

Fixation and consensus times on a network: a unified approach

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We investigate a set of stochastic models of biodiversity, population genetics, language evolution and opinion dynamics on a network within a common framework. Each node has a state, $0 < x_i < 1$, with interactions specified by strengths m_{ij} . For any set of m_{ij} we derive an approximate expression for the mean time to reach fixation or consensus (all $x_i = 0$ or 1). Remarkably in a case relevant to language change this time is independent of the network structure. A more rigorous result, in the form of a bound, is found by mapping to particle coalescence dynamics on a network.

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Mathematical models predicting biological and social change are becoming increasingly commonplace, with the last few years having seen an explosion of activity among statistical physicists in cultural dynamics [1]. One aspect of this work which is not widely appreciated is that several seemingly distinct phenomena can be described by very similar models: in some cases they can even be exactly mapped into each other [2]. Examples include biodiversity [3], population genetics [4], opinion dynamics [1] and language change [5]. The common thread is that objects that come in different variants are copied from one place (an “island”) to another according to some stochastic rule. If no new variants are created in the process (e.g., by mutation) and the number of objects does not grow without bound, one variant is eventually guaranteed to take over an entire population, or go to fixation in the genetics parlance. Changes in the network structure connecting different islands, and the stochastic rules used to choose the source and target islands, lead to a variety of scaling laws relating the number of islands and time to reach fixation (see, e.g., [6, 7, 8]). In this Letter, we present a theoretical treatment of a very general stochastic copying model that includes many previously-studied cases and unifies the diverse fixation time results obtained so far. By mapping to a particle reaction system we show that our prediction for the fixation time, obtained by making various approximations, can in many cases be stated as a bound that simulations show is often saturated. We also discuss the consequences of our findings on a current theory of new-dialect formation [9].

To establish the basic features of the large class of models we consider, we describe a prominent special case, Hubbell’s model of biodiversity and biogeography [3]. Here there are only two islands: a metacommunity or mainland (island 1) and a local community (island 2). The objects are individuals which compete for a common resource (e.g. trees competing for space, sunlight and nutrients [10]) and the variants are different species. At regular time intervals an individual in island 2 is picked

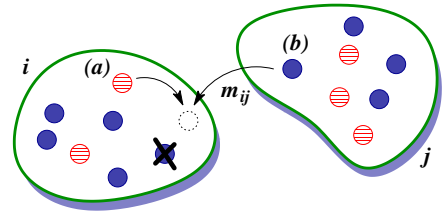


FIG. 1: Stochastic copying dynamics between two islands i and j forming part of a larger network. After a death on i , an object is replaced either with a copy from (a) the same island i or (b) a different island j (rate m_{ij}).

at random to die and to be replaced by a copy of either (a) another individual picked at random from island 2, or (b) a *migrant* from island 1. Process (b) is assumed to happen less frequently than (a), and as mentioned above, if (b) is absent then the final state of the system is one which contains individuals of only one species. The number of individuals on island 2 is a constant, n , and new species are created on island 1, but not island 2, by mutation-like events. This model is a *neutral* theory; no one species is assumed to be “fitter” than another.

The relationship between this model and simple neutral models of population genetics is well known [3]: individuals are analogous to genes and species are types of genes (alleles). A more general model comprises a set of islands labeled $i = 1, \dots, N$ each of which contains n genes (in reality, n individuals each containing one copy of the gene of interest). For simplicity we assume that there is no mutation, so that no new alleles may be created. The alleles are labeled by $\alpha = 1, \dots, M$. The dynamical processes, illustrated in Fig. 1 are as before: a death on island i followed by (a) a birth on island i , or (b) a migrant offspring from island j arriving on island i . There are various ways to parametrize these dynamics. As in [2], we let the parent (copied object) be taken from island j with probability f_j . In process (b) the probability the offspring (copy) lands on island i is taken to

be proportional to m_{ij} , which specifies a *migration rate* within a standard continuous-time limit described in [2], but whose details are unimportant here. At any time t , the state of the system can be given in terms of the fraction $x_{i\alpha}(t)$ of genes on island i that are allele α . Then, the islands can be represented as nodes on a network, which in the opinion dynamics and language change models are individuals i with opinions or language variants α expressed with frequency $x_{i\alpha}$. In these social contexts, fixation is sometimes called consensus.

Using the formalism first developed for these systems in population genetics [4], we describe the evolution in terms of a Fokker-Planck equation. Suppose, first of all, that there is only one island and no mutation. Then the only dynamical process is *random genetic drift* in which the frequencies $x_\alpha(t)$ diffuse on the interval $[0, 1]$ due to the random sampling in the death/birth process. For simplicity, we will assume that there are only two alleles which have frequencies x and $(1-x)$, so the state of the system is described by the single stochastic variable $x \in [0, 1]$. The probability that the system is in the state x at time t , $P(x, t)$, satisfies the Fokker-Planck equation $\partial_t P(x, t) = \partial_x^2 [D(x)P(x, t)]$ where the diffusion constant is state dependent: $D(x) = x(1-x)/2$ [4]. Moving to the case of N islands, with migration rate m_{ij} from j to i , the Fokker-Planck equation for $P(x_i, t)$ now reads [2]

$$\begin{aligned} \frac{\partial P}{\partial t} &= \sum_{\langle ij \rangle} \left(m_{ij} \frac{\partial}{\partial x_i} - m_{ji} \frac{\partial}{\partial x_j} \right) [(x_i - x_j) P] \\ &+ \frac{1}{2} \sum_{i=1}^N f_i \frac{\partial^2}{\partial x_i^2} [x_i (1 - x_i) P], \end{aligned} \quad (1)$$

where $\langle ij \rangle$ means sum over distinct pairs i, j . This may be generalized to $M > 2$ and to include mutation [2], but Eq. (1) will be sufficient for our purposes.

Analysis of Eq. (1) is, on the face of it, a hopeless task since it has many degrees of freedom, x_i , interacting with arbitrary strengths m_{ij} . However, much of the macroscopic dynamics is captured by the first and second moments of $x_i(t)$. The mean, $\alpha_i(t) = \langle x_i(t) \rangle$ can be found from Eq. (1) to evolve according to

$$\frac{d\alpha_i}{dt} = \sum_{j \neq i} m_{ij} (\alpha_j - \alpha_i) \equiv \sum_{i=1}^N m_{ij} \alpha_i, \quad (2)$$

where the equivalence holds if the diagonal elements m_{ii} are defined to be $-\sum_{j \neq i} m_{ij}$. This matrix has a zero eigenvalue, which we will assume is non-degenerate. The associated right eigenvector has all elements equal to one, and the left eigenvector we denote Q_i , so that $\sum_i Q_i m_{ij} = 0$, and normalized such that $\sum_i Q_i = 1$. Then we find from Eq. (2) that the ensemble (noise-history) average of the collective variable

$$\xi(t) = \sum_{i=1}^N Q_i x_i(t) \quad (3)$$

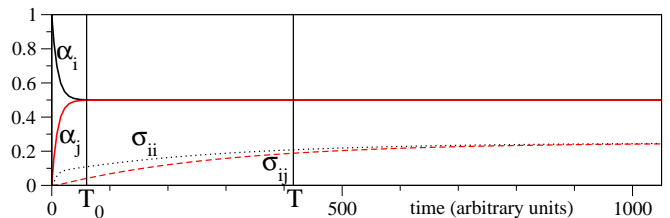


FIG. 2: Numerical solution for means α_i, α_j and (co)variances $\sigma_{ij} \equiv \beta_{ij} - \alpha_i \alpha_j$ on a fully-connected network of $N = 20$ sites. Note the α s converge at a time T_0 much less than the mean fixation time T , and at time T_0 , $\sigma_{ij} \approx 0$ for $i \neq j$. These features become more pronounced as N is increased.

is conserved by the dynamics. Decomposing $\alpha_i(t)$ in terms of its right eigenvectors we see that it approaches a constant independent of i as $t \rightarrow \infty$. Since all $x_i(t)$ tend to 0 or 1 as $t \rightarrow \infty$, this is the probability of the allele fixing. From (3) we see $\langle \xi(t) \rangle$ also approaches this value in this limit and since ξ is conserved, the fixation probability is $\xi(0)$ [6, 11].

Numerical studies suggest that convergence of the ensemble average $\alpha_i(t)$ to its asymptote $\xi(0)$ occurs on a much shorter timescale than the ultimate fixation of a variant, which in turn governs the rate of change of the second moments $\beta_{ij}(t) = \langle x_i(t)x_j(t) \rangle$, see Fig. 2. Eq. (1) implies for the latter

$$\frac{d\beta_{ij}}{dt} = \sum_k m_{ik} \beta_{kj} + \sum_l m_{jl} \beta_{il} + \delta_{ij} f_i (\alpha_i - \beta_{ii}) \quad (4)$$

whilst the mean time to fixation, T , is given by the solution of a backward version of the Fokker-Planck equation (1) [12]

$$\begin{aligned} -1 &= - \sum_{\langle ij \rangle} (x_i - x_j) \left(m_{ij} \frac{\partial T}{\partial x_i} - m_{ji} \frac{\partial T}{\partial x_j} \right) \\ &+ \frac{1}{2} \sum_{i=1}^N f_i [x_i (1 - x_i)] \frac{\partial^2 T}{\partial x_i^2}. \end{aligned} \quad (5)$$

The assumption that the time over which all the α_i converge, T_0 , is much less than T (see Fig. 2) leads to the following approximate treatment of this equation. We assume that T depends *only* on the state of the system at time T_0 , and principally through $\xi(0)$. Changing to the $\xi(0)$ variable using Eq. (3) we find that the first term on the right-hand side of Eq. (5) vanishes [6] giving

$$-2 = \sum_{i=1}^N f_i Q_i^2 x_i(T_0) [1 - x_i(T_0)] \frac{d^2 T}{d\xi(0)^2}. \quad (6)$$

This equation still depends on the variables x_i at time T_0 . We can estimate these by assuming that correlations between the nodes are absent, i.e. $\beta_{ij} = \alpha_i \alpha_j = \xi(0)^2$ $i \neq j$, and that the rate of change of the variance of x_i is

sufficiently slow that the time derivative in Eq. (4) when $i = j$ can be neglected (see again Fig. 2). Then β_{ii} at time T_0 can be estimated from Eq. (4).

By replacing $x_i(1 - x_i)$ in Eq. (6) by $\alpha_i - \beta_{ii}$ at time T_0 , we find $[\xi(0)(1 - \xi(0))] d^2 T / d\xi(0)^2 = -2/r$ where

$$r \approx \sum_i Q_i^2 f_i \frac{2 \sum_{j \neq i} m_{ij}}{2 \sum_{j \neq i} m_{ij} + f_i}. \quad (7)$$

The mean fixation time is obtained by integrating the equation for $T(\xi(0))$, with the boundary conditions $T(0) = T(1) = 0$ to give

$$T(\xi(0)) = -\frac{2}{r} [\xi(0) \ln \xi(0) + (1 - \xi(0)) \ln(1 - \xi(0))], \quad (8)$$

which in tandem with (7) is our main result, derived for a large class of stochastic-copying processes on any network and arbitrary migration rates. The parameter r , and the form of (7), admits a physical interpretation within an interacting particle picture which we describe below.

First we remark that if the rates m_{ij} are chosen to mimic the voter dynamics described in [6, 7], viz, $f_i = 1/N$ and $m_{ij} \propto 1/(Nk_j)$, where k_i is the degree of node i , we obtain (modulo choice of time units) the same expression for the fixation time in terms of moments of the degree distribution. We also recover the various scaling forms found in [8]. A more stringent test of our results can be constructed by choosing f_i and m_{ij} from various random distributions in such a way that the numerators and denominators in (7) are of similar magnitudes. Simulation results (not shown) on Erdős-Rényi random graphs of varying densities [13] are consistent with the predictions of Eqs. (7) and (8), except when T and T_0 turn out to be of a similar order in N .

More interesting is a remarkable result for the utterance selection model of language change [5], in which m_{ij} is proportional to two factors, the frequency speakers i and j meet, and a social weight speaker i gives to speaker j 's utterances. A socially-neutral model, as proposed in [9] for new-dialect formation, is obtained if the latter weights are all equal. Then, m_{ij} is symmetric for any set of interaction frequencies, and one finds the time to fixation is completely independent of the network structure! This is because the symmetry of m_{ij} implies that its left and right eigenvectors are proportional to one another; hence $Q_i = 1/N$, and $\sum_j m_{ij} \propto f_i$. This network independence of r , and hence T , is confirmed by simulation results shown in Fig. 3 (although see below for some caveats). To evaluate the plausibility of this socially-neutral model as a mechanism for new dialect formation requires in addition to this result detailed consideration of human memory lifetimes, to be discussed elsewhere [14]. Ultimately, we find that a purely neutral model is hard to reconcile with available empirical data.

A more solid understanding of Eq. (7) and its validity is obtained by considering a mapping of the stochastic-

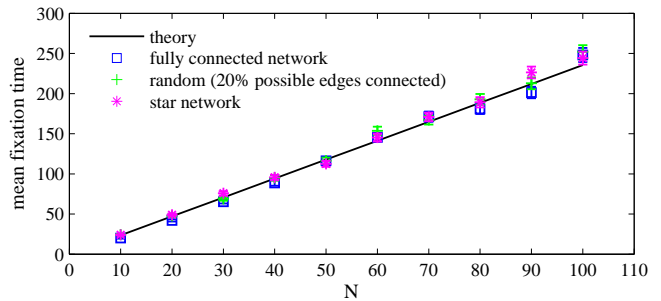


FIG. 3: Fixation times within the socially-neutral utterance selection model (defined in the text) on various networks with N nodes (see legend).

copying dynamics to the $A + A \rightarrow A$ particle coalescence reaction of non-equilibrium statistical mechanics [15] on a network, also called the *coalescent* in population genetics [16]. Here we sketch the main ideas of this approach, with full details appearing elsewhere [17]. One considers the history of two present-day objects, which we now call particles. Looking backward in time, each particle hops from node i to j at rate m_{ij} . Eventually, a particle reaches the stationary distribution previously denoted Q_i . Two particles on the same site coalesce at rate f_i . If the reactions did not induce any correlations in the particle positions, then asymptotically the mean reaction rate r would approach $\sum_i Q_i^2 f_i$, since two particles would be on node i with probability Q_i^2 . This result is valid when the hop rates m_{ij} are large compared to the coalescence rates f_i [18]. The additional factor appearing in (7) can thus be interpreted as a correction due to correlations.

More formally, one can show [17] that the asymptotic relative probability $Q_{(ij)}$ of finding one particle on island i and the other on j , given that they have not coalesced, satisfies

$$\sum_{kl} Q_{(kl)} M_{(kl)(ij)} = -r Q_{(ij)}, \quad (9)$$

where $M_{(ij)(kl)} = m_{ik} \delta_{jl} + m_{jl} \delta_{ik} - f_i \delta_{ijkl}$ and δ_{ijkl} is zero unless all the indices are the same, in which case it is unity. In other words, $Q_{(ij)}$ is the left eigenvector of the matrix M with eigenvalue $-r$. This equation is hard to solve in general, but a variational approach is possible if the single-particle process satisfies the detailed balance condition $Q_i m_{ij} = Q_j m_{ji}$ (this holds if m_{ij} is symmetric, for instance). Then, if $p_{(ij)}^\lambda$ is a right eigenvector with eigenvalue λ , $q_{(ij)}^\lambda = Q_i Q_j p_{(ij)}^\lambda$ is the corresponding left eigenvector, which can be shown from the fact that $Q_i Q_j M_{(ij)(kl)} = Q_k Q_l M_{(kl)(ij)}$. Furthermore, one can show (in the usual fashion [19]) that all the eigenvalues are real and negative and form an orthonormal set, i.e.,

$$(p^\lambda, p^{\lambda'}) \equiv \sum_{ij} Q_i Q_j (p_{(ij)}^\lambda)^* (p_{(ij)}^{\lambda'}) = \delta_{\lambda, \lambda'} \quad (10)$$

in which the equivalence defines a scalar product and the asterisk denotes complex conjugation. It then follows that any vector p can be expanded as $p = \sum_{\lambda} (p^{\lambda}, p) p^{\lambda}$ from which one obtains in the usual way the variational result [19] $(p, Mp) \leq -r(p, p)$, which provides an upper bound on the magnitude of the reaction rate r through a specific choice of p . From Eq. (8), we see that it will provide a *lower* bound for the mean time to fixation.

The parameters $p_{(ij)}$ account for correlations between particle pairs through the relation $Q_{(ij)} = Q_i Q_j p_{(ij)}$. Hence the variational approach allows a systematic treatment of these correlations. For example, we can assume no correlations between different islands, $p_{(ij)} = 1$ for all $i \neq j$, and leave $p_i \equiv p_{(ii)}$ as variational parameters. Minimising $r = -(p, Mp)/(p, p)$ yields, after some calculations, the pair of equations

$$p_i = \frac{2 \sum_{j \neq i} m_{ij}}{2 \sum_{j \neq i} m_{ij} + f_i - \tilde{r}}, \quad \tilde{r} = \frac{\sum_i Q_i^2 p_i (f_i - \tilde{r})}{1 - \sum_i Q_i^2} \quad (11)$$

that must be simultaneously solved for the optimum value of r , denoted \tilde{r} . Analysis of these equations [17] shows that there is a unique solution with all positive p_i , and that \tilde{r} itself satisfies a slightly weaker bound

$$r \leq \tilde{r} \leq \frac{1}{1 - \sum_{\ell} Q_{\ell}^2} \sum_i Q_i^2 f_i \frac{2 \sum_{j \neq i} m_{ij}}{2 \sum_{j \neq i} m_{ij} + f_i}, \quad (12)$$

which is the right-hand side of Eq. (7) with an extra factor $[1 - \sum_i Q_i^2]^{-1}$ included. In many cases, this factor contributes only to sub-leading order in N as $N \rightarrow \infty$, and (7) is recovered; additionally, numerical solution of Eqs. (11) shows that for many networks and parameter choices, \tilde{r} approaches (7) as $N \rightarrow \infty$. The value of the results (11) comes instead from the more controlled nature of the approximations made in deriving them, and the fact that they are in the form of a bound that is valid for models that satisfy detailed balance.

We have discussed above a number of cases where this lower bound on the fixation time is saturated. One may thus ask under what circumstances the fixation time is underestimated. We have observed this to occur on some networks exhibiting local structure: for example, on Watts-Strogatz small-world networks [20] each node is connected to a vanishing fraction of non-neighbor nodes. To improve the bound, one would need to build this local structure into the variational ansatz, which we suggest as a task for future work, along with establishing criteria for determining when the assumption that $T_0 \ll T$ is invalidated.

In summary, we have shown how to find the fixation time for a very broad class of stochastic-copying models that have applications in a wide range of physical, biological, and social contexts. Although approximate, the analytic result shows good agreement with simula-

tion data for a range of networks. We have also developed a more systematic treatment via a mapping to the coalescence reaction $A + A \rightarrow A$ on an arbitrary network, and hope that the variational principle outlined here can be extended to examine the effects of, for example, local structure on particle correlations. This approach relies on an underlying detailed-balance symmetry, and it would be interesting to try to extend to cases where this is violated. Finally, we have briefly discussed how a particularly striking result—that fixation time is independent of network structure—is of direct relevance to current linguistic theory [9, 14] and hope that in the future many other mathematical results for formal models of social behavior will be applied in empirical contexts.

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