Metastability and anomalous fixation in evolutionary games on scale-free networks

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We study the influence of complex spatial structure on the metastability and fixation properties of a set of evolutionary processes characterized by frequency-dependent selection. In the framework of evolutionary game theory, we analyze the dynamics of snowdrift games (characterized by a metastable coexistence state) on scale-free networks. Using an effective diffusion theory we demonstrate how the complex structure of the network affects the system’s metastable state and leads to anomalous fixation. In particular, we analytically and numerically show that the probability and mean time of fixation are characterized by stretched exponential behaviors with exponents depending nontrivially on the network’s degree distribution. Our approach is also shown to be applicable to models, like coordination games, characterized by the absence of metastability prior to fixation.

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The dynamics of systems where successful traits spread at the expense of others is naturally modeled in the framework of evolutionary game theory (EGT)\textsuperscript{[1]}. EGT involves frequency-dependent selection, where selection depends on the species instantaneous concentration. Traditionally EGT is studied in terms of differential equations, and is an approach transcending almost every aspect of evolutionary biology\textsuperscript{[1,2]}. While the EGT classic setting was originally proposed to describe the evolution of infinitely large and spatially homogeneous populations, it is known that evolutionary dynamics is affected by demographic noise and by the population’s spatial arrangement (structure)\textsuperscript{[3–5]}. Evolutionary dynamics is often characterized by the central notion of fixation, first introduced in population genetics\textsuperscript{[6]}, that refers to the possibility that a “mutant type” takes over the entire population. In contrast to spatially-homogeneous (well-mixed) populations, accounting for the population’s spatial arrangement can give rise to various scenarios:\textit{e.g.}, in games modeling social dilemmas, the local interactions on regular lattices may enhance or inhibit the resistance of “cooperators” against the invasion by “defectors”\textsuperscript{[3]}. In this context, evolutionary dynamics on networks\textsuperscript{\textsuperscript{[3]}} provides a general and unifying framework to describe the dynamics of both well-mixed and spatially-structured populations\textsuperscript{[5]}. In spite of their importance, fixation of evolutionary processes on networks have been mostly studied in idealized situations,\textit{e.g.}, for two-state systems under a constant weak selective bias\textsuperscript{[6,11]}. In these works, it has been shown that the update rules and the network structure effectively renormalize the population size and affect the fixation properties. While these results are of great interest, they do not account for frequency-dependent selection, which is an important evolutionary mechanism\textsuperscript{[1,8]}, and may lead to a long-lived metastable (or coexistence) state prior to fixation\textsuperscript{[12,13]}. As a firm understanding of metastability on complex networks is still lacking, we here study metastability and fixation on a class of scale-free networks in the EGT framework. Our findings will also be directly relevant to the dynamics of epidemic outbreaks\textsuperscript{[14]} and population genetics\textsuperscript{[15]}.

Here, we study “snowdrift games” (SGs, see below)\textsuperscript{[1] 13} that are the paradigmatic EGT models exhibiting metastability (see\textsuperscript{[16]} for their experimental relevance). In the case of well-mixed populations (complete graphs), the fixation properties of SGs typically exhibit an exponential dependence on the population size, see\textit{e.g.}\textsuperscript{[13]}. Using an individual-based approach, we show that the spatial structure of scale-free networks yields anomalous fixation and metastability characterized by a stretched exponential dependence on the population size, in stark contrast with their non-spatial counterparts. We also show that such a dependence characterizes fixation in models like coordination games which do not possess a long-lived metastable state prior to fixation\textsuperscript{[1]}.

The model. We consider a network comprising\textit{N} nodes, each of which is either occupied by an individual of type C (cooperator) or by a D-individual (defector). The occupancy of the node $i$ is encoded by the random variable $\eta_i$, with $\eta_i = 1$ if the node $i$ is occupied by a C and $\eta_i = 0$ otherwise. The state of the system is thus described by $\{\eta\} = \{\eta_i\}^N$ and the density of cooperators present in the system is $\rho = \sum_{i=1}^{N} \eta_i/N$. The network is specified by its adjacency matrix $A = [A_{ij}]$, whose elements are 1 if the nodes $ij$ are connected and 0 otherwise. The network is also characterized by its degree distribution $n_k = N_k/N$, where $N_k$ is the number of nodes of degree $k$. EGT is traditionally concerned with large and homogeneous populations (i.e., $N \rightarrow \infty$ and $A_{ij} = 1, \forall ij$) whose mean field dynamics is described by the celebrated replicator equation\textsuperscript{[1,2]}: $(d/dt)\rho(t) = \rho(t)(1 - \rho(t))[(\Pi^C(\rho) - \Pi^D(\rho))]$, where $\Pi^C/D(\rho)$ are the cooperator/defector average payoffs derived from the game’s payoff matrix. For a generic two-strategy cooper-
ation dilemma, the payoff of C against another C is denoted a and that of D playing against D is d. When C and D play against each other, the former gets payoff b and the latter gets c [1]. Here, we are particularly interested in SGs, for which ρ = (d − b)/(a − b + c + d) and unstable absorbing states ρ = 0 (all-D) and ρ = 1 (all-C). When the population size is finite (N < ∞), the role of fluctuations is important and ρ∗ becomes a metastable state whose decay time on complete graphs (Aij = 1, Vij) grows exponentially with N [12].

In a spatial setting, the interactions are among nearest-neighbor individuals and the species payoffs are defined locally: C and D players at node i interacting with a neighbor at site j respectively receive payoffs Π^C_{ij} = an_j + b(1 − η_j) and Π^D_{ij} = cn_j + d(1 − η_j). In the spirit of the Moran model (in the weak selection limit) [2, 3, 6], each species local reproductive potential, or fitness, is given by the difference of Π^C/D relative to the population mean payoff Π̄_{ij}(t). Here, we make the mean-field-like choice Π̄_{ij}(t) = ρ(t)Π^C_{ij} + (1 − ρ(t))Π^D_{ij} to include what arguably is the simplest mechanism ensuring the formation of metastability. It is customary to introduce a selection strength s in the definition of the fitness to unravel the interplay between random fluctuations and selection [2, 5, 6]. Here, the fitnesses of C/D at node i interacting with a neighbor at site j are

\[f^C_{ij} = 1 + s[Π^C_{ij} − Π̄_{ij}] \quad \text{and} \quad f^D_{ij} = 1 + s[Π^D_{ij} − Π̄_{ij}]. \quad (1)\]

These expressions comprise a baseline contribution (set to 1) and a selection term proportional to the relative payoffs. Moreover, we consider a system evolving according to the so-called “link dynamics” (LD) [3, 10]: a link is randomly selected at each time step and if it connects a CD pair, one of the neighbors is randomly selected for reproduction with a rate proportional to its fitness while the other is replaced by the offspring [17]. Fixation under LD is unaffected by the network topology when the selection is frequency-independent [10]. However, in the more generic case of frequency-dependent selection considered here, metastability and fixation properties are drastically altered by the network’s structure, as shown below.

The evolutionary dynamics of the system will be analyzed in terms of the (subgraph) density ρ_k = Σ_i^k η_i/N_k of cooperators C on nodes of degree k (the prime means that the sum is restricted to nodes of degree k). Quantities necessary for our analysis are the mth—moment of the degree distribution, \(\mu_m = \sum_k k^m n_k = \sum_i k^m N / N\), where \(k\) denotes the degree of node \(i\), and the degree-weighted density of cooperators \(ω = Σ_i^k (k/\mu_1)n_k ρ_k\).

Effective diffusion theory. To implement the evolutionary dynamics, we introduce Ψ_{ij} = η_i(1 − η_j)f^C_{ij} and Ψ_{ji} = (1 − η_i)η_j f^D_{ij}, where η_i(1 − η_j) is non-zero only when the nodes \(ij\) are occupied by a CD pair. In the LD, the probability to select the neighbor \(j\) of node \(i\) for an update is \(A_{ij}/(N\mu_1)\) and the transition \(η_i \rightarrow 1 − η_i\) hence occurs with probability \(Σ_i A_{ij}/N\mu_1 [Ψ_{ij} + Ψ_{ji}]\ [14]\). The subgraph density \(ρ_k\) changes by \(±\delta ρ_k = ±1/N_k\) according to a birth-death process [18] defined by the transition rates \(T^+(ρ_k) = Σ_j A_{ij}Ψ_{ij}/(N\mu_1)\) and \(T^−(ρ_k) = Σ_j A_{ij}Ψ_{ji}/(N\mu_1)\), respectively. For our analytical treatment, we focused on degree-heterogeneous networks with degree-uncorrelated nodes, as in Molloy-Reed networks (MRN) [14], yielding \(A_{ij} = k_i k_j/(N\mu_1)\). Our numerical simulations were performed using the “redirection algorithm” that generates degree-correlated scale-free networks [20]. Yet, it has been shown that the dynamics of the latter is close to that on MRN [10]. With \(Σ_j N_j = n_k ρ_k\), the transition rates become

\[T^+(ρ_k) = \frac{n_k}{(N\mu_1)} \left[1 + s(b − d)(1 − ρ)\right] k(1 − ρ)ω \quad \text{and} \quad T^−(ρ_k) = \frac{n_k}{(N\mu_1)} \left[1 − s(a − c)ρ\right] kρ(1 − ω). \quad (2)\]

We notice that \(T^±_k\) are nonzero provided that the mean degree \(μ_1\) does not diverge with \(N \rightarrow ∞\). In the limit of weak selection intensity (s ≪ 1) [13], one can use the diffusion theory to treat the birth-death process defined by [2]. This yields a multivariate backward Fokker-Planck equation (FPE) whose generator reads

\[G(\{ρ_k\}) = \sum_k \left[\frac{(T^+ − T^-)}{n_k} \frac{∂}{∂ρ_k} + \frac{(T^+ + T^-)}{2Nn_k} \frac{∂^2}{∂ρ_k^2}\right], \quad (3)\]

with time increments \(δt = N^{-1} [6, 18]\). Moreover, when the selection intensity is weak (s ≪ 1), a timescale separation allows to greatly simplify the
Indeed, when $t \ll s^{-1}$ the selection pressure is negligible and the quantity $\rho$ is conserved. In fact, using Eq. (2) at mean field level gives
\[
(d/dt)\tilde{\rho} = s(a - b - c + d)\omega(1 - \tilde{\omega})(\tilde{\rho} - \rho_s)
\] (where the upper bar denotes the ensemble average). This indicates that $\tilde{\rho}$ relaxes to its metastable value $\rho_s$, on a timescale $t \sim s^{-1}$, see Fig. 11. At mean field level, Eqs. (2) also yields
\[
(d/dt)\tilde{\rho}_k = (T_k^0(\tilde{\rho}_k) - T_k^0(\tilde{\rho})) / n_k = (k(\mu_1)) \times \frac{\omega - \tilde{\rho}_k + s(b - d)\omega(1 - \tilde{\rho}_k)(1 - \tilde{\rho}) + (a - c)(1 - \tilde{\rho})\tilde{\rho}_k}{\tilde{\rho}_k - \rho_s}.
\] This indicates that after a timescale of order $\mathcal{O}(1)$, $\tilde{\rho}_k \approx \tilde{\omega}$, and also $\tilde{\rho} \approx \tilde{\omega}$ since $\tilde{\rho} = \sum_k \tilde{\rho}_k n_k$. With $\tilde{\rho}_k \approx \tilde{\omega} \approx \tilde{\rho}$, the rate equation for $\tilde{\rho}_k$ becomes
\[
(d/dt)\tilde{\rho}_k \simeq -(k(\mu_1)) \omega(1 - \tilde{\rho}_k)\tilde{\rho}_k / \tilde{\rho}_k - 1.
\] Hence, while after a time of order $\mathcal{O}(1)$, $\tilde{\rho}_k \approx \tilde{\omega} \approx \tilde{\rho}$, all these quantities approach $\rho_s$ on a longer timescale $t \sim s^{-1}$. This behavior is corroborated by numerical simulations, see Fig. 11. Because fixation occurs on much longer time-scales than $s^{-1}$ (see below), we henceforth use the approximation that on average $\rho_k \approx \rho_s \approx \omega$. Using Eq. (3), changing variables $\rho_k \rightarrow \omega$ and using the definition of $\omega$ that yields $\partial_{\rho_k} \rightarrow (kn_k / \mu_1) \partial_{\omega}$, we arrive at the effective single-coordinate FPE generator
\[
\mathcal{G}_{\text{eff}}(\omega) = \omega(1 - \omega) / N_{\text{eff}} \left[-\sigma(\omega - \rho_s) \frac{\partial}{\partial \omega} + \frac{1}{2} \frac{\partial^2}{\partial \omega^2} \right].
\] Here $\sigma \equiv 2(b - d) / \rho_s$, and the effective population size and selection intensity are given by $N_{\text{eff}} = N(\mu_1)^3 / \mu_3$ and $s_{\text{eff}} = s / \mu_2(\mu_1)^2$. For scale-free networks with degree distribution $k_\xi \propto k^{-\nu}$ and finite average degree (i.e. $\gamma > 2$) [22], the maximum degree is $k_{\text{max}} \sim N^{(1/\nu - 1)}$ [23]. This can be used to calculate the moments $\mu_m$ [10] and obtain the scaling of $N_{\text{eff}} / s_{\text{eff}}$:
\[
\sigma = \frac{2(b - d)}{\rho_s} sN \frac{\mu_1 \mu_2}{\mu_3} \sim \frac{sN}{N \ln N}, \quad \mu_4 = 4
\]
\[
\frac{sN^2}{\ln N}, \quad \mu_4 = 4
\]
\[
\frac{sN^2}{\ln N}, \quad \mu_3 = 3 < \nu < 4
\]
\[
\frac{sN^2}{\ln N}, \quad \mu_2 = 2 < \nu < 3.
\] We have checked analytically and by numerical simulations that our theory is valid when $s_{\text{eff}}^2 \ll N_{\text{eff}}^{-1}$. Hence, for $2 < \nu < 4$ it is applicable over a broader range of values of $s$ than on complete graphs; e.g. $s^2 \ll N^{-1/\nu - 1}$ when $2 < \nu < 3$ ($s^2 \ll N^{-1}$ on complete graphs [13]).

Fixation properties. Evolutionary dynamics is characterized by the fixation probability $\phi^C(\omega)$ that a system with initial degree-weighted density $\omega$ is taken over by cooperators. In the framework of the effective diffusion theory and using [44] the fixation probability obeys $\mathcal{G}_{\text{eff}}(\omega)\phi^C(\omega) = 0$ with the boundary conditions $\phi^C(0) = 1 - \phi^C(1) = 0$. The solution of this equation is
\[
\phi^C(\omega) = \frac{\text{erfi}[\rho_s / \sqrt{\sigma}] - \text{erfi}[(\rho_s - \omega) / \sqrt{\sigma}]}{\text{erfi}[\rho_s / \sqrt{\sigma}] + \text{erfi}[(1 - \rho_s) / \sqrt{\sigma}]},
\] where $\text{erfi}(z) \equiv \frac{2}{\sqrt{\pi}} \int_0^z e^{u^2} du$. Let us consider the (biologically relevant) case of a small initial density of cooperators such that $\omega \ll 1$, weak selection [3, 4], and a large population such that $\rho^2 \sigma \gg 1$ and metastability is guaranteed. Using the asymptote $\text{erfi}(z) \sim e^{z^2}$ for $x \gg 1$ in Eq. (10), we distinguish two cases: (i) when $\rho_s < 1/2$, $\ln(1 - \phi^C) \sim -(1 - 2\rho_s) / \sigma$; (ii) when $\rho_s > 1/2$ and $\omega > 2\rho_s - 1$, $\ln(1 - \phi^C) \sim -(2\rho_s - 1) / \sigma$, while $\ln(1 - \phi^C) \sim -\omega(2\rho_s - \omega) / \sigma$ if $\rho_s > 1/2$ and $\omega < 2\rho_s - 1$. The stretched-exponential dependence of $\phi^C$ on $N$ is shown in Fig. 2 where (as in Figs. 3 and 4) data have been rescaled and collapsed with $\sigma \propto sN_{\mu_1 / \mu_3}$ along a single line. Since $\ln(1 - \phi^C) \sim -N$ on complete graphs [13], our results demonstrate how the complex structure of the network drastically affects the fixation probability.

Another quantity of great interest is the (unconditional) mean fixation time (MFT) $\tau(\omega)$ – the mean time necessary to reach an absorbing boundary. Here, using Eq. (11) the MFT is obtained by solving $\mathcal{G}_{\text{eff}}(\omega)\tau^C(\omega) = 0$ with the boundary conditions $\tau(0) = \tau(1) = 0$. Using standard methods [6, 18], we obtain
\[
\tau(\omega) = 2N_{\text{eff}} \left[\left(1 - \phi^C(\omega)\right) \int_0^\omega dy e^{-\Theta(y)} \int_0^y dz e^{\Theta(z)} + \phi^C(\omega) \int_\omega^1 dy e^{-\Theta(y)} \int_0^1 dz e^{-\Theta(z)}\right]; \quad \Theta(z) \equiv \sigma(z - 2\rho_s).
\] For $\rho^2_s \sigma \gg 1$ the inner integrals can be computed by expanding $\Theta(z)$ around its extremal values $z = 0$ for $z \in [0, \rho_s]$ and $z = 1$ for $z \in [\rho_s, 1]$, while the outer integral is computed via the saddle-point approximation around $\omega = \rho_s$. To leading order, one thus obtains
\[
\tau(\omega) \sim (1 - \phi^C(\omega)) e^{\sigma \rho^2_s / 2} \text{ when } \omega > \rho_s \text{ and } \tau(\omega) \sim \phi^C(\omega) e^{\sigma(1 - \rho_s)^2 / 2} \text{ otherwise}.
\] When $\sigma \gg 1$ and $\rho_s < 1/2$ (as in Fig. 5), we
find that $\tau(\omega)$ grows with $N$ as a stretched exponential:

$$\ln \tau(\omega) \simeq \sigma \rho^2_*.$$  \hspace{1cm} (7)

When the initial number of cooperators is not too low, the long-lived metastable state is entered prior to fixation and the MFT (7) is independent of the initial condition \[12, 13\]. Eq. (7), confirmed by Fig. 3, implies that for scale-free networks with $2 < \nu < 4$ fixation occurs much more rapidly than on complete graphs, a phenomenon called “hyperfixation” in population genetics \[15\].

For completeness, we have also studied the class of “coordination games” (CGs) characterized (at mean-field level) by an unstable interior (coexistence) fixed point and two stable absorbing states \[1\]. The fixation probability of CGs evolving under the LD on scale-free graphs has been found to have the same stretched-exponential dependence on $N$ as in the SGs \[13\], see Fig. 4.

Discussion & conclusion. We have studied metastability and fixation of evolutionary processes on scale-free networks in the realm of EGT. Within an individual-based approach, we have focused on “snowdrift games” with frequency-dependent selection evolving according to the LD \[10\] and characterized by long-lived (metastable) coexistence. Exploiting a timescale separation occurring at weak selection intensity, we have devised an effective (single-coordinate) diffusion theory and, from the corresponding backward Fokker-Planck equation, calculated the probability and mean time of fixation. These quantities exhibit an stretched-exponential dependence on the population size, in stark contrast with their non-spatial counterparts. Here, important consequences of the stretched-exponential behaviors are a drastic reduction of the mean fixation time and the possible enhancement of the fixation probability of a few mutants with respect to a non-spatial setting. These anomalous fixation properties reflect the influence of the network’s complex structure on the evolutionary dynamics.

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