

Stochastic Dynamics through Hierarchically Embedded Markov Chains

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(Received 27 July 2016; revised manuscript received 15 September 2016; published 1 February 2017)

Studying dynamical phenomena in finite populations often involves Markov processes of significant mathematical and/or computational complexity, which rapidly becomes prohibitive with increasing population size or an increasing number of individual configuration states. Here, we develop a framework that allows us to define a hierarchy of approximations to the stationary distribution of general systems that can be described as discrete Markov processes with time invariant transition probabilities and (possibly) a large number of states. This results in an efficient method for studying social and biological communities in the presence of stochastic effects—such as mutations in evolutionary dynamics and a random exploration of choices in social systems—including situations where the dynamics encompasses the existence of stable polymorphic configurations, thus overcoming the limitations of existing methods. The present formalism is shown to be general in scope, widely applicable, and of relevance to a variety of interdisciplinary problems.

DOI: 10.1103/PhysRevLett.118.058301

Many complex time-dependent processes, from the evolution of cooperation [1] to genetic drift and evolution of ecosystems [2], flocking behavior [3], voter dynamics [4], disease spread [5], diffusion of innovations [6], consensus formation [7], and peer influence [8], have been modeled by stochastic Markov processes. The nonlinear nature of the dynamics often precludes a full analysis, even under continuous approximations, in which case (quasi)stationary distributions of the Markov chain still provide insightful information [9–11]. However, with an increasing number of states, determining these distributions leads to chains of a prohibitive size (see below). As a result, the so-called small mutation approximation (SMA) was introduced, defining a minimal (embedded) Markov chain whose solution estimates the limiting stationary distribution of the population [9].

To reveal the savings obtained under the SMA, let us consider a population of size Z where each individual adopts one of S different strategies (states), $\sigma_1, \sigma_2, \dots, \sigma_S$. The (mean-field) population configurations are characterized by the number of individuals adopting each strategy, with $\{i_1, i_2, \dots, i_S\}$ adding up to $|s| = \binom{Z+S-1}{S-1}$ possible configurations, requiring us to solve a Markov chain of that size. The complexity obtained for large finite S turns the complete analysis unfeasible, even for a small Z . In the absence of mutations, this stochastic process has S absorbing states, the so-called monomorphic [9,12,13] configurations, in which all individuals play the same strategy. Starting at a given monomorphic configuration, the population will remain there until a mutation happens that flips the state of one individual. This new behavior either spreads, leading to another monomorphic configuration, or goes extinct, leading to the starting configuration. If mutations are rare, the time scales of selection (fast) and

mutation (slow) become separated. This allows us to define an embedded Markov chain consisting only of S monomorphic configurations. The transition matrix is given by the fixation probability of a single mutant in a homogeneous population of resident individuals [14]. Thus, under the SMA the (embedded) configuration space has a size S and all transitions are computed through processes involving only two states at a time.

The SMA has been employed with success in different areas of research [10,12,15], its validity requiring the mutation probability μ to be small [16], depending on the population size and the underlying dynamics of the system. Thus, many time-dependent processes of interest cannot be described in the SMA [15,17].

Here, we develop a new framework leading to a hierarchy of approximations to the stationary distribution of a general population Markov process. At each level, our framework involves implementing the following process: (1) Choose an (ideally) small set of configurations of interest (COIs), thus separating the set of all possible configurations $s = \{s_1, s_2, \dots, s_{|s|}\}$ into two disjoint sets— $A = \{a_1, a_2, \dots, a_{|A|}\}$, the COIs, and $B = \{b_1, b_2, \dots, b_{|B|}\}$, the neglected configurations (NCs)—such that $|s| = |A| + |B|$ and $|A| \ll |B|$. The goal is to infer the full dynamics considering only the COIs. The stable fixed points constitute ideal choices to include in the COIs. If they cannot be determined analytically or numerically, one may use a sample of the state space. Both cases are illustrated below. The hierarchical nature of the approximation stems from the location of the COIs in the state space (the simplex): H_n corresponds to when all points in the COIs belong to hyperfaces of dimension at most n . In this case, the approximation is of the order n in the exploration parameter, μ (typically, mutation), restricting the phase space

to those configurations accessible through n cumulative transitions in μ , starting at the vertices. (2) Calculate the transition probabilities among the COIs, $\rho_{a_i \rightarrow a_j}$, from the known one-step transitions between the states s_i and s_j , $T_{s_i s_j}$. The probability of reaching a COI, a_j , starting from one of the NCs, b_n , can be computed through an absorbing Markov chain and reads $P_{b_n a_j} = \sum_{\{b_m\}} T_{b_n b_m} P_{b_m a_j} + T_{b_n a_j}$. Thus, for nonadjacent COIs, $\rho_{a_i a_j} = \sum_{\{b_n\}} T_{a_i b_n} P_{b_n a_j}$, allowing the computation of an unnormalized stationary distribution, p , over the COIs through $p = \rho^T p$. (3) p reflects the relative time spent in each COI, yet it ignores the prevalence in the COIs relative to the NCs. Thus, a renormalization is in order to allocate the right strength to each point in the COIs. We write the distribution over the whole phase space as $P(x) \propto \sum_{i=1}^{|A|} p(a_i) f_i(x) / f_i(a_i)$, where f_i represents locally defined distributions that characterize $P(x)$ around each COI. This way, we associate with each COI the moments of the distribution around it, reflecting its shape around these configurations. This can be achieved by using local information and/or the remaining COIs.

Whenever analytical approaches are not available, the complexity of Hn is dominated by the computation of ρ , involving the inversion of a matrix of size $\approx Z^n/n!$, still much smaller than the original Markov chain for any $n < s - 1$ (see the original chain size above). Below, we provide an efficient alternative for $H1$.

Let us illustrate the method with some examples. We consider a one-dimensional system ($S = 2$) to motivate our first-order approximation ($H1$) and the limitations of the SMA ($H0$). Specifically, consider the evolutionary dynamics of a population of size Z where individuals are either **C** or **D** and they interact with all others via a two-person game that posits a social dilemma of cooperation, with the associated payoff matrix

$$\begin{array}{cc|cc} & & C & D \\ \hline C & & 1 & f \\ D & & 1+g & 0 \end{array},$$

with $\{f, g\} \in [-1, 1]$ [18]. The states s_i are defined by the number i of **C** individuals ($Z - i$ are **D** individuals). Time evolution proceeds via a discrete-time *birth-death* process [19], characterized by the probabilities that, in each time step, the number of individuals adopting strategy **C** changes by ± 1 or 0. We employ a stochastic imitation process inspired in the Fermi distribution of statistical physics [20], allowing the analytical computation of the transition probabilities: $T_i^\pm \equiv T_{(i \rightarrow i \pm 1)} = (1 - \mu) [i(Z - i) / Z(Z - 1)] \{1 / [1 + e^{\mp \beta (f_C(i) - f_D(i))}]\} + \mu \{[(Z - i) / Z] \delta_{(1, \pm 1)} + (i / Z) \delta_{(-1, \pm 1)}\}$, where f_C (f_D) is the average payoff of a **C** (**D**), and the inverse temperature, $\beta \geq 0$, mimics the intensity of natural selection [19], to which we added a mutation probability μ that accounts for the possibility of (unanticipated) random exploration of strategies, an important process in social and cultural evolution [21].

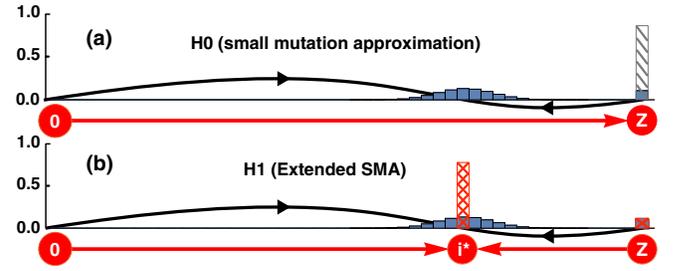


FIG. 1. Stationary distributions associated with a coexistence game ($f = 0.7$, $g = 0.3$). The gradient of selection is represented by the black curves, whereas the exact stationary distribution, computed for $\mu = 10^{-10}$, is depicted by the solid (blue) bars. Two levels of approximation are considered: (i) zeroth order, $H0$ or SMA (the dashed gray bars) and (ii) first order, $H1$ (the crossed red bars). In (a), we compare the exact solution with $H0$ (SMA). In $H0$, the COIs include only the configurations $i = 0$ and $i = Z$, and the most probable transitions between the COIs—indicated by the red arrows—suggest why the full strength is concentrated at $i = Z$. Clearly, $\mu = 10^{-10}$ in a population of size $Z = 50$ is not small enough to bring the exact result into the SMA domain of validity. In (b), the crossed red bars represent the stationary distribution yielded by $H1$, where i^* was added to the COIs. The other parameters are $Z = 50$, $\beta = 10$.

Naturally, different assumptions regarding the time evolution of the population will result in different expressions for the transition probabilities, but the method remains valid for any population Markov chain.

In Fig. 1(a) we show results for a coexistence game, known as the snowdrift game in physics and economics [22], the hawk-dove game in evolutionary biology [23], and the chicken game in other contexts [24]. The full stationary distribution is depicted by the blue histogram bars. There are two monomorphic states, associated with configurations in which all individuals are either **D** ($i = 0$) or **C** ($i = Z$). The existence of a probability attractor at $i^* = 0.7Z = 35$ reflects the coexistence dynamics. $H0$ (SMA) leads to the dashed gray bar in Fig. 1(a). The solid line represents the so-called gradient of selection, given by $G(i) = T_i^+ - T_i^-$. Clearly, SMA leads to a distribution that differs substantially from the full distribution. Indeed, Fig. 2(a) shows that the existence of an interior attractor means that, to get a good agreement between the SMA and the full distribution, μ must be less than 10^{-13} —leading to μ values unreasonably small, both in biological and social contexts. Importantly, as μ increases, the SMA quickly fails to account for the changes introduced in the stationary distribution by nonzero mutations.

Figure 1(b), in turn, shows the result of employing $H1$. The first step consists of adding the attractor i^* to the COIs already including $i = 0$ and $i = Z$. This additional point is trivial to find [19]. The second step implies calculation of the probabilities $\rho_{a_i \rightarrow a_j}$ within the COIs, merely requiring a repartition of the terms already computed in $H0$, bringing no additional overhead to the computation. Indeed, an ordering

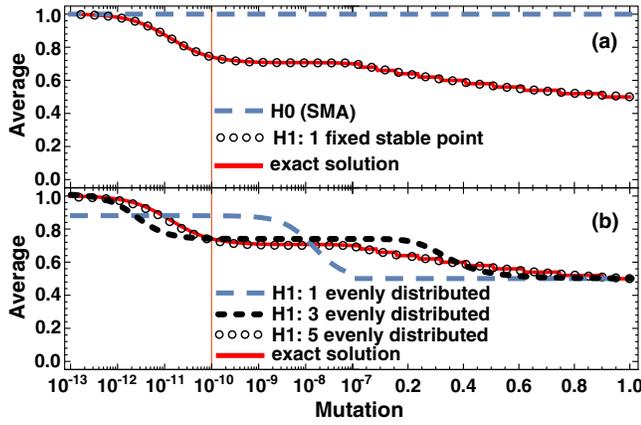


FIG. 2. Same system as Fig. 1. (a) We compare the results of $H0$ and $H1$ with the exact solution. (b) We add one, three, and five homogeneously distributed points to the $H0$ COIs, assuming a flat distribution around each COI. With five equidistant points, we reproduce the full distribution, disregarding any information about the dynamics and its fixed points. The vertical line indicates the value of μ employed in Fig. 1.

can be defined over configurations in A such that transition probabilities from a_i to $a_{(i\pm 1)}$ are written as $\rho_{a_i}^{\pm} \equiv \rho_{a_i \rightarrow a_{(i\pm 1)}}$. These correspond to the probability of having a one-step transition in the direction of $a_{(i\pm 1)}$ and then being absorbed by it, resulting in $\rho_{a_i}^{\pm} = T_{a_i}^{\pm} [1 + \sum_{j=a_i \mp 1}^{a_i \mp 1} \prod_{k=a_i \pm 1}^j (T_k^{\mp} / T_k^{\pm})]^{-1}$ [see the Supplemental Material (SM) [25] for additional details].

With $\rho_{a_i}^{\pm}$, the unnormalized stationary distribution over configurations in A , $p(a_i)$, is calculated through an eigenvector search [26]. The histogram shown with crossed red bars in Fig. 1(b) results from a proper renormalization of $p(a_i)$ via the implementation of step 3 above. Indeed, as a_2 is a probability attractor, it should carry an associated strength that mimics the weight of the full stationary distribution (the solid blue bars) in its vicinity. The natural choice (and the one we propose and adopt throughout) is to derive this renormalization factor from a normal distribution whose expected value is equal to (the value of the process at) a_2 and whose variance can be calculated from the Kramers-Moyal expansion of the associated master equation [19]. We may therefore write the distribution as

$$P(i) \approx \alpha^{-1} [p(a_1)\delta_{i a_1} + Z\sqrt{2\pi\sigma^2}p(a_2)\delta_{i a_2} + p(a_3)\delta_{i a_3}],$$

where $\alpha = p(a_1) + Z\sqrt{2\pi\sigma^2}p(a_2) + p(a_3)$, and σ^2 can be derived from the transition probabilities T_x^+ and T_x^- around a_2/Z as $\sigma^2 = F/|J|$, with $J = d(T_x^+ - T_x^-)/dx|_{x=a_2}$ and $F = (T_{a_2}^+ + T_{a_2}^-)/(2Z)$. In the SM [25] we prove these results and discuss the validity and accuracy of these estimates.

Whenever the game at stake is not one of coexistence but, instead, one of coordination [22,27]—thus characterized by the occurrence of a probability repeller instead of an

attractor—our approach remains unchanged, as detailed in the SM [25].

The choice of the COIs (and hierarchy order n) dictates the complexity and accuracy of the whole procedure, as the problem is reduced from solving a chain of size $\sim Z^{s-1}$ to one of size $\sim Z^n$, $n < s$. Any choice of COIs optimizing the trade-off between complexity and accuracy will depend on the specifics of each model, such as the characteristic mutation rate, number, and position of fixed points and their basins of attraction. In general, choosing as COIs the stable fixed points of the gradient of selection provides the most natural choice to minimize the size of the embedded chain that leads to an accurate approximation. These fixed points are often easy to find by resorting to numerical methods whose complexity scales linearly with $|s| \sim Z^n$ [28].

Nonetheless, our framework can still be applied whenever the fixed points are unknown. In Fig. 2(b) we provide results analogous to Fig. 2(a) by defining the COIs in the simplest possible way: a homogeneous grid including one, three, or five intermediate configurations. Clearly, depending on the problem, other methods (such as importance sampling) may be employed to improve the choice of COIs.

In terms of accuracy, $H0$ (SMA) leads to the smallest COI set, accurate for $\mu \rightarrow 0$. At $H1$, one enlarges the set A , including in the COIs points located along the edges of the simplex. A comparison of Figs. 2(a) and 2(b) shows that including the fixed points in the COIs minimizes its size for a given order. Whenever an increase in the order leads to a mismatch between the results, we identify the region of validity of the previous orders. This mismatch occurs whenever a stable fixed point is present at the newly included dimension and exploration rates allow the system to reach them. In turn, this means that, if there are no internal fixed points above a given order n , this order will suffice to describe the system for any exploration rates. Indeed, order Hn will be exact to the extent that the probability of reaching dimension $m > n$ from n ($\propto \mu^{(m-n)}$) is much lower than the probability of going back (model dependent). As we increase μ , retaining accuracy will require increasing the hierarchy level.

It is worth pointing out at this stage that, already at $H1$, one is able to study explicitly the role of mutations, whose occurrence is ubiquitous in, e.g., (noisy) social systems [29]. Indeed, whereas in the SMA ($H0$) mutation is a tool to enforce that the embedded Markov chain is irreducible, in our case nothing prevents mutations from occurring *at par* with the selection process.

Consider now a population in which Z individuals may adopt (be in) one of three possible strategies (states) (σ_k , $k = 1, 2, 3$). This higher dimension problem may call for higher order approximations, as we discuss next. Each configuration $s_1 = (i_1, i_2)$ is one in which i_1 (i_2) individuals have the strategy σ_1 (σ_2) (and $Z - i_1 - i_2$ have the strategy σ_3). Both G and the stationary distribution can be represented using the two-dimensional simplex portrayed in Fig. 3. We consider the evolutionary dynamics of a three-strategy game

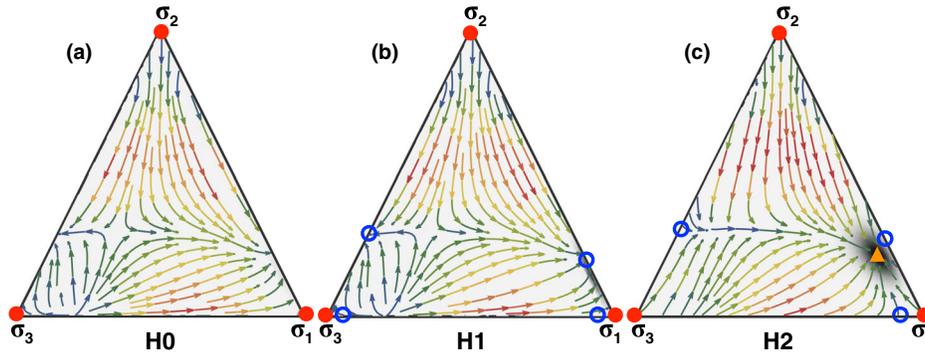


FIG. 3. COIs at different levels of the hierarchical approximation. The arrows represent the most likely direction of evolution of the system (the gradient of selection, G , with warm colors representing larger magnitudes), whereas the background gray shading represents the stationary distribution (darker areas correspond to states with higher probability). As mutation increases, the population explores configurations deviating gradually from the vertices. For the dynamics and parameters specified below, this trend starts (a) at $\mu = 10^{-4}$, exploration of the phase space extending mostly along the edges (b) up to $\mu = 10^{-2}$, to finally explore the interior of the simplex for higher values of μ [$\mu = 10^{-1}$ in (c)]. The probabilities of updates from strategies σ_i to σ_j are given by $T_{(\sigma_i \rightarrow \sigma_j)} = [Z/(Z - 1)]x_i x_j (1 - \mu)(1 + e^{\Delta f_{\sigma_i \sigma_j}})^{-1} + x_i(\mu/d)$, with $\Delta f_{\sigma_i \sigma_j} = \beta_{ijx}(x_1 - x_1^*) + \beta_{ijy}(x_2 - x_2^*)$, with x_i being the frequency of strategy σ_j and d the number of accessible strategies, given the restriction of the phase space considered. The parameters are $Z = 50$, $\beta_{12x} = 2$, $\beta_{12y} = \beta_{13x} = 10$, $\beta_{23y} = -10$, $\beta_{13y} = \beta_{23x} = 0$, $x_1^* = 2/10$, and $x_2^* = 3/10$.

(see the caption to Fig. 3), characterized by an interior saddle point, while exhibiting both coexistence and coordination dynamics along the edges of the simplex, a problem reminiscent of the evolutionary dynamics of multiple myeloma cancer cells [30,31]. Under $H0$ (SMA), the COIs include the three monomorphic configurations [vertices of the triangles and the red solid circles in Fig. 3(a)], confining the evolutionary trajectories to the edges of the simplex. Under $H1$, the COIs now include additional configurations along the edges, as illustrated by the blue

open circles in Fig. 3(b). Importantly, the criteria adopted in choosing these COIs follow straightforwardly from the one-dimensional cases already discussed, given the constraints that apply to the trajectories at this level of approximation.

At level $H2$, we add to the COIs one configuration in the interior of the simplex (in which three strategies are present), identified by the (interior) solid orange triangle in Fig. 3(c). The results obtained are shown in Fig. 4, where we compare the exact solution (the black open circles) with the results provided by successive orders of approximation, for a wide range of mutation values. As expected, $H0$ (SMA) is unable to provide an overall accurate description of the stationary distribution. As μ increases, the stable fixed points move away from the vertices, first along the edges, a feature which is nicely captured at the level of $H1$, and subsequently to the interior of the simplex, requiring one to move to $H2$.

Notably, both $H1$ and $H2$ provide accurate results for the average distribution. This, for a large μ , is an artifact of averaging, as the variance of the distribution will be different. Indeed, $H1$ imposes a dynamics along the edges, whereas $H2$ allows exploration of the interior of the simplex.

In summary, as is well known in many areas of science, a judicious choice of COIs proves instrumental in minimizing the workload necessary to reach a good description of a system. In this Letter we show how this concept applies to nonlinear population dynamics where individuals may be equipped with complex physical, biological, or social repertoires. In dealing with population Markov chains, we establish an approximation order associated with the dimensionality of the simplex points to be included as COIs, an approach that allows the explicit inclusion of mutations in the dynamics, leading to, among other features, an explicit

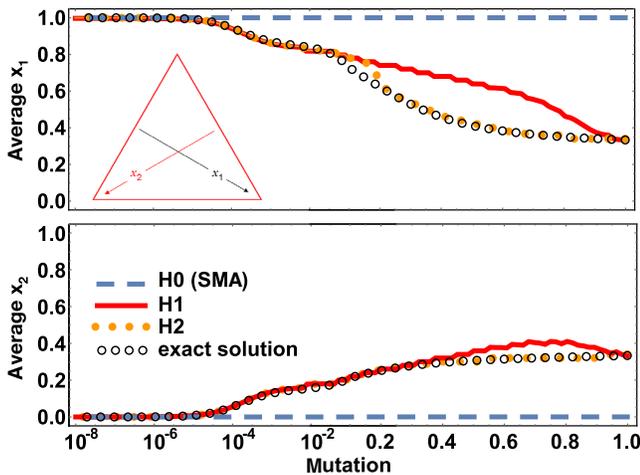


FIG. 4. We plot the average of the stationary distributions as a function of mutation probability for the system depicted in Fig. 3, and at different levels of the hierarchical approximation. At the $H0$ level (SMA), accurate average values are obtained whenever $\mu < 10^{-5}$. As mutation increases, the polymorphic configurations attract higher probabilities, requiring the inclusion of COIs along the edges of the simplex ($H1$) and in its interior ($H2$)—see the text for details.

dependence of the weight and location of the fixed points on μ . Although reminiscent of the approach of Freidlin and Wentzell [32], these features of our framework make it different and especially well suited to treat not so large deviations, mostly when mutations induce deviations with time scales comparable to those of the dynamical process, having a direct impact on G , as well as on higher moments. By dramatically reducing the complexity of the multidimensional Markov processes we aim to describe, the present framework allows one to retain analytical and/or numerical tractability, being general in scope, and thus of a potential applicability in a wide variety of problems that transcend pure physics applications.

This research was supported by FCT-Portugal through Grants No. SFRH/BD/86465/2012, No. SFRH/BD/94736/2013, No. PTDC/EEI-SII/5081/2014, No. PTDC/MAT/STA/3358/2014, No. UID/BIA/04050/2013, and No. UID/CEC/50021/2013. We also thank three anonymous referees for their insightful comments and suggestions.

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