ON THE METASTABILITY OF QUADRATIC MAJORITY DYNAMICS ON CLUSTERED GRAPHS AND ITS BIOLOGICAL IMPLICATIONS*

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A preprint version [12] is available at `https://arxiv.org/abs/1805.01406`.

Introduction

Dynamics are simple stochastic processes on graphs in which nodes update their own state according to a symmetric function of the state of their neighbors and of their current state, with no dependency on time or on the topology of the graph [15, 23]. In previous decades the computational power of this kind of systems has been investigated in the context of automata networks from mathematicians and physicists. Recently it has been subject to a renewed interest from the theoretical computer science community, as new algorithmic techniques made the analysis of dynamics as distributed algorithms possible [13, 2, 9, 10, 4, 3].

In this work, we consider the 2-CHOICES dynamics, where in each discrete-time step each node samples two random neighbors with replacement and, if they have the same state, the node adopts that state. In [9, 10], the authors show that this process rapidly converges to *consensus*, i.e., all nodes having the same state, if the proportion of nodes supporting a given state exceeds a given function of the second eigenvalue of the graph. Their proofs leverage an interesting property of the 2-CHOICES dynamics, namely the fact that the expected number of nodes supporting a given state can be expressed as a quadratic form of the transition matrix of a simple random walk on the graph, for an inner product given by the stationary distribution of such random walk. In turn, the previous relation between the dynamics and the transition matrix allows to relate the behavior of the process to the eigenspaces of the graph. Motivated by biological questions that we discuss in the following sections, we exploit the aforementioned relation to show a more

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fine-grained understanding of the consensus behavior of the 2-Choices, which should also extend to similar dynamics. Our new analysis combines symmetry-breaking techniques [4, 8] and concentration of probability arguments with the linear algebraic approach of [9, 10] to obtain the first symmetry-breaking analysis for dynamics on non-complete topologies.

Main Theorem. Consider a *clustered* regular graph[1] [5] in which the nodes are divided in two sets V_1 and V_2 of equal size, such that each node in V_i has a neighbors in V_i and b neighbors in V_j, for each $i, j = 1, 2$ s.t. $i \neq j$. Assume that

- the ratio d/b is $\Omega(n^{\frac{1}{2}})$;
- the second eigenvalues of the subgraphs induced by V_1 and V_2 are $\mathcal{O}(n^{-\frac{1}{4}})$;
- the initial state of each node is *red* or *blue*, according to the toss of a fair coin (namely an independent Bernoulli($\frac{1}{2}$) random variable).

Then, with constant probability, after $\mathcal{O}(\log n)$ rounds all nodes in V_1 and V_2 but $\mathcal{O}(\log n)$ nodes have the same color and the the predominant colors in V_1 and V_2 are different. Moreover, with high probability,[2] the process remains in such *almost-clustered* configuration for n^c rounds, for any positive constant c.

In the next sections, we discuss two biological implications of our result.

An Evolutionary Graph-Theoretic Explanation for Speciation

Evolutionary dynamics is the branch of genetics which studies how populations evolve genetically as a result of the interactions among the individuals [14]. In its seminal paper on evolutionary graph theory [21], Lieberman et al. initiated the study of evolutionary dynamics on graphs by investigating the *fixation probability* of the *Moran process* on different families of graphs, namely the probability that a new mutation with increased fitness eventually spreads across all individuals in the population. Since then, the Moran process has attracted the attention of the computer science community due to the algorithmic questions associated to its fixation probability [19, 16]. However, no simple dynamics has been proposed so far in the context of evolutionary graph theory to explain one of evolution's fundamental phenomena, namely *speciation* [11].

> "What is needed now is a shift in focus to identifying more general rules and patterns in the dynamics of speciation. Theoretical studies of speciation have been dominated by numerical simulations. [...] The crucial step in achieving this goal is the development of simple and general dynamical models that can be studied not only numerically but analytically as well. [...] A number of important conclusions have emerged from analytical studies. [...] If transition does happen, it is very quick. Speciation can occur by mutation and random drift alone with no contribution from

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[1] In the full version [12], we discuss how the proof might generalize to a wider class of graphs.

[2] An event E happens *with high probability* if $\Pr(E) = 1 - \mathcal{O}(n^{-c})$, for some constant $c > 0$.

> selection as different populations accumulate incompatible genes. [...] Speciation can be understood as the divergence along nearly neutral networks and holey adaptive landscapes [...] accompanied by the accumulation of reproductive isolation as a by-product." - S. Gavrilets [18]

Two fundamental classes of driving forces for speciation can be distinguished: *allopatric* speciation and *sympatric/parapatric* speciations. The former, which refers to the divergence of species resulting from geographical isolation, is well understood [24]; the latter, namely divergence of species without complete geographical isolation, is still controversial [24, 7, 6].

In several evolutionary settings, the spread of a mutation appears nonlinear w.r.t. the number of interacting individuals carrying the mutation, exhibiting a drift towards the most frequent phenotypes [18, 11]. We look at the 2-Choices dynamics on clustered graphs as a quadratic evolutionary dynamics on sympatric and parapatric scenarios. The random initialization of the 2-Choices can be regarded as two inter-mixed populations of individuals with different genetic pools. The interactions for reproduction purposes between the two populations can be categorized in frequent interactions among individuals within a equal-size bipartition of the populations (the clusters) and less frequent interactions between the two populations (which, in later stages of the differentiation process, may be interpreted as genetic admixture, i.e., interbreeding between two genetically-diverging populations [22]).

Within such framework, our theorem provides an analytical evolutionary graph-theoretic proof of concept on how speciation can emerge from the simple nonlinear underlying dynamics of the evolutionary process on the population level.

On the Process of Innervation in Muscular Junctions

During mammalian development, neuromuscular junctions and some other postsynaptic cells transition from having multiple neurons innervating onto them into being subject to innervation from a single neuron only [17, 25, 26]. This process takes place as synaptic sites are exchanged between different axons: Locations on the surface of the cell on which neurons innervate transition from being freed by the current innervating neuron to be occupied again by a new one [26].

In [26], it is shown that soon-to-be-eliminated axons rapidly reverse fate and grow to occupy vacant sites at a neuromuscular junction after they are artificially damaged in laboratory. Such evidence is argued to support the hypothesis that the process is driven by a form of competition at the level of neural terminations:

> "This reversal supports the idea that axons take over sites that were previously vacated. Indeed, during normal development we observed withdrawal followed by takeover. The stimulus for axon growth is not postsynaptic cell inactivity because axons grow into unoccupied sites even when target cells are functionally innervated. These results demonstrate competition at the synaptic level and enable us to provide

> a conceptual framework for understanding this form of synaptic plasticity." - Turney et al. [26]

The author then provides a simplistic model for the aforementioned process based on evolutionary graph theory (discussed in the previous section). Such model is equivalent to the Voter dynamics[3] when the underlying graph is regular.

We argue that our theorem provides evidence for the fact that, in order for a model based on dynamics[4] to comply with experimental evidence on the outcome of the innervation process, either the innervation sites do not exhibit spatial bottlenecks or the dynamics cannot be based on majority-like mechanisms. Our analysis shows that, when the 2-Choices dynamics takes place on a clustered graph and starts from a random configuration, there is a constant probability that the system will converge to a configuration in which the two clusters maintain an almost consensus on two different values. This is in contrast with the aforementioned phenomenon of synapse elimination when developing neuromuscular junctions [25, 26], where the outcome is a *consensus* configuration in which the whole neuromuscular junction is innervated by a single axon only. Hence, our result suggests that, if the competition among axons for innervating a postsynaptic cell follows a local behavior akin to the 2-Choices dynamics, the topology of the sites as formalized in [26] should not exhibit a clustered structure, i.e., a partition into two clusters with good expansion properties that are separated by a sparse cut (as in the clustered graphs used in our theorem). On the other hand, if experimental evidence would confirm that the graph associated to the innervation site can indeed exhibit a structure similar to the graphs of our theorem, then the dynamics implemented by axons should qualitatively differ from a super-linear majority dynamics such as the 2-Choices.

We complement our previous argument with simulations on stochastic block models with two clusters [20] on a class of dynamics which generalizes the 2-Choices dynamics. We call such class *y-degree majority dynamics*, in which each node u updates its current state with state σ with probability $\left(\frac{|N(u)\cap S_\sigma|}{d_u}\right)^y$, for a real value $y \geq 1$ and where S_σ is the set of nodes with state σ, $N(u)$ is the set of neighbors of u, and d_u is the degree of u. Observe that the node does not update its current state to σ with probability $1 - \left(\frac{|N(u)\cap S_\sigma|}{d_u}\right)^y$. As a special case with only two states, for $y = 2$ we get the 2-Choices and for $y = 1$ we get the Voter. Our numerical experiments on the stochastic block models show that the probability that the dynamics converges to (and maintains) a configuration in which the two clusters support different colors deteriorates towards 0 as y decreases from 2 to 1.

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[3] In each discrete-time step each node updates its state to that of a random neighbor.

[4] We remark that we did not find any decisive evidence in the experimental literature that the process could not be better explained through other factors such as communication among axons via molecular clues (similarly to other developmental neural process such as [1]).

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