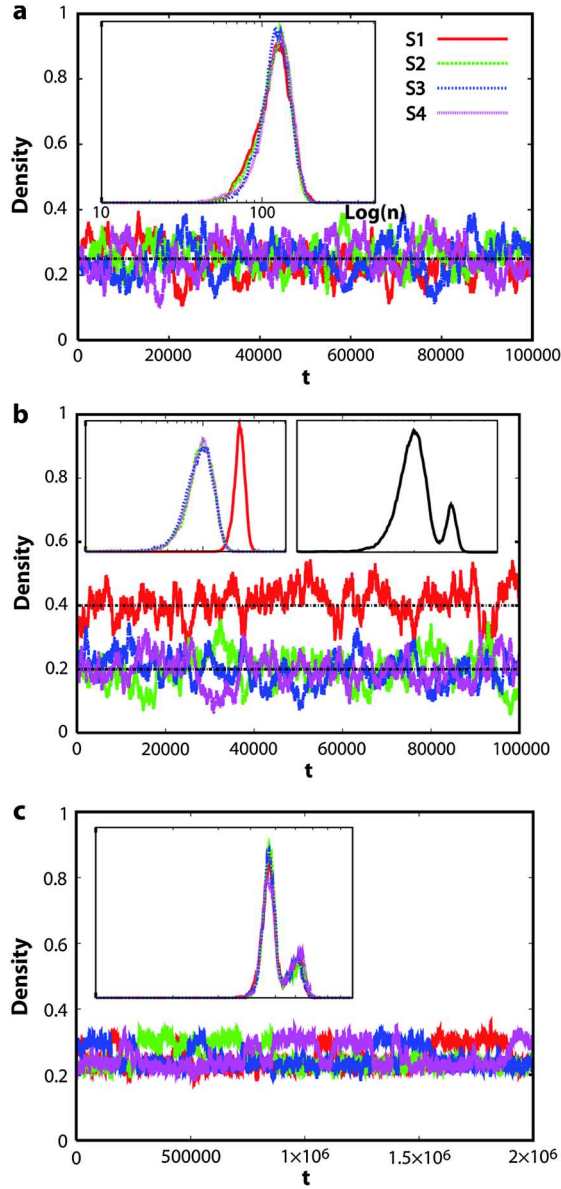
FIG. 1 (color online). Example of the evolution of a neutral ecological model with four species with global dispersal (see the main text) for (a) neutral symmetry. All the species are indistinguishable and fluctuate around the average value $1/4$. In the inset (colors are the same as in the main picture), we show the probabilities $P_i(n)$, and the superposition is perfect within statistical errors. (b) Nonsymmetric dynamics. Species 1 has a different set of birth and death rates with respect to the other three species, and fluctuates around an average density of $2/5$, while the others fluctuate around $1/5$. The probability $P_1(n)$ differs from the others, as shown in the left inset; in the inset on the right, the global probability $P(n)$ is shown. (b) Spontaneously broken neutral symmetry. Here, the system behaves differently, depending on the observation window of its evolution: for small time scales, the system appears nonsymmetric, whereas, for longer time scales, the symmetry is recovered. Unlike case (b), all the species show a bimodal distribution. The probability $P(n)$ in this case superpose virtually exactly on the probabilities $P_i(n)$. The total population is $N = 512$ individuals for cases (a) and (b), and $N = 2048$ individuals for (c).

symmetry characterizing the model. The idea that dynamical symmetry among species can be broken is not new in population biology. For instance, speciation can be interpreted as a form of bifurcation [9]. However, here we introduce a new concept in community ecology borrowed from the statistical mechanics of phase transitions [10], i.e., spontaneously broken neutral symmetry. As shown in Fig. 1(c), when the symmetry of the model is broken spontaneously, species behave as in the nonsymmetric case on time intervals shorter than the characteristic temporal scale, which will be calculated later on. On larger time scales, instead, species' identities can be swapped, and eventually neutral dynamics is recovered. These large temporal scales are also comparable to those at which speciation can occur thereby sustaining biodiversity.

We now turn to the mathematical details of our model. Let $n_x^\alpha \geq 0$ be the population at site x of the αth species, where $\alpha = 1, \ldots, S$, S being the total number of species. Thus $\sum_{\alpha=1}^{S} n_x^\alpha = M$ holds for all x, and the total number of individuals in the whole community is $N = ML^2$. In the following, we shall also use the alternative variable $\rho_x^\alpha = n_x^\alpha/M$, the fraction or density of individuals of the αth species at site x. Suppose that at time t and site x an individual belonging to a certain species γ is picked at random for removal. Then, call β the label of the species of the individual from one of the neighboring sites of x, say y, selected to replace the individual. Note that the dynamics keep the total population per site constant at every time step. Thus, a generic n_z^α evolves according to

$$n_z^\alpha \rightarrow n_z'^\alpha = n_z^\alpha + \delta_{x,z}(\delta^{\beta,\alpha} - \delta^{\gamma,\alpha}). \qquad (1)$$

The effective transition rate for this process is proportional to the population of the γth species at site x, n_x^γ, and to the population of the βth species in the chosen neighboring site, n_y^β. Mathematically, this means that the probability of colonization is $P(n_x^\gamma \rightarrow n_x'^\gamma) = K_{xy}^{\gamma\beta} n_x^\gamma n_y^\beta$. If the proportionality constant, $K_{xy}^{\gamma\beta}$, is chosen independently of the population of species at x and y and independently of the kind of species involved, we get a voterlike model [7,8] with neutral dynamics (the standard voter model has $M = 1$; i.e., only one individual is allowed to live on each site). In this case, regardless of the initial conditions, an infinite-size system would inexorably evolve toward a monodominant state, i.e., an absorbing state, where only one of the S species survives. This is a trivial example of spontaneously broken neutral symmetry. In a more realistic perspective, however, different competing effects influence species interactions favoring or hampering colonization [11], such as, for instance, the Janzen-Connell effect in tropical forests [12], stating that the reproduction rate of a given species decreases with its local population size, or the Allee effect, a positive density dependence in a small density range [13,14]. Altogether, these effects may result in an effective, in general nonlinear and nonmonotonic [11,13,14] dependence on the population sizes, so that

we encode in the proportionality constant $K_{xy}^{\gamma\beta}$, now
dependent, in principle, on the population sizes at both
positions x and y. However, if the dynamics has to be
neutral or symmetric, then $K_{xy}^{\gamma\beta}$ (i) cannot depend explic-
itly on the species' labels γ and β and (ii) can at best
depend only on the densities of species β and γ. Indeed,
because the population of every site is fixed, we obtain the
constraint $\sum_{\alpha\neq\beta,\gamma}\rho_x^\alpha = 1 - (\rho_x^\beta + \rho_x^\gamma)$, which is valid for
every x and plays an important role in the calculations.
In order to keep the discussion simple, we consider the
case $K_{xy}^{\gamma\beta} = K_{xy}(\rho_y^\beta)$, where ρ_y^β represents the density of
species β at y replacing one individual of species γ at x.

To get an insight into the evolution of the ecosystem
described above, following the standard approach for sta-
tistical mechanics systems, we assume infinite dispersal
or, equivalently, a well mixed system. This assumption—
referred to as the mean field limit in the physics
literature—is useful to simplify the treatment, while still
capturing the qualitative behavior of the model in any finite
dimension. In this case, the description is simple since
$\rho_x^\gamma = \rho^\gamma$ for all $\gamma = 1, \ldots, S$, the average birth rate of a
generic species ν is proportional to $\rho^\nu(t)K(\rho^\nu(t))$, and the
time derivative of $\sum_{\mu=1}^S \rho^\mu(t)$ has to vanish. Thus, the
evolution equation for the average density $\rho^\nu(t)$ can be
derived by a standard Kramers-Moyal expansion [15] of
the master equation of our system up to the second order:

$$\dot{\rho}^\nu = N\rho^\nu\left[(1-\rho^\nu)K(\rho^\nu) - \sum_{\mu\neq\nu}\rho^\mu K(\rho^\mu)\right]$$
$$+ \left\{\rho^\nu\left[(1-\rho^\nu)K(\rho^\nu) + \sum_{\mu\neq\nu}\rho^\mu K(\rho^\mu)\right]\right\}^{1/2}\xi, \quad (2)$$

where $\xi = \xi(t)$ is a Gaussian white noise δ-correlated in
time. Focusing on the deterministic evolution, we set
from here on $\xi(t) \equiv 0$. This is equivalent to neglecting
fluctuations—of $O(1/N)$ smaller than the deterministic
term—in the analytical treatment. The simulations are
performed by means of Gillespie's algorithm [16] consid-
ering directly the full master equation of the system.

The neutrality or symmetry of the dynamics is reflected
in the stationary states obtained when $\frac{d}{dt}\rho^\nu(t) = 0$. Note
that the drift term on the right-hand side of Eq. (2) cannot
be derived from a potential function, and therefore the
stationary states cannot be thought of as minima of an
analytical function. However, regardless of the form of
K, there are always $S + 1$ steady states: one neutral-
symmetric case, $\rho^\nu = 1/S$, $\nu = 1, 2, \ldots, S$, and S mono-
dominant situations, where only one of the ρ's is 1 and the
remaining ones are 0. By using local stability analysis, one
can prove that the monodominant states are stable only
when $K(1) > K(0)$, whereas the condition $K'(\frac{1}{S}) < 0$ guar-
antees the stability of the symmetric coexistence. If the
function $K(z)$ is linear, Eq. (2) has no other stationary
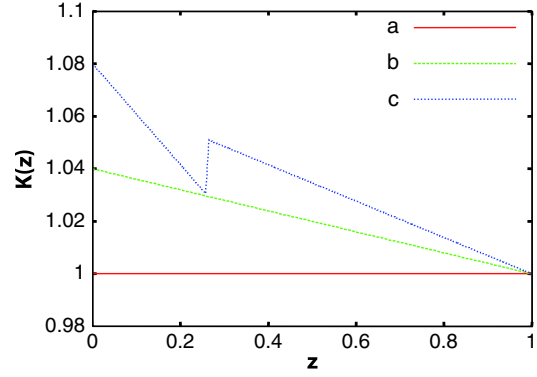stable solutions. However, in a more general nonlinear

FIG. 2 (color online).   (a) (Red solid line) $K(z) \equiv 1$, corre-
sponding to the standard voter model with many species.
(b) (Green dashed line) $K(z) = a(b - z)$: This definition of the
function $K(z)$ makes the symmetric state stable against pertur-
bations, and the monodominant states unstable, provided $a > 0$.
(c) (Blue dotted line) $K(z)$ allowing S stable stationary states
where the neutral symmetry is spontaneously broken by one of
the S species.

case, new stable solutions can show up. It is this nonline-
arity that allows a spontaneous breaking of the neutral
symmetry. The simplest situation of coexistence within a
broken-symmetry scenario is obtained when a given spe-
cies has density $\varphi > 1/S$ and all the other species have
the same density $\zeta = (1 - \varphi)/(S - 1) < 1/S$, which can
occur in S different ways. These densities correspond to
the stationary solutions of Eq. (2) if $K(\varphi) = K(\zeta)$ and are
also stable when $K'(\zeta) < 0$ and $K'(\varphi) < -K'(\zeta)/(S - 1)$.
We now discuss three paradigmatic cases.

(A) $K = $ constant.—This corresponds to the classic
voter model [7,8] [see Fig. 2(a)]. The deterministic evolu-
tion, given by Eq. (2), is trivial because any initial value of
the population of each species remains invariant across
evolution. However, the stochastic dynamics lead to a
monodominant state with only one surviving species, a
trivial case of spontaneously broken neutral symmetry.
For a finite system size, the time $\tau(N)$ to reach one of the
S absorbing states, starting from a random initial condition,
scales as $\tau(N) \sim N^\zeta$, where $\zeta = 2$, as shown in Fig. 3
(purple line) where $\log\tau(N)$ versus $\log N$ is plotted.

(B) $K(z) = a(b - z)$ with a, $b > 0$.—This is a more
interesting case [see Fig. 2(b)], in which the colonization
ability of a given species at some position decreases as its
population—at the same position—increases (negative
density dependence), and becomes zero when it reaches
the maximum value b. Therefore, abundant species are
relatively not as effective in colonizing different regions
compared to those with small populations. The symmetric
state is the stable stationary state of the deterministic
evolution, whereas the S monodominant states are un-
stable. When the full stochastic dynamics is considered,
the symmetric stationary state is typically reached after an
initial transient (depending on initial conditions). Once
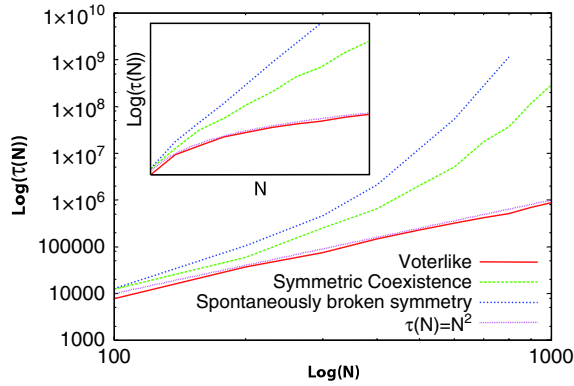the stationary state is reached, it lasts for a typical time

FIG. 3 (color online). Mean time to extinction $\tau(N)$ for the three different definitions of $K(z)$ in Fig. 2, calculated in the mean field approximation and plotted in a double logarithmic scale varying N from $N = 100$ to $N = 1000$. For $K = $ const (red solid line), $\tau(N) \sim N^{\alpha}$ with $\alpha \simeq 2$ (red dotted line) as expected for a voterlike model, while the two cases of $K = b - az$ (green dashed line), where we chose $a = 0.04$ and $b = 1.04$, and $K(z)$ allowing for a spontaneous breaking of the neutral symmetry (blue dotted line) show an exponential behavior $\tau(N) \sim e^{kN}$. In the inset, we show the same plot in a logarithmic-linear scale, to emphasize the exponential growth.

$\tau(N) \sim \exp\{\kappa N\}$, as shown in Fig. 3 (green line), and then the system evolves toward one of the S monodominant states through a gradual extinction of species (observe that this exponential behavior is at variance with what happens in the $K = $ constant case, where $\tau(N) \sim N^{\zeta}$). The constant $\kappa > 0$ depends on the specific choice of $K(z)$. The exponential behavior can be easily understood by focusing on the limiting case of $S = 2$ species, where a description in terms of a potential exists. Introducing a density dependence in the voter model dynamical rule generates an effective potential in the equations of motion for ρ^{ν}, $\nu = 1, 2$, that in the case of linear $K(z)$ discussed above has a minimum for $\rho = 1/2$ [17–20]. Thus, applying the well-known Arrhenius law and noting that the stochastic term is of order $1/N$ smaller than the deterministic part [see Eq. (2)], we recover the exponential behavior for $\tau(N)$. For time scales much smaller than $\tau(N)$ or for all times in the infinite size limit, $N \to \infty$, an active stationary state exists where all species symmetrically coexist. Therefore, negative density dependence strongly enhances species coexistence.

We have calculated the relative species abundance (RSA) in the steady state, i.e., the probability $P(n)$ to find a species with population n. The population $n^{\nu}(t)$ of the νth species is followed for a sufficiently long time, and the frequency, $P^{\nu}(n)\Delta n$, in each interval $(n, n + \Delta n)$ is recorded and the RSA is obtained as $P(n) = \sum_{\nu=1}^{S} P^{\nu}(n)/S$. In the neutral or symmetric case, P^{ν} is independent of ν and the corresponding RSA is equivalent to those in Fig. 1(a). Note that at variance with the $K = $ constant case—where the RSA is not well defined as a consequence of the lack of metastable active states [21]—in the case $K(z) = a(b - z)$

[see Fig. 1(a)], we obtain a mode, as typically found in the RSA of several tropical forests [1,3,4] and other ecosystems [22].

(C) $K(z)$ has the S shape shown in Fig. 2(c) [11,14] in order to satisfy the stability conditions for the broken symmetry scenario given above [this particular shape is for convenience, but it is also valid for $K(z)$ of the generic cubic form $K(z) = az^3 + bz^2 + cz + d$ with suitably chosen coefficients; note that a cubic nonlinearity in density dependence is usually called a *Nagumo* term and is employed to describe populations experiencing the Allee effect [13]]. Here, broken-symmetry coexistence is the stable stationary state of the deterministic evolution. Turning on the stochastic dynamics—after an initial transient—the system reaches one of the S stationary states of the deterministic dynamics with broken symmetry. Again, on a typical time scale $\tau(N) \sim \exp\{\kappa' N\}$, there is gradual extinction of species, till one gets a monodominant situation. Once more, the constant $\kappa' > 0$ depends on the specific choice of $K(z)$. When the system is in a broken-symmetry case, the species whose density fluctuates around the average $\varphi > 1/S$ interchanges with one of the $S - 1$ species fluctuating around the average $\zeta = (1 - \varphi)/(S - 1) < 1/S$ on time scales $\tau_{\text{switch}}(N) \sim \exp\{k_s N\}$. Thus, in a finite system $N < \infty$ and on a time scale $\gg \tau_{\text{switch}}(N)$ the ecosystem looks neutral or symmetric; i.e., the species behave like they were interchangeable. However, for time scales $\ll \tau_{\text{switch}}(N)$ or for all times within an infinite system $N = \infty$, the neutral symmetry is spontaneously broken and the ecosystem looks as if the species were not all interchangeable. We have calculated the probability, $P^{\nu}(n)$, that the νth species has population n on a time scale smaller than $\tau_{\text{switch}}(N)$ so as to exhibit the characteristics of a broken-symmetry state. The results are indistinguishable from those of the case where there is no neutral symmetry [Fig. 1(b)], in which we run the model with two different functions $K(z)$ depending on species label: for $\nu = 1$ we set $K(z) = K_1(z) = a_1 - b_1 z$ with $a_1 = 3$ and $b_1 = 2$, while for $\nu = 2, 3, 4$ we set $K(z) = K_2(z) = a_2 - b_2 z$ with $a_2 = 2.5$ and $b_2 = 1.5$. The RSA for the spontaneous symmetry breaking case calculated for time scales $\gg \tau_{\text{switch}}(N)$ is displayed in the inset of Fig. 1(c), where two peaks appear, showing that one of the species behaves differently from the others. In a more general pattern of spontaneous symmetry breaking, one can have up to S distinct P^{ν}'s producing an S-peak RSA. Multiple peaks would be resolved in the RSA depending on the width and separation of the peaks: this scenario is consistent with some recent studies on several different ecological communities [23], pointing out the possibility of a multimodal distribution of $P(n)$ in real systems.

In conclusion, we have shown that a simple nonequilibrium microscopic model for a general S-species ecological community driven by a density-dependent but otherwise completely neutral or symmetric dynamics—i.e., the

dynamic rules governing the stochastic microscopic process are insensitive to the species' labels—can show a rich and stable heterogeneous biodiversity even at very long times. The striking fact is that species can behave distinctly by spontaneously breaking the neutral symmetry.

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