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LETTER TO THE EDITOR

Effects of mobility on ordering dynamics

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Abstract. Models of ordering dynamics allow to understand natural systems in which an initially disordered population homogenizes some traits via local interactions. The simplest of these models, with wide applications ranging from evolutionary to social dynamics, are the Voter and Moran processes, usually defined in terms of static or randomly mixed individuals that interact with a neighbor to copy or modify a discrete trait. Here we study the effects of diffusion in Voter/Moran processes by proposing a generalization of ordering dynamics in a metapopulation framework, in which individuals are endowed with mobility and diffuse through a spatial structure represented as a graph of patches upon which interactions take place. We show that diffusion dramatically affects the time to reach the homogeneous state, independently of the underlying network's topology, while the final consensus emerges through different local/global mechanisms, depending on the mobility strength. Our results highlight the crucial role played by mobility in ordering processes and set up a general framework that allows to study its effect on a large class of models, with implications in the understanding of evolutionary and social phenomena.

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Initially heterogeneous individuals in isolated groups often end up homogenizing their characteristic traits: People tend to align their opinions (1), segregated populations gradually lose their genetic diversity (2), different social groups spontaneously develop their own seemingly arbitrary traits, such as distinctive styles of dress or jargons (3), etc. In all these cases a global order emerges through local interactions in a self-organized way, without any central coordination. Several statistical models have been put forward to capture the main features of this kind of ordering processes. Among the simplest ones range the Voter model (VM) (4) and the Moran process (MP) (5), designed to address issues of social (1) and evolutionary (6) dynamics, respectively. In the VM, individuals hold one of two mutually exclusive opinions, and are subject to pairwise interactions in which a randomly selected individual adopts the opinion of a nearest neighbor peer. In the MP, on the other hand, individuals belong to one (out of two) species and reproduce generating an equal offspring which replaces a randomly selected nearest neighbor. Due to their abstraction and simplicity, both models are now well established paradigms of ordering dynamics (1; 6).

Previous statistical studies of VM/MP dynamics have mainly considered the randomly mixed (5) (mean-field) case or a static (*fermionic*) distribution of individuals, identified with the sites of a lattice (1). More recently, after the discovery that the topological environment of many social and ecological processes is highly heterogeneous (7), fermionic dynamics on complex networks have also been considered (8; 9; 10). While interesting results have been obtained in all these cases, the analysis of the effects of the *mobility* of individuals has been mostly neglected, even though it is a crucial feature of many real biological and social systems. For example, human migration guarantees cultural contamination (11), while small exchanges between separated groups yield spatially synchronized population oscillations (12), and mobility of individuals promotes biodiversity (13). In an evolutionary context, moreover, migration is the force that increases the inter-population similarity reducing the intra-population homogeneity, thus contrasting the effects of random drift and adaptation (14).

Here we explore the role of mobility in ordering dynamics by considering the VM/MP within a generalized metapopulation (*bosonic*) framework (15; 16). As in classical studies in population genetics (17), and recent generalizations (18), we consider individuals of different species placed on a geographical substrate, represented for generality in terms of a random graph or network (7), whose vertices can host a population of any desired size. Individuals are endowed with mobility and at each time step they can either interact with the local population or migrate to a nearest neighbor vertex. To take mobility quantitatively into account, we introduce a species-specific parameter, representing the ratio between the mobility and interaction strengths, that determines the probability that an individual performs one of these two steps. We present evidence that mobility can strongly affect the ordering process, determining the onset of different mechanisms leading the system to the final homogeneous state and dramatically affecting the average time needed to reach it. Our results imply that the coupling between mobility and interactions leads to novel properties of the dynamics of

ordering, and should be explicitly taken into account when aiming at realistic modeling in general social or biological contexts.

In our metapopulation scheme, individuals interact inside the vertices of a network, while they can diffuse along the edges connecting pairs of vertices. From a statistical point of view, the underlying network is described by means of its degree distribution $P(k)$ (probability that a vertex has degree k —i.e. is connected to k other vertices) (7) and its degree-degree correlations $P(k'|k)$ (conditional probability that a vertex of degree k is connected to a vertex of degree k') (19). Individuals belong in general to S different species, each defined by a given trait (opinion, genotype, etc.) α and characterized by a parameter p_α (the *mobility ratio*), representing the ratio between the mobility (diffusion coefficient) and the propensity of species α to interact with other species. The dynamics of the processes is defined in the spirit of discrete time stochastic particle systems (20): At time t , one individual is randomly selected, belonging to class α . With probability p_α , the individual migrates, performing a random jump to a nearest neighbor vertex. Otherwise, with probability $1 - p_\alpha$, the individual chooses a peer inside its same vertex (the peer belonging to the species α') and reacts with it according to the dynamical rules describing the corresponding model: **(i)** Metapopulation VM (MVM): The individual copies the trait of the peer and becomes of species α' . **(ii)** Metapopulation MP (MMP): The individual reproduces, generating an offspring of the same species α , which replaces the peer. In any case, time is updated as $t \rightarrow t + 1/N$, where N is the (fixed) number of individuals. For each species α the occupation number of any vertex is unbounded and can assume any integer value, including zero $\ddagger$. When $p_\alpha = p_{\alpha'} \ \forall \alpha, \alpha'$ the MVM and the MMP are obviously equivalent (21).

Both dynamics are characterized by the presence of S ordered states in which all individuals belong to the same species, and interest lies in studying how the final ordered state is reached (1; 6). The relevant quantities are thus the *fixation probability* (or exit probability) ϕ_α and the *consensus* or *fixation time* $\bar{t}_\alpha$, defined as the probability that a population ends up formed by all α individuals and the average time until the eventual fixation (1). To gain insight on these quantities, it is useful to first consider the time evolution of the density of individuals. To do so, we consider as usual the partial densities of individuals of species α in vertices of degree k , defined as (15) $\rho_k^\alpha(t) = n_k^\alpha(t)/[VP(k)]$, where $n_k^\alpha(t)$ is the number of individuals of species α in vertices of degree k , at time t , and V is the network size. The total density of species α is then $\rho^\alpha(t) = \sum_k P(k)\rho_k^\alpha(t)$, satisfying the normalization condition $\sum_\alpha \rho^\alpha(t) = \frac{N}{V} \equiv \rho$, being ρ the total density of individuals in the network. Let us focus on the simplest case in which only two species are present in the system, $+1$ and -1 , with mobility ratios p_{+1} and p_{-1} , respectively. Within a mean-field approximation (16), we can see that the quantities $\rho_k^\alpha(t)$ fulfill the

$\ddagger$ We note that, with our definition, the occupation number of each vertex is not fixed, as in previous metapopulation models (18), but it is in fact a stochastic variable whose average value depends in general on the network structure.

rate equations

$$\partial_t \rho_k^\alpha(t) = -p_\alpha \rho_k^\alpha(t) + p_\alpha k \sum_{k'} \frac{P(k|k')}{k'} \rho_{k'}^\alpha(t) + \varepsilon(p_{-\alpha} - p_\alpha) \frac{\rho_k^\alpha(t) \rho_k^{-\alpha}(t)}{\rho_k^\alpha(t) + \rho_k^{-\alpha}(t)}, \quad (1)$$

where ε takes the values -1 and $+1$ for the MVM and the MMP, respectively. In Eq. (1), the first two terms stand for the diffusion of individuals, while the third one accounts for the interactions inside each vertex. Since the total number of individuals is conserved, the latter disappear in the equation for the density of individuals, $\rho_k(t) = \sum_\alpha \rho_k^\alpha(t)$, that takes the form of a weighted diffusion equation for the different species (15; 16). A quasi-stationary approximation, assuming that the diffusion process is so fast that it can stabilize the particle distribution in a few time steps, leads to the functional form for the partial densities, $\rho_k^\alpha(t) = k \rho^\alpha(t) / \langle k \rangle$. The existence of this diffusion-limited regime (16), whose presence is confirmed in numerical simulations (see Fig. 1(a)), is expected to hold for not too small values of p_α . This approximation allows to write the equation for the total species density

$$\partial_t \rho^\alpha(t) = \varepsilon(p_{-\alpha} - p_\alpha) \rho^\alpha(t) [1 - \rho^\alpha(t) / \rho], \quad (2)$$

where we have used the normalization condition $\rho^{+1}(t) + \rho^{-1}(t) = \rho$. Remarkably, this expression is valid for any degree distribution and correlation pattern.

When $p_\alpha = p_{-\alpha}$ the total species density is conserved ($\partial_t \rho^\alpha(t) = 0$), and the ordering process proceeds via density fluctuations (1), see Fig. 1(b). For $p_\alpha \neq p_{-\alpha}$, if $\varepsilon(p_{-\alpha} - p_\alpha) < 0$ the ordered state corresponds to a population of the $-\alpha$ species. The time evolution of the species α going extinct is given by an exponential decay, $\rho^\alpha(t) \sim \rho^\alpha(0) \exp(-t|p_{-\alpha} - p_\alpha|)$, see Fig. 1(c) and (d). Extinction becomes almost sure when ρ^α takes its minimum value, namely N^{-1} . Therefore, final ordering takes place in a time of the order $\ln N / |p_{-\alpha} - p_\alpha|$, independently of the network structure, for both MVM and MMP.

In order to obtain information on the fixation probability, we can take advantage of the topology independence of the MVM and MMP, evidenced in Eq. (2), and focus on a fully connected network, in which the particle distribution is homogeneous in all vertices. Both MVM and MMP can therefore be mapped to a biased one-dimensional random walk, in which the transition probabilities $p_{n',n}$ from n individuals of species $+1$ to n' individuals take the form

$$p_{n+1,n} = A_+ \frac{n(N-n)}{N^2}, \quad p_{n-1,n} = A_- \frac{n(N-n)}{N^2}, \quad (3)$$

all the rest being zero except $p_{n,n} = 1 - p_{n+1,n} - p_{n-1,n}$, and where $A_\pm = 1 - [p_{+1} + p_{-1} \pm \varepsilon(p_{+1} - p_{-1})]/2$. Applying standard stochastic techniques (23; 24) one recovers the fixation probability

$$\phi_{+1}(\rho^{+1}) = \frac{1 - r^{-V\rho^{+1}}}{1 - r^{-V\rho}} \quad (4)$$

where $r = A_+/A_-$. This result yields a neat evolutionary interpretation for the MMP. The fixation probability takes indeed the same form as in the fermionic MP in any

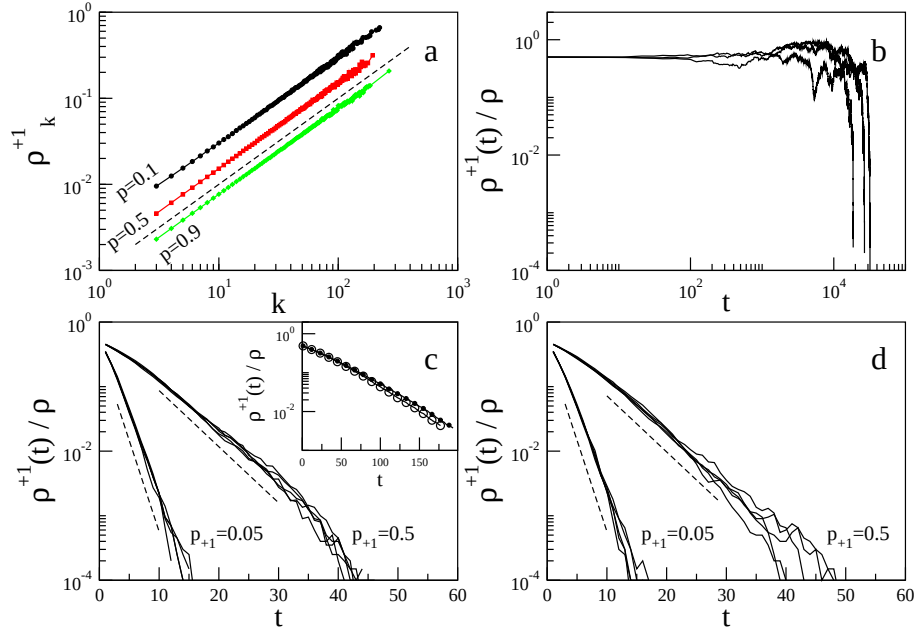


Figure 1. (a) Density of +1 individuals as a function of the degree in MVM and MMP on heterogeneous scale-free networks generated with the (uncorrelated) configuration model (22) with degree distribution $P(k) \sim k^{-2.5}$ for different values of $p = p_{+1} = p_{-1}$ (curves are shifted vertically for clarity). (b) Partial density of +1 individuals as a function of time ($p_{+1} = p_{-1} = 0.5$) in scale-free networks. (c, main) and (d) Partial density of +1 individuals as a function of time for the MVM in scale-free and fully connected networks, respectively. Dashed lines represent the theoretical slope $|p_{+1} - p_{-1}|^{-1}$ ($p_{-1} = 0.7$). Data from single runs with homogeneous initial conditions $\rho^{+1}(0) = \rho^{-1}(0) = 10$, in networks of size $V = 10^3$. (c, inset) Also in the low mobility case ($p_{+1} = 0.05$, $p_{-1} = 0.1$) averaged curves for fully connected (empty circles) and scale free networks (full circles) collapse well to an exponential decay.

undirected underlying network (9), provided the factor $r = (1 - p_{+1})/(1 - p_{-1})$ is interpreted as the relative selective *fitness* (6) of species +1 over species -1, defined as the relative number of offspring contributed to the next generation by both species §. In the case $p_{+1} = p_{-1}$, corresponding to the limit $r \rightarrow 1$, in which both species are equivalent, we recover $\phi_{+1} = \rho^{+1}$ (6). For $p_{+1} \neq p_{-1}$, on the other hand, homogeneous initial conditions ($\rho^{+1} = 1/2$) in the limit of large V yield $\phi_{+1} \rightarrow \Theta[\varepsilon(p_{-1} - p_{+1})]$ where $\Theta[x]$ is the Heaviside theta function; that is, the population becomes, as expected from the analysis of the density evolution, fixated to the species with the largest (smallest) p_α value for the MVM (MMP).

An analysis on general networks (24) confirms the results from fully connected ones, and implies that the MMP represents therefore a rigorous generalization of the classical evolutionary MP. Moreover, since the same fitness r can be achieved for different values of the mobility ratios, the metapopulation framework allows to explore the independent effects of mobility for a fixed selective advantage. This is particularly explicit in the form

§ An analogous interpretation can be made for a VM dynamics with fitness (21).

of the fixation time. To compute it, we extend the backwards Fokker-Planck approach presented in Refs.(10; 25; 21) to the bosonic case. Focusing for simplicity in the case of $p_{+1} = p_{-1} \equiv p$ ||, we recast the stochastic processes defined by the MVM and MMP in terms of a master equation. The state of the system can be described by the occupation number vectors $\vec{n}^\alpha = \{n_q^\alpha\}$, $q = 1, \dots, k_c$, where k_c is the largest degree in the network, that allow to keep track of the actual occupation number of the vertices of different degree. Transitions from one state to another can proceed therefore both when an individual diffuses and when it changes its state. Thus, defining the vector $\vec{\delta}_k = \{\delta_{q,k}\}$, the transitions rates due to the diffusion of an individual from vertex k' to k take the form

$$T(\vec{n}^\alpha + \vec{\delta}_k - \vec{\delta}_{k'}, \vec{n}^{-\alpha} | \vec{n}^\alpha, \vec{n}^{-\alpha}) = N \frac{p_\alpha}{\rho} P(k') \rho_{k'}^\alpha P(k|k'),$$

while the transitions rates due to reaction are

$$T(\vec{n}^\alpha \pm \vec{\delta}_k, \vec{n}^{-\alpha} \mp \vec{\delta}_k | \vec{n}^\alpha, \vec{n}^{-\alpha}) = N \frac{1-p}{\rho} P(k) \frac{\rho_k^\alpha \rho_k^{-\alpha}}{\rho_k^\alpha + \rho_k^{-\alpha}}.$$

From these transition probabilities it is straightforward to write the corresponding master equation, which can then be translated into a backwards Fokker-Planck equation, by expanding it up to second order in the inverse network size V^{-1} . Resorting again to the quasi-stationary condition $\rho_k^\alpha = k\rho^\alpha / \langle k \rangle$, the backwards Fokker-Planck becomes a function of the densities ρ^α only, and its different terms can be conveniently simplified. From the backwards Fokker-Planck equation, finally, we obtain the consensus time, which, as a function of the reduced initial density $x = \rho^{+1}/\rho$, satisfies the equation (10)

$$4 \frac{1-p}{N} x(1-x) \frac{\partial^2 \bar{t}_{+1}(x)}{\partial x^2} = -1, \quad (5)$$

subject to the boundary conditions $\bar{t}_{+1}(0) = \bar{t}_{+1}(1) = 0$ (24). Strikingly, this equation is the same for both MVM and MMP, and again independent of the topological details of the network, that therefore turn out to be an irrelevant parameter as far as the asymptotic results for fixation probability are concerned (provided that the diffusion rates are not too small, and the quasi-stationary approximation assumed above is valid (24)). The solution of Eq. (5) is

$$\bar{t}_{+1}(x) \sim -\frac{N}{1-p} [x \ln x + (1-x) \ln(1-x)]. \quad (6)$$

Therefore, for homogeneous initial conditions, $x = 1/2$, we obtain a fixation time scaling as $\bar{t}_{+1}(1/2) \sim N/(1-p)$. This result recovers the standard scaling linear in N of the fermionic VM and MP in fully connected networks (1; 6), and is in opposition to the topological dependent scaling shown by the VM in heterogeneous networks (21). The most interesting feature of this fixation time, however, is that, even though it has been computed for fixed $r = 1$, it shows a strong dependence on the individuals' mobility p . In particular, it is a growing function of p , which, in the limit $p \rightarrow 1$ tends to infinity, evidencing a dramatic slowing down in the ordering process, see Fig. 2. Numerical

|| The general case $p_{+1} \neq p_{-1}$ will be considered elsewhere (24).

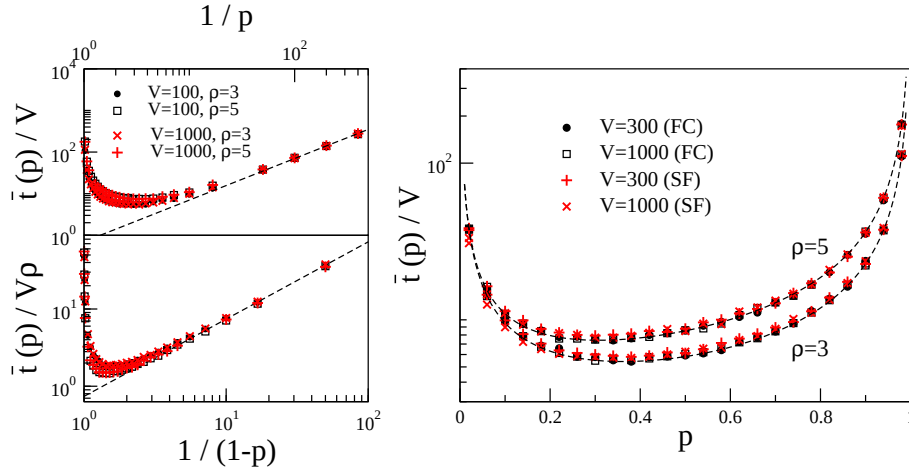


Figure 2. Left: Scaling of the fixation time for the MVM and MMP with mobility $p_{+1} = p_{-1} = p$, in the limit $p \rightarrow 0$ (top) and $p \rightarrow 1$ (bottom), in fully connected networks. Right: Rescaled fixation time for the MVM and MMP with mobility $p_{+1} = p_{-1} = p$ in fully connected (FC) and scale free (SF) networks of different sizes. Dashed lines are nonlinear fits to the functional form Eq. (7), for $A \simeq 0.70$ and $B \simeq 0.72$. Data refer to homogeneous initial conditions.

simulations of the fixation time in the full range of mobility values, Fig. 2 (right panel), yield, however, an asymmetric concave form, in contrast with the hyperbolic form predicted by the diffusion approximation. A detailed numerical analysis, see Fig. 2 (left panel), allows us to conjecture the functional form of the fixation time as a function of the mobility p , $\bar{t}_{+1} = \bar{t}_{-1} \equiv \bar{t}(p)$, as given by

$$\bar{t}(p) \approx A \frac{V}{p} + B \frac{V\rho}{1-p}, \quad (7)$$

where A and B are constants, approximately independent the population size and mobility ratio. The functional form in Eq. (7) is corroborated by the scaling analysis performed in Fig. 2 (right panel), where we observe that curves for fully connected and heterogeneous networks collapse, when properly scaled, for the same value of ρ . The concave form of the fixation time implies additionally the presence a minimum for a value p_{min} of the mobility ratio for which the systems orders more quickly. According with the estimated functional form in Eq. (7), this minimum takes the form $p_{min} \sim \rho^{-1/2}$. This indicates the striking presence of an optimum global level of mobility that maximizes the speed at which an opinion consensus is reached or a neutral mutant dominates a population (6). Possibly against intuition, moreover, according to Eq. (7) in the thermodynamic limit the fastest fixation regime is associated to almost still particles ($p_{min} \rightarrow 0$ as $\rho \rightarrow \infty$).

The asymmetry of the fixation time for $p_{+1} = p_{-1}$, Eq. (7), hints towards different mechanisms in operation on the way in which convergence is reached in the two limits $p \rightarrow 0$ and $p \rightarrow 1$ (26). To quantify this intuition it is helpful to consider the global order parameter $\psi(t) = |N_{+1}(t) - N_{-1}(t)|/N(t)$, measuring the global difference between

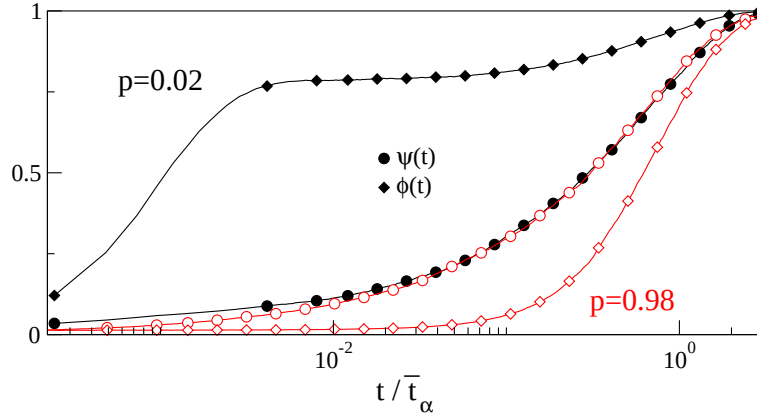


Figure 3. Ordering mechanisms as a function of mobility. In the limit $p \rightarrow 0$ (black curves) local order ($\phi(t)$) grows in short time, while global order ($\psi(t)$) emerges as a result of vertex-vertex competition. When $p \rightarrow 1$ (red curves), on the other hand, local order emerges only as a result of global ordering at late times. Data refer to a fully connected network with $V = 100$ with homogeneous initial conditions $\rho^{+1}(0) = \rho^{-1}(0) = 10$.

the number of individuals belonging to the two species, and the local order parameter $\phi(t)$ given by the fraction of vertices in which a local convergence has been reached and only one species is present. Fig. 3 shows the behavior of these quantities. When p is small, intra-vertex order rapidly emerges but different species prevail in different vertices, as reflected by the low value of the global order parameter. The process then proceeds through a vertex-vertex competition leading in the end to global convergence thanks to the successive contamination of different vertices. When particle mobility is high, on the other hand, convergence emerges instead by the sudden prevalence of one of the two species, so that local and global order rise almost simultaneously.

In conclusion, we have studied a metapopulation scheme that allows to consider the effects of mobility in ordering dynamics. Focusing on the Voter/Moran processes as simple yet paradigmatic examples, we have found expressions for the fixation probability and time, which are independent from the topological details of the underlying network. While the fixation probability takes the same form as in the usual fermionic counterparts, the fixation time depends strongly on mobility when all species share the same mobility ratio (actually diverging when the mobility tends to very large or small values). Additionally, in this regime we have identified two different mechanisms leading to local and global convergence in the limit of low and high diffusion ratios. Our work opens the way to a better understanding of mobility in a wide class of models of ordering dynamics, with consequences touching the broad spectrum of disciplines that have borrowed from this field over time. In particular, a challenging task for future work will consider the implementation of mobility in more complex and realistic models of social dynamics (1).

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