

Stochastic game dynamics under demographic fluctuations

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Frequency-dependent selection and demographic fluctuations play important roles in evolutionary and ecological processes. Under frequency-dependent selection, the average fitness of the population may increase or decrease based on interactions between individuals within the population. This should be reflected in fluctuations of the population size even in constant environments. Here, we propose a stochastic model that naturally combines these two evolutionary ingredients by assuming frequency-dependent competition between different types in an individual-based model. In contrast to previous game theoretic models, the carrying capacity of the population, and thus the population size, is determined by pairwise competition of individuals mediated by evolutionary games and demographic stochasticity. In the limit of infinite population size, the averaged stochastic dynamics is captured by deterministic competitive Lotka–Volterra equations. In small populations, demographic stochasticity may instead lead to the extinction of the entire population. Because the population size is driven by fitness in evolutionary games, a population of cooperators is less prone to go extinct than a population of defectors, whereas in the usual systems of fixed size the population would thrive regardless of its average payoff.

evolutionary games | stochastic dynamics | changing population size

All natural populations are composed of a finite number of individuals. These individuals can reproduce, interact, die, or migrate, which leads to changes in the population size over time. In many theoretical models, it is convenient and possible to neglect the effect of demographic fluctuations by assuming infinite populations when population sizes are sufficiently large (1) or by assuming constant population size as in the Moran or Wright–Fisher process (2). However, such simplifications may be invalid when considering additional ecological processes including oscillations in population size of predator and prey systems (3–5), periodic fluctuations and outbreaks of infectious diseases in humans (6), or chaotic dynamics under multispecies interactions (7). The Lotka–Volterra equations provide a deterministic description of the abundances of species as continuous densities but they are not designed to include the impact of random drift. Theoretical models coupling changing population size and stochastic dynamics arising from individual based models have become more popular only recently (8–12).

The Lotka–Volterra equations naturally take frequency-dependent selection into consideration. Under frequency-dependent selection, the fitness of a given type (or species) depends on the composition of the entire population (or community) (13). Different kinds of frequency dependence can lead to different dynamical patterns. Most prominently, negative frequency-dependent selection can result in a stable coexistence of different types (14–18). One elegant way to describe such frequency dependence is through evolutionary game dynamics (13, 19). Evolutionary game theory has extensively developed the theory of stochastic dynamics in the past decade (2). However, most progress has been accomplished for constant, finite population sizes, which is mathematically convenient but does not always reflect biologically appropriate scenarios. Game theoretic models that take changing population sizes into account mostly focus on deterministic dynamics (20)—similar to traditional

ecological models. Here we introduce a simple and elegant model of stochastic evolutionary game dynamics that explicitly allows for changing population size through a natural interpretation of payoffs in terms of competition between individuals.

Traditional game theoretic models assume that individuals obtain payoffs from interactions with other members in the population, which are translated into fitness. Individuals with higher fitness are assumed to have more offspring and hence reproduction is frequency-dependent. Conversely, death rates are assumed to be constant or normalized so as to keep the population size constant. In contrast, here we focus on a microscopic description of the dynamics in terms of reaction kinetics equations. Assuming constant birth rates and frequency-dependent death rates allows one to interpret payoffs directly and naturally in terms of reaction rates, where selection acts on survival rather than reproduction. The present setup lends itself to a straightforward derivation of the deterministic dynamics in the limit of large population sizes in the form of competitive Lotka–Volterra equations but equally allows one to model the stochastic dynamics in finite populations of variable sizes, which may even lead to the extinction of the population.

Model and Results

Stochastic Dynamics. Most models for stochastic evolutionary game dynamics consider a fixed population size, such that every birth is balanced by the death of another individual (2). Simply decoupling birth and death events in such models leads to random fluctuations in the population size and thus eventually to stochastic extinction (21). Instead, here we propose a framework based on the microscopic processes of birth, death, and competition. For simplicity, we focus on two types of individuals, X and Y , but note that the generalization to arbitrary numbers is straightforward. Every individual reproduces

Significance

This contribution breaks with the tradition to restrict stochastic evolutionary game dynamics to populations of constant size and introduces a theoretical framework to investigate relevant and natural changes arising in populations that vary in size according to fitness—a feature common to many real biological systems. Explicitly including ecological variation can result in significant effects on the stochastic evolutionary trajectories while providing a transparent link to the established, deterministic Lotka–Volterra systems.

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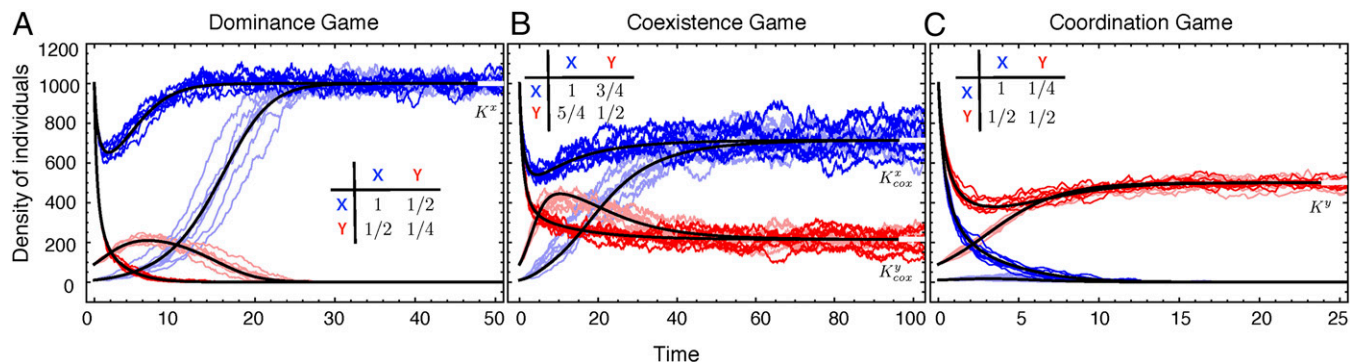


Fig. 1. The stochastic dynamics fluctuates around the deterministic predictions in large populations (black lines). Each panel refers to one of the three characteristic classes of interactions as determined by the ranking of payoffs. Evolutionary trajectories for X (blue) and Y (red) types are shown for initially small ($x_0 = 10$, $y_0 = 90$, pale colors) and large ($x_0 = 1,000$, $y_0 = 1,000$ saturated colors) populations. Regardless of the game both types tend to increase for low initial population sizes, whereas both types decrease in densities at large initial sizes. In all cases the deterministic predictions agrees well with the stochastic dynamics in that the stochastic trajectories fluctuate around the deterministic average [parameters $M = 2,000$, $\lambda_{x \rightarrow x} = \lambda_{y \rightarrow y} = 0.6$, and $\lambda_{x \rightarrow 0} = \lambda_{y \rightarrow 0} = 0.1$, which translates into $K^x = 1,000$ and $K^y = 250$ (A) and $K^y = 500$ (B and C)].

heterogeneous populations, where the total equilibrium density is K_{cox} and the densities of type X and type Y individuals at this equilibrium are K_{cox}^x and K_{cox}^y , respectively.

If $r_x < 0$ or $r_y < 0$, the corresponding type will invariably decline and disappear. Including competition only speeds up their demise. For example, this applies to the predators in the famous, oscillating Lotka–Volterra predator–prey dynamics. Because negative interaction rates are not meaningful, at least three different types are required to observe oscillations in a competitive system (25, 33).

Equilibria of the Deterministic System. The deterministic mean-field dynamics of our model serves as a valuable reference for the underlying stochastic evolutionary process. Birth and death rates, Eqs. 1 and 2, may differ for different types, but for the sake of simplicity and to highlight effects arising from evolutionary games we discuss interactions of two types, X and Y , with $r_x = r_y = r$. The evolutionary fate of each type depends on a combination of the strength of intratype competition (a and d) and intertype competition (b and c). In general, we can classify three different scenarios based on the payoff matrix. First, for $a > c$ and $b > d$, type X individuals invariably achieve higher payoffs (i.e., longer life expectancy) than Y types and hence type X dominates type Y . Similarly, type Y dominates type X whenever $a < c$ and $b < d$ (Fig. 1A). The prisoner’s dilemma is the most prominent example of a dominance game (19). Second, for $a > c$ and $b < d$ both types are at a disadvantage compared with the other type when rare. This reflects coordination games such as the stag-hunt game (34). Third, for $a < c$ and $b > d$ both types have an advantage when rare but are at a disadvantage when abundant. Thus, an interior equilibrium exists where the two types coexist (Fig. 1B). The hawk–dove or snowdrift games are examples of such scenarios (35). Note that even though the classification of the dynamics for two types is based on their payoffs in the same way as in the classical replicator dynamics (and the stability remains the same; see *SI Appendix, section 3*), the position of the rest points in our deterministic system are naturally different. For example, in the replicator dynamics a coexistence game as in Fig. 1B exhibits a stable rest point at $x^* = (d - b) / (a - b - c + d) = 1/2$. In contrast, according to Eq. 6, the frequency of X at equilibrium is $x^* = 10/13$. An intuitive reason for this increase in the relative abundance of X is that the total number of individuals at the mixed equilibrium is lower than the carrying capacity for a population of only X types.

Therefore, the only possible equilibria are either homogenous X or Y populations or a stable heterogeneous mixture of the two. According to Eq. 5 with $r_x = r_y = r$, the densities of individuals at the three

equilibria are $K^x = aMr$ and $K^y = dMr$ as well as $K_{\text{cox}} = K_{\text{cox}}^x + K_{\text{cox}}^y$ with $K_{\text{cox}}^x = [ac(b - d) / (bc - ad)]Mr$ and $K_{\text{cox}}^y = [bd(c - a) / (bc - ad)]Mr$, which can be rewritten as $K_{\text{cox}} = K^x + [(c - a)(b - a) / (bc - ad)]K^y$. Note that in the coexistence equilibrium the density of individuals of each type is always lower than its carrying capacity in isolation, that is, $K_{\text{cox}}^x < K^x$ and $K_{\text{cox}}^y < K^y$. However, the total number of individuals in mixed equilibria can either exceed or fall short of homogenous carrying capacities: If $b > a$, $K_{\text{cox}} > K^x$; if $b < a$, $K_{\text{cox}} < K^x$; if $c > d$, $K_{\text{cox}} > K^y$; and if $c < d$, $K_{\text{cox}} < K^y$. More specifically, in coexistence games $b > a$ and $c > d$ holds such that the total number of individuals is highest in the mixed equilibrium, $K_{\text{cox}} > K^x, K^y$. Conversely, the reverse ranking is impossible: It would require $b < a$ and $c < d$, but this refers to coordination games where the mixed state is unstable and the population approaches either one of the homogenous configurations. Of course, in the corresponding stochastic realizations the population size at equilibrium is not fixed and instead fluctuates around the carrying capacity (Fig. 1). For identical birth and death rates, the evolutionary game controls the relative growth or decline of the two types through competition, but regardless of the game the numbers of both types can increase or decrease if the current state of the population is far from equilibrium. All possible rankings of equilibrium densities are summarized in *SI Appendix, Table 1*.

Stochastic Simulations. In contrast to the deterministic equilibrium predictions, the only evolutionary outcome in stochastic simulations is the eventual extinction of the entire population—all other states are transient. Fortunately, the expected times to extinction rapidly grow with the density of individuals in equilibrium, controlled by M (Fig. 2). Hence, predictions based on deterministic dynamics, Eq. 5, keep providing valuable insights for the stochastic dynamics, Eqs. 1–3, especially for large population sizes. Substantial quantitative and even qualitative differences arise, as illustrated in Fig. 1 for three characteristic types of interactions. The stochastic dynamics is implemented through the Gillespie algorithm (36). For the relatively large carrying capacity $K^x = 1,000$ in Fig. 1, each realization of the stochastic dynamics fluctuates around the deterministic trajectory. Fluctuations represent an integral part of natural populations and hence stochastic evolutionary models provide a more natural way to study evolutionary trajectories, especially to capture the interplay between ecological and evolutionary processes (10, 11, 37, 38).

In small populations, competition for survival is weak and the dynamics is mainly determined by the intrinsic growth rate, r (i.e., individual birth and death events). Consequently, small r results in higher stochasticity but also tends to decrease the number of

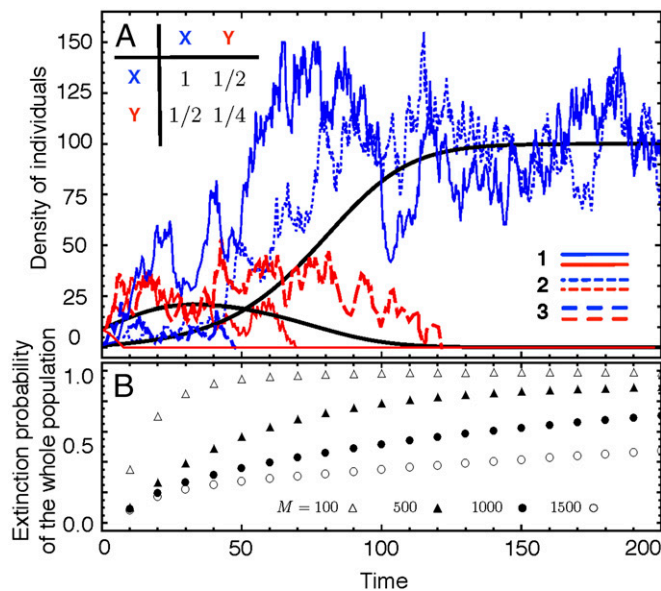


Fig. 2. Stochastic dynamics of a dominance game in small populations. (A) Three realizations of the stochastic dynamics in a small population with two types, X (blue) and Y (red) for $M=1,000$. Stochastic trajectories deviate significantly from the deterministic dynamics (solid black lines). For example, in the third realization both types go extinct, first the dominant type X followed by type Y a little later. (B) Cumulative probability for the extinction of the entire population over time, averaged over 10^5 realizations for different M (parameters $\lambda_{x-xx} = \lambda_{y-yy} = 0.6$, $\lambda_{x-0} = \lambda_{y-0} = 0.5$, $x_0 = 1$, and $y_0 = 9$; this yields $K^x = 100$ and $K^y = 25$ in the upper panel).

individuals at equilibria, which further amplifies the effect. As the population grows and approaches its carrying capacity, competition becomes increasingly important and competition rates (payoff matrix, Eq. 4) also control the size of fluctuations. Strong competition (small payoffs) reduces stochasticity but also tends to decrease the population size, which may offset the reduction in terms of fluctuations.

Furthermore, if the numbers of the two types in the stochastic process are far away from the deterministic equilibrium, even the averaged stochastic dynamics can be very different from deterministic predictions. For example, in the deterministic case a dominant mutant always succeeds in invading and eventually fixating in the population. In contrast, in the stochastic case a single mutant often fails to invade and fixate even if it is dominant. Note that fixation of a single mutant becomes even less likely in larger populations—despite the fact that fluctuations decrease and the deterministic dynamics is recovered in the limit of large populations.

Extinction. In ecological models the risk of extinction of a population owing to demographic stochasticity has recently received considerable attention (see, e.g., refs. 10, 37, and 38). Evolutionary game theory models demonstrated that stochastic fluctuations are important determinants for the fixation and extinction of individual traits even under constant population sizes (2) but remained unable to address the more dramatic possibility of the extinction of the entire population.

In a dominance game, the deterministic dynamics predicts that the dominant type invariably takes over the entire population and approaches its carrying capacity (Fig. 2A). However, in stochastic models the two types X and Y may go extinct sequentially owing to fluctuations. Especially when starting from small populations, the extinction probability is not negligible (Fig. 2B). Note that the (cumulative) extinction probability converges to 1 as time goes on regardless of the population size.

Only for larger populations extinction typically takes much longer and the extinction probability increases slowly with time. The smaller the population size—owing to small carrying capacities, fluctuations, or initial configurations—the higher the risk of extinction.

In Fig. 2A, the dominant X type has a higher carrying capacity than the Y type and, hence, provided that the X mutant successfully invades and fixates, the population ends up more persistent. In the third realization in Fig. 2A, the X type is lost first and the entire population vanishes soon after. An essential factor for the persistence of small populations are the birth and death rates, Eqs. 1 and 2, or, more specifically, their difference: For large intrinsic growth rates, small populations are more likely to escape extinction because the population can more readily recover and return to its carrying capacity.

In coexistence games, the two types X and Y typically coexist and their densities fluctuate around their respective (deterministic) densities of individuals in equilibrium, K_{cox}^x and K_{cox}^y (Fig. 1B). Whenever stochastic fluctuations drive one type to extinction, the carrying capacity of the remaining type changes to K^x or K^y , respectively. Thus, the density of individuals in the entire population changes and is driven by the interplay of demographic fluctuations arising from intrinsic growth rates and the strength of competition (Fig. 3).

In this case the extinction of the entire population is a two-step process: First one type goes extinct—typically the type with the lower density in equilibrium—and then the population fluctuates around the homogenous carrying capacity of the remaining type such that the extinction dynamics is now governed by the stochastic equivalent for the logistic growth of a single type, which is well understood (10, 24, 37).

Snowdrift Game. As a concrete example of a coexistence game, we consider the stochastic dynamics of the snowdrift game (35) [or, equivalently, the hawk–dove game (19)]. In the snowdrift game two individuals need to finish a task, which provides benefits β to both. The costs of the task, γ , are shared equally if both cooperate (i.e., participate in completing the task). If only one participates, the cooperator has to bear the entire costs but the defector still receives the benefits. Finally, if both defect and refuse to participate, the payoffs for both individuals are close to zero. Hence, the payoffs of cooperators, X, and defectors, Y, are $a = \beta - \gamma/2$, $b = \beta - \gamma$, $c = \beta$, and $d = \epsilon$, where $\beta - \gamma \gg \epsilon > 0$ and $\beta > \gamma > 0$. Note that in the limit $\epsilon \rightarrow 0$ the death rate of Y types due to competition diverges and they are no longer able to persist in isolation. To maximize its own gain, each player should do the opposite of what its opponent does. A population of cooperators fluctuates around $K^x = (\beta - \gamma/2)r_x M$. A defecting mutant has a selective advantage and hence is likely to successfully invade and the population typically starts fluctuating around a new equilibrium, where the total density of individuals is lower—from $b < a$ follows $K_{\text{cox}} < K^x$ (SI Appendix, Table 1). For sufficiently small ϵ , the conditions for the ranking $K^x > K_{\text{cox}}^x > K^y > K_{\text{cox}}^y$ are satisfied. Thus, even though defecting mutants are favored, their abundances in the coexistence equilibrium are even lower than when in isolation. Consequently, stochastic fluctuations are more likely to eliminate defectors and reestablish cooperation at the original carrying capacity, K^x . For example, for $M = 2,000$, $r_x = r_y = 0.5$, $\beta = 1.5$, $\gamma = 1$, and $\epsilon = 0.05$, the density of cooperators $K_{\text{cox}}^x \approx 964$ in the mixed equilibrium is much larger than that of defectors $K_{\text{cox}}^y \approx 18$ and hence the odds of persistence are clearly in favor of cooperators.

Discussion

Demographic fluctuations based on ecological interactions capture important aspects and represent crucial determinants of evolutionary trajectories, especially in smaller populations. Here, we introduce a simple stochastic framework built on the microscopic events of birth, death and competition. This framework admits a

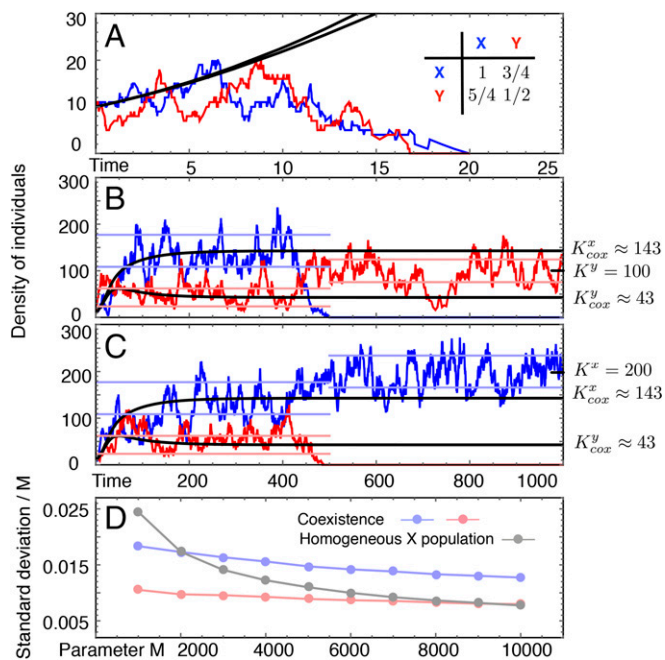


Fig. 3. Stochastic dynamics and large demographic fluctuations in a coexistence game. (A–C) ($M=2,000$): According to the deterministic dynamics (solid black lines) the two types X (blue) and Y (red) coexist at their respective equilibrium, K_{coex}^X and K_{coex}^Y . The three stochastic realizations, however, reveal a different picture: In the first case (A), both types go extinct early on. In the second case (B), type X goes extinct first, which benefits type Y and results in a higher carrying capacity than the density of type Y individuals in the coexistence equilibrium, $K^Y > K_{\text{coex}}^Y$. In the third case (C), type Y goes extinct first and the new carrying capacity K^X even exceeds the whole population size in the coexistence equilibrium, $K^X > K_{\text{coex}}^X$. Pale lines represent the simulated SD (averaged over 500 independent simulations with $\geq 10^6$ data points each). (D) The SD scaled by M in the coexistence equilibrium decreases with M , but differently for the two types (parameters $\lambda_{X \rightarrow XX} = \lambda_{Y \rightarrow YY} = 0.6$, $\lambda_{X \rightarrow 0} = \lambda_{Y \rightarrow 0} = 0.5$, $x_0 = 10$, and $y_0 = 10$, the same payoff matrix for all panels).

simple yet elegant way to implement evolutionary games through payoff based competition rates, which results in selection on survival instead of the more traditional fecundity based selection (30). This yields a stochastic model for evolutionary games in populations of changing and fluctuating finite size. In the limit of infinite population sizes, this framework recovers the deterministic dynamics of the competitive Lotka–Volterra equations and hence allows to pinpoint and emphasize differences that arise due to stochastic effects. The deterministic limit of the stochastic framework also highlights that, in contrast to the classical r - K -selection theory, the ecological carrying capacity of a population is an emergent quantity (27, 28), which depends on the population configuration and is determined by the underlying processes of birth, death, and

competition. In particular, mutations that alter the rates of any of these processes trigger a change in the (deterministic) carrying capacities of the mutant population, provided that it succeeds to take over, or of the mixed population in the case of coexistence. Our model implies that adaptation is not a simple process of accumulating beneficial mutations with higher carrying capacities in isolation, but instead an adaptive process that can favor invasion and fixation of mutations that are disadvantageous for the entire population including evolutionary suicide (39).

Dominant mutations are bound to take over with certainty under deterministic dynamics. However, in the stochastic scenario, the chances for a single beneficial mutant to successfully invade and take over remain small, even for a dominant strategy. At first it might be surprising that the chances of success decrease for increasing population sizes—despite the fact that the limit of large populations recovers the deterministic dynamics. However, of course, in this limit the mutant density converges to zero, which resolves the apparent contradiction. Similar results can be found in classical models of finite populations with constant fitness values (40). Here we investigated stochastic dynamics in well-mixed populations but a natural extension is to consider spatial dimensions, which may increase stochastic effects due to small local subpopulations (41–43).

Here, we have focused on the paradigmatic case of one population and two types, but it is straightforward to extend the framework to include multiple types. In a population with three types, oscillations can persist in the stochastic process, whereas the deterministic limit suggests cycles spiraling toward an internal equilibrium (44, 45) (SI Appendix, Fig. 1). Moreover, our framework extends to group interactions, such as public goods games, by allowing for competitive interactions that involve more than two individuals. However, in either case, the number of microscopic interactions tends to increase rapidly and hence hampers a more general yet compact and intuitive presentation.

The stochastic framework also emphasizes that in the long run populations invariably go extinct, which means that the deterministic equilibria merely indicate fleeting states—albeit the expected time to extinction can be exceedingly long, especially for larger populations. Therefore, it remains reasonable to consider the deterministic predictions as a baseline superimposed by fluctuations of stochastic realizations. At the same time it is crucial, especially in smaller populations, to consider the persistence of individual traits or the viability of the entire population. For example, in the snowdrift game an invasion attempt by defectors triggers ecological feedback, which alters the carrying capacities in favor of cooperators, such that stochastic fluctuations help to eliminate defectors and reestablish homogenous cooperation.

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