Variety Is the Spice of Life: Irrational Behavior as Adaptation to Stochastic Environments[*]

Thomas J. Brennan[†], Andrew W. Lo[‡], and Ruixun Zhang[§]

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Abstract

The debate between rational models of behavior and their systematic deviations, often referred to as "irrational behavior", has attracted an enormous amount of research. Here we reconcile the debate by proposing an evolutionary explanation for irrational behavior. In the context of a simple binary choice model, we show that irrational behaviors are necessary for evolution in stochastic environments. Furthermore, there is an optimal degree of irrationality in the population depending on the degree of environmental randomness. In this process, mutation provides the important link between rational and irrational behaviors, and hence the variety in evolution. Simulation confirms the generality of these implications in a wide range of stochastic environments. Our results yield widespread implications for science, management, and public policy. The simplicity and generality of our model also suggest that these implications are primitive and cut across species, physiology, and genetic origins.

Keywords: Behavioral Bias; Behavioral Finance; Adaptive Markets Hypothesis; Evolutionary Game Theory

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[†] Stanley S. Surrey Professor of Law, Harvard Law School, Cambridge, MA, USA, `tbrennan@law.harvard.edu` (email).

[‡] Charles E. and Susan T. Harris Professor, MIT Sloan School of Management; director, MIT Laboratory for Financial Engineering; Principal Investigator, MIT Computer Science and Artificial Intelligence Laboratory. Please direct all correspondence to: MIT Sloan School, 100 Main Street E62-618, Cambridge, MA 02142–1347, (617) 253–0920 (voice), `alo-admin@mit.edu` (email).

[§] Research Affiliate, MIT Laboratory for Financial Engineering, Cambridge, MA, USA, `zhangruixun@gmail.com` (email).

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1 Introduction

Rationality is the key assumption behind standard economic models of human behavior. The idea that individuals maximize their own self-interest subject to resource constraints has led to numerous breakthroughs, including expected utility theory (von Neumann and Morgenstern, 1944), game theory (von Neumann and Morgenstern, 1944; Nash, 1950), rational expectations (Lucas Jr, 1972), the efficient markets hypothesis (Samuelson, 1965; Fama, 1970), and the option pricing theory (Black and Scholes, 1973; Merton, 1973). The influence of this paradigm goes far beyond academia — it underlies current macroeconomic and monetary policies, and has also become an integral part of the rules and regulations that govern financial markets today (Kocherlakota, 2010; Hu, 2012).

On the other hand, psychologists and economists have documented many violations of rational models in human behavior, often referred to as "cognitive biases". These systematic deviations from rational behaviors are hard to reconcile with the standard economic models, and are therefore considered irrational behaviors. Representatives of these cognitive biases include probability matching (Grant, Hake, and Hornseth, 1951; Herrnstein, 1961) (the tendency to choose randomly between heads and tails when asked to guess the outcomes of a series of independent biased-coin tosses, where the randomization matches the probability of the biased coin), loss aversion (Tversky and Kahneman, 1974; Tom, Fox, Trepel, and Poldrack, 2007) (the tendency to take greater risk when choosing between two potential losses, and less risk when choosing between two potential gains), uncertainty effect (Gneezy, List, and Wu, 2006) (a risky prospect is valued less than its worst possible outcome), and confirmation bias (Mahoney, 1977) (the tendency to search for or interpret information in a way that confirms one's preconceptions). Such anomalous behaviors have also been observed in many non-human subjects ranging from bacteria to primates (Harder and Real, 1987; Pasteels, Deneubourg, and Goss, 1987; Kirman, 1993; Smallwood, 1996; Chen, Lakshminarayanan, and Santos, 2006; Ben-Jacob, 2008; Santos and Chen, 2009), which suggests that they may have a common and ancient origin, and an evolutionary role that belies their apparent shortcomings.

The debate between rational models of behavior and their systematic deviations has attracted an enormous amount of research in economics, psychology, and evolutionary biology (Becker, 1962; Stanovich and West, 2000; Rabin and Thaler, 2001; McKenzie, 2003; Burnham, 2013; Gneezy and

List, 2013). For instance, bounded rationality (Simon, 1955) and prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) provide alternative perspectives for understanding human behavior beyond the maximization of expected utility. At the same time, numerous empirical studies are devoted to understanding the relationship between individual rationality and decision-making in the real world (Hsu, Bhatt, Adolphs, Tranel, and Camerer, 2005; Camerer and Fehr, 2006; Gneezy and List, 2006; Apicella, Dreber, Campbell, Gray, Hoffman, and Little, 2008; Dreber, Apicella, Eisenberg, Garcia, Zamore, Lum, and Campbell, 2009; Chen and Chen, 2011; Bednar, Chen, Liu, and Page, 2012; Fershtman, Gneezy, and List, 2012; Gneezy and Imas, 2014).

Evolutionary principles have been adopted by economists and psychologists to explain these counterintuitive behaviors (Cooper and Kaplan, 1982; McDermott, Fowler, and Smirnov, 2008; Kenrick, Griskevicius, Sundie, Li, Li, and Neuberg, 2009; Brennan and Lo, 2011; Brennan and Lo, 2012), as well as altruism and sociobiology (Alexander, 1974; Becker, 1976; Hirshleifer, 1977; Almenberg and Dreber, 2013; Zhang, Brennan, and Lo, 2014a), the biological origin of utility functions and time preference (Campbell, 1986; Rogers, 1994; Waldman, 1994; Robson, 1996a; Samuelson, 2001; Zhang, Brennan, and Lo, 2014b), and the dynamics of financial markets (Blume and Easley, 1992; Luo, 1995; Lo, 2004; Kogan, Ross, Wang, and Westerfield, 2006; Hirshleifer and Teoh, 2009). In particular, irrational behavior—as opposed to utility-maximizing behavior—has been found useful and persistent in a variety of environments in evolution (Belavkin, 2006; Houston, McNamara, and Steer, 2007; Waksberg, Smith, and Burd, 2009; Ross and Wilke, 2011; Okasha and Binmore, 2012). However, it is unclear how these behaviors relate to standard economic theories of individual rationality, and why they emerge in some instances and not others.

On the other hand, evolutionary biologists have studied the role of stochastic environments (Ishii, H., Iwasa, and Sasaki, 1989; Kussell and Leibler, 2005; Acar, Mettetal, and van Oudenaarden, 2008; Gaal, Pitchford, and Wood, 2010; Frank, 2011) and mutation in evolution (King, 1972; Taddei, Radman, Maynard-Smith, Toupance, Gouyon, and Godelle, 1997; Drake, Charlesworth, Charlesworth, and Crow, 1998). Several quantitative models have been developed to understand the magnitude of mutation rates (Kimura, 1960; Levins, 1967; Leigh Jr., 1970; Gillespie, 1981; Travis and Travis, 2002; Desai and Fisher, 2011; Liberman, Van Cleve, and Feldman, 2011). While some of our results will be familiar to evolutionary biologists, they do not appear to be widely known in a economic context. For completeness, we derive them from first principles and provide the link between mutation and rationality.

In this article, we reconcile the rationality debate by proposing an evolutionary explanation for irrational behavior. The rational behavior is a function of the particular environment, and different environments lead to different rational behaviors in evolution. As a result, irrational behaviors not only persist in evolution, but are also necessary for robust growth of population in stochastic environments. Furthermore, we show that there is an optimal degree of irrationality in the entire population depending on the degree of environmental stochasticity. This is a novel implication of natural selection that has not appeared in prior studies of human or animal rationality.

In contrast to game theory, the model considered in this article does not require any strategic interactions, and individual decision-making is deliberately mindless, allowing us to determine the most primitive and fundamental links between stochastic environments and adaptive behavior. Even in such a simple setting, we find a range of randomized behaviors—including behaviors that do not always conform to common economic intuition about rationality—can arise and persist via natural selection. Simon (1981) illustrated this principle vividly with the example of a single ant traversing a mixed terrain of sand, rocks, and grass. The ant's path seems highly complex, but the complexity is due more to the environment than the ant's navigational algorithm.

Much of the rationality debate among economists and psychologists focuses on whether the rational models can help people make better inferences and decisions in the real world (McKenzie, 2003). Instead, our framework provides an evolutionary explanation of seemingly irrational behaviors and different degrees of irrationality in the population. The results have widespread implications for science, management, and public policy. For example, our framework has a different explanation for the entry of new firms and technologies in an industry, a well-studied phenomenon in industrial economics (Klepper and Graddy, 1990; Audretsch and Mahmood, 1994; Geroski, 1995; Mata, Portugal, and Guimaraes, 1995; Campbell, 1998). Even if new entrants appear to be suboptimal with respect to their current context, they facilitate more robust growth of the entire industry in the face of a stochastically shifting environment. Furthermore, our results yield the optimal amount of entrants as a function of environmental stability.

Our model consists of an initial population of individuals, each assigned a purely arbitrary behavior with respect to a binary choice problem. Assuming that offspring have behaviors identical to their parents, only those behaviors linked to reproductive success will survive. The key is the interaction between individual behavior and the stochastic environment in which reproductive success is determined. On the other hand, by assuming that a small fraction of offspring have behaviors different from their parents, irrational behavior emerges as a result of mutation. Mutation provides diversity of behaviors in the entire population, and therefore, the important link between rational and irrational behaviors. Over time, only a certain degree of mutation and irrationality in the population will persist in the limit.

By studying the impact of selection on behavior rather than on genes, we are able to derive evolutionary implications that cut across species, physiology, and genetic origins. In the same way that different magnifications of a microscope reveal different details of a specimen, applying evolutionary principles to behavioral variations leads to different insights that may be more relevant for economics, psychology, and behavioral ecology. Our focus on behavior as the object of selection is a different lens through which the effects of evolution may be studied.

In the remainder of this article, we first describe the binary choice model with mutation. Then we show that mutation and irrational behaviors are essential in evolution. Furthermore, the degree of irrationality is determined by evolution to match the degree of environmental stochasticity. We conclude with a brief discussion and provide additional technical details and proofs in the Supporting Information.

2 Binary Choice Model with Mutation

We begin with the binary choice model (Brennan and Lo, 2011). Consider a population of individuals that live for one period, produce a random number of offspring asexually, and then die. During their lives, individuals make only one decision: they choose from two actions a and b, and this results in one of two corresponding random numbers of offspring x_a and x_b, described by some well-behaved probability distribution function $\Phi(x_a, x_b)$. We assume that x_a and x_b are not perfectly correlated, and

Assumption 1. *x_a and x_b are bounded non-negative random variables, and $\mathbb{P}(x_a = x_b = 0) = 0$.*

Assumption 2. *(x_a, x_b) is IID over time and identical for all individuals in a given generation.*

Note that Assumption 1 simply rules out the degenerate case that no offspring is produced at all. Now suppose that each individual chooses a with some probability $f \in [0,1]$ and b with probability $1-f$, denoted by the Bernoulli variable I^f, hence the offspring of an individual is given by:

$$x^f = I^f x_a + (1 - I^f) x_b, \;\; I^f = \begin{cases} 1 & \text{with prob } f \\ 0 & \text{with prob } 1-f. \end{cases}$$

We shall henceforth refer to f as the individual's behavior since it completely determines how the individual chooses between a and b. Assume for the moment that there is no mutation, so that offspring from a type f individual are still of type f. The following proposition (Brennan and Lo, 2011) summarizes the population dynamics of the binary choice model without mutation.

Proposition 1. *Under Assumptions 1-2, suppose that the total number of type f individuals in generation T is n_T^f. As both the number of generations and the number of individuals in each generation increases without bound, $T^{-1} \log n_T^f$ converges almost surely to the log-geometric-average growth rate*

$$\mu(f) = \mathbb{E}\left[\log\left(f x_a + (1-f) x_b\right)\right]. \tag{1}$$

Furthermore, the growth-optimal behavior f^* is given by:

$$f^* = \begin{cases} 1 & \textit{if } \mathbb{E}\left[x_a/x_b\right] > 1 \textit{ and } \mathbb{E}\left[x_b/x_a\right] < 1 \\ \textit{solution to (3)} & \textit{if } \mathbb{E}\left[x_a/x_b\right] \geq 1 \textit{ and } \mathbb{E}\left[x_b/x_a\right] \geq 1 \\ 0 & \textit{if } \mathbb{E}\left[x_a/x_b\right] < 1 \textit{ and } \mathbb{E}\left[x_b/x_a\right] > 1 \end{cases} \tag{2}$$

where f^* is defined implicitly in the second case of (2) by

$$\mathbb{E}\left[\frac{x_a}{f^* x_a + (1-f^*) x_b}\right] = \mathbb{E}\left[\frac{x_b}{f^* x_a + (1-f^*) x_b}\right], \tag{3}$$

and the expectations in (1)-(3) are with respect to $\Phi(x_a, x_b)$.

The growth-optimal behavior f^* is a function of the particular environment $\Phi(x_a, x_b)$. The role of Φ is critical in our framework, as it represents the entirety of the implications of an individual's actions for reproductive success. Embedded in Φ is the biological machinery that is fundamental to evolution, i.e., genetics. However, this machinery is of less interest to economists than the link between behavior and reproductive success, which is summarized compactly by Φ. The specification of Φ also captures the fundamental distinction between traditional models of population genetics (Levins, 1968; Wilson and Bossert, 1971; Dawkins, 1976) and more recent applications of evolution to behavior (Hamilton, 1964; Trivers, 1971; Wilson, 1975; Maynard Smith, 1982); the former focuses on the natural selection of traits (determined by genetics), whereas the latter focuses on the natural selection of behavior. Although behavior is obviously linked to genetics, the specific genes involved, their loci, and the mechanisms by which they are transmitted from one generation to the next are of less relevance to economic analysis than the ultimate implications of behavior for reproduction, i.e., Φ. In the jargon of econometrics, Φ may be viewed as a "reduced form" representation of an individual's biology.

This simple and general model generates a remarkably rich set of behaviors. For example, the three possible behaviors in (2) reflect the relative reproductive success of the two choices and is a generalization of the "adaptive coin-flipping" strategies of Cooper and Kaplan (Cooper and Kaplan, 1982). The behavior f^* that emerges through the forces of natural selection is quite distinct from the neoclassical economic framework of expected utility in one important respect: expected utility theory implies deterministic behavior. Furthermore, intelligence has a natural definition in our framework—any type of behavior that is positively correlated with reproductive success—and bounds on the level of intelligence arise organically from physiological and environmental constraints on this correlation (Brennan and Lo, 2012). By considering different sources of randomness in reproductive success, risk aversion can be derived in this framework as a consequence of systematic reproductive risks (Zhang, Brennan, and Lo, 2014b). Proposition 1 may also be interpreted as a primitive form of group selection, in which natural selection appears to operate at the group level instead of, or in addition to, the level of individuals, traits, or genes (Zhang, Brennan, and Lo, 2014a).

2.1 Mutation: a link between optimal and sub-optimal behavior

Now we add mutation to the binary choice model to provide a link between optimal and sub-optimal behaviors in evolution. In general, mutation implies that the offspring of type-f individuals are not necessarily of type-f, but assume a probability distribution over all possible types. We consider a simple form of mutation, namely that an offspring of type-f mutates equally likely to all types.

To be more specific, consider a discrete type space. Let f takes value in a finite set $\{f_1, f_2, \cdots, f_{K+1}\}$ (for example, $\{0, \frac{1}{K}, \frac{2}{K}, \ldots, \frac{K-1}{K}, 1\}$) where K is a positive integer. The world has $K+1$ types in total. In addition to Assumptions 1-2, we further assume that:

Assumption 3. *Each type f individual mutates with a small probability $\epsilon > 0$ to type $g \neq f$. Once it mutates, it mutates with equal probability $\frac{\epsilon}{K}$ to any type $g \in \{f_1, f_2, \cdots, f_{K+1}\} \setminus \{f\}$.*

Note that Assumption 3 is a simple and special form of mutation. From the behavioral point of view, it is general enough to capture the most important characteristics of mutation, which is to provide the link between different behaviors. With this particular structure, we are able to parametrize the degree of mutation with a single parameter ϵ.

We would like to emphasize that each individual lives for only one period in our model, and therefore its mutant offspring may be viewed as "new entrants" in the next generation's population because they represent different behaviors than their predecessors. Also, there is no intelligence or volition ascribed to the behavior f; we are simply providing a formal representation for it, and then investigating its evolutionary implications. To that end, individuals choosing between a and b according to the same f may be viewed as consisting of the same "type", where types are indexed by f and range continuously from 0 to 1, including the endpoints. In this manner, we are able to study the evolutionary dynamics of each type of individual over many generations.

Once mutation is introduced into the population, it is no longer possible to analyze the population dynamics of each type f separately. The entire system is a multi-type branching process in random environments (Smith and Wilkinson, 1969; Tanny, 1981). Let $\mathbf{n}_t = \left(n_t^{f_1}, \cdots, n_t^{f_{K+1}}\right)'$ be the column vector of number of individuals of all $K+1$ types in generation t. The following proposition describes the population dynamics between two generations.

Proposition 2. *Under Assumptions 1-3, as n_{t-1}^{g} increases without bound for all $g \in \{f_1, f_2, \cdots, f_{K+1}\}$,*

$\mathbf{n}_t$ *can be written as:*

$$\mathbf{n}_t = \mathbf{A}_t \cdot \mathbf{n}_{t-1} \quad a.s. \tag{4}$$

where $\mathbf{A}_t := \mathbf{M} \cdot \mathbf{F}_t$. *Here* $\mathbf{M}$ *is a constant mutation matrix:*

$$\mathbf{M} = \begin{pmatrix} 1-\epsilon & \frac{\epsilon}{K} & \cdots & \frac{\epsilon}{K} \\ \frac{\epsilon}{K} & 1-\epsilon & \cdots & \frac{\epsilon}{K} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\epsilon}{K} & \frac{\epsilon}{K} & \cdots & 1-\epsilon \end{pmatrix},$$

and $\mathbf{F}_t$ *is a stochastic fecundity matrix:*

$$\mathbf{F}_t = \begin{pmatrix} f_1 x_{a,t} + (1-f_1)x_{b,t} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & f_{K+1}x_{a,t} + (1-f_{K+1})x_{b,t} \end{pmatrix},$$

with $0 = f_1 < f_2 < \cdots < f_{K+1} = 1$.

Equation (4) gives the fundamental relationship between individuals in two consecutive generations. With probability 1, $\mathbf{n}_t$ can be written as the product of two matrices and $\mathbf{n}_{t-1}$. $\mathbf{F}_t$ represents the reproducibility of different types of individuals, and $\mathbf{M}$ represents a re-distribution of types because of mutation. Then the natural question is: how does $\mathbf{n}_t$ behave in the limit? We summarize the asymptotic behavior of population with mutation in the following proposition.

Proposition 3 (Growth rate)**.** *Under Assumptions 1-3, there exists a number* μ_ϵ *such that:*

$$\mu_\epsilon = \lim_{T\to\infty} \frac{1}{T} \log \mathbf{c}'\mathbf{n}_T = \lim_{T\to\infty} \frac{1}{T} \log ||\mathbf{A}_t\mathbf{A}_{t-1}\cdots\mathbf{A}_1||$$

almost surely, where $||\cdot||$ *is any matrix norm,* $\mathbf{c}$ *is any vector of bounded non-negative numbers* ($\mathbf{c} \neq \mathbf{0}$)*.*

In particular, when $\mathbf{c}$ is a vector of 1's, we get the growth rate of total population; when $\mathbf{c} = \mathbf{e}_i$ (the vector with i-th coordinate equals to 1 and 0 otherwise), we get the growth rate of the i-th type individuals. A direct corollary is that all types of behaviors grow at the same exponential rate μ_ϵ.

This is an important difference of population with mutation compared to non-mutation populations. To understand this fact, suppose a long time has elapsed, because the positive mutation rate is fixed, any behavior that is not favored by the current environment still gets a fixed proportion of the offspring from the behavior that grows the fastest. Therefore the ratio of the individuals of any two behaviors can be lower bounded by some positive constant, and no single behavior can grow exponentially faster than any other behaviors. Note that μ_ϵ is called the *maximum Liapunov characteristic exponent* of matrix $\mathbf{A}_t$ in the probability literature, and Corollary 1 in the next section gives an estimate of μ_ϵ.

Another difference between the mutation and non-mutation population is the asymptotic ratio between different types of population. Without mutation, $\mu(f)$ is different for different f, and therefore the ratio $n_T^f/n_T^{f^*}$ converges to 0 for any $f \neq f^*$ (see Proposition 1). However, μ_ϵ is the same with mutation for all types f, and the ratio $n_T^{f_1}/n_T^{f_2}$ is typically stochastic even in the long run as T increases without bound. Fortunately, we have ergodic theorems to characterize the asymptotic behavior of this ratio.

2.2 Asymptotic population dynamics

Under Assumptions 1-3, let $P_t = \mathbf{1}'\mathbf{n}_t$ be the total population size at time t and

$$\mathbf{y}_t := \frac{\mathbf{n}_t}{P_t} = \left(\frac{n_T^{f_1}}{\sum_g n_T^g}, \cdots, \frac{n_T^{f_{K+1}}}{\sum_g n_T^g} \right)' \tag{5}$$

be the normalized population vector in generation t. Because of the dynamics between two consecutive generations (4), $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is a vector-valued Markov process, with a compact state space:

$$\mathscr{Y} := \left\{ \mathbf{y} = (y_1, \cdots, y_{K+1})' \middle| \mathbf{y} \geq 0, \sum_{i=1}^{K+1} y_i = 1 \right\}.$$

The 1-step transition probability for $\mathbf{y} \in \mathscr{Y}$ and $B \subseteq \mathscr{Y}$ is:

$$p_1(\mathbf{y}, B) := \mathbb{P}_\Phi \left(\frac{\mathbf{A}\mathbf{y}}{||\mathbf{A}\mathbf{y}||} \in B \right). \tag{6}$$

Without mutation, because different behaviors grow at different exponential rates, $\mathbf{y}_t$ converges almost surely to a basis vector $\mathbf{e}_i = (0, \cdots, 1, \cdots, 0)$ as $T \to \infty$. In the case of positive mutation rates, similar result exists only for non-random matrices $\mathbf{F}_t$ in (4), in which case the long run proportion vector converges to the eigenvector of $\mathbf{F}_t$ (see models in Robson (Robson, 1996a) and Gaal et al (Gaal, Pitchford, and Wood, 2010) for example). In the case of positive mutation rates when $\mathbf{F}_t$ are random matrices, environmental uncertainty implies that $\mathbf{y}_t$ is typically stochastic even in the long run (see simulation results in the Appendix). However, we have the following ergodic theorem (Tuljapurkar, 1990) to characterize the asymptotic behavior of $\mathbf{y}_t$:

Proposition 4 (Stochastic ergodic theorem)**.** *Under Assumptions 1-3, let $\mathscr{L}_t(\cdot)$ be the distribution of $\mathbf{y}_t$, then $\mathscr{L}_t(\cdot)$ converges to a stationary distribution $\mathscr{L}(\cdot)$ pointwisely as T increases without bound:*

$$\lim_{T \to \infty} \mathscr{L}_T = \mathscr{L}.$$

Proposition 4 asserts that the proportion vector $\mathbf{y}_t$ converges weakly as $T \to \infty$. In addition, by basic properties of Markov chains, the stationary distribution $\mathscr{L}$ satisfies the following equation:

$$\mathscr{L}(B) = \int_{\mathscr{Y}} p_1(\mathbf{y}, B)\mathscr{L}(d\mathbf{y})$$

for any $B \subseteq \mathscr{Y}$. An important application of Proposition 4 is that it provides a formula to estimate the exponential growth rate μ_ϵ. Note that the total population size

$$P_t = \mathbf{1}'\mathbf{n}_t = \mathbf{1}'\mathbf{M}\mathbf{F}_t\mathbf{n}_{t-1} = \mathbf{1}'\mathbf{F}_t\mathbf{n}_{t-1} = P_{t-1}\mathbf{1}'\mathbf{F}_t\mathbf{y}_{t-1},$$

so the log-geometric-average growth rate μ_ϵ can be expressed as:

$$\mu_\epsilon = \mathbb{E}\left[\log(\mathbf{1}'\mathbf{F}_t\mathbf{y}_{t-1})\right] \tag{7}$$

where the expectation is taken over the joint stationary distribution of $(\mathbf{F}_t, \mathbf{y}_{t-1})$.

Corollary 1 (Bounds of growth rate)**.** *Let f^* be the optimal behavior without mutation (see Proposition 1). Under Assumptions 1-3, if the type space is dense enough such that $f^* \in \{f_1, f_2, \cdots, f_{K+1}\}$, then:*

$$\mu(f^*) - |\log(1-\epsilon)| \leq \mu_\epsilon \leq \mu(f^*). \tag{8}$$

Corollary 1 asserts that the growth rate μ_ϵ is slightly less than the optimal growth rate of population without mutation. Note that this is different from the mutation modeled in Robson (Robson, 1996a), where population growth could be increased by randomizing between different types of individuals to create a new "behavior". We will identify the case where mutation does speed up growth in non-stationary environments in the next section.

The Appendix gives additional results for population dynamics with mutation. In particular, we give the asymptotic distribution of total population size P_t, the rate of convergence for the limit distribution $\mathscr{L}(\cdot)$, and the optimal behavior with mutation in the probabilistic sense.

2.3 Extinction probability

When the population is extinct in evolution, the stochastic processes $\mathbf{n}_t$ and $\mathbf{y}_t$ become degenerate. Therefore, all results so far are implicitly conditional on non-extinction sample paths. However, extinction is important in evolution, and particularly of interest with mutation. In this section, we investigate the extinction probability of different behaviors f in different environments $\Phi(x_a, x_b)$.

Consider a specific behavior $f \in \{f_1, f_2, \cdots, f_{K+1}\}$ starting with an initial population $n_0^f > 0$, we define that the type f is *extinct* if $n_T^f = 0$ for some $T > 0$, and *surviving* otherwise. There are two scenarios in terms of extinction when the number of generation T increases without bound:

(i) $\lim_{T\to\infty} \mathbb{P}\left(n_T^f > 0\right) = 0$: the population is extinct with probability 1;

(ii) $\lim_{T\to\infty} \mathbb{P}\left(n_T^f > 0\right) > 0$: the population survives with positive probability.

Note that in case (ii), if $\lim_{T\to\infty} \mathbb{P}\left(n_T^f > 0\right) < 1$, then the extinction probability depends on the initial population n_0. However, when n_0 is relatively large, the survival probability is close to 1. To be more specific, we define that the type f is *immortal* if the extinction probability is strictly less than 1 as $T \to \infty$, and the extinction probability goes to 0 as the initial number of individuals n_0 increases without bound. Mathematically, A type f is immortal if $\mathbb{P}(n_T^f = 0) < 1$ as $T \to \infty$, and $\mathbb{P}(n_T^f = 0) \to 0$ as $T \to \infty$ and $n_0 \to \infty$.

For an immortal population, case (ii) can be essentially treated as almost sure survival with a large initial population. Proposition 1-4 are implicitly conditional on non-extinction sample paths. The probability of non-extinction in these results is close to 1 for a large initial population, because immortality is a common feature for non-degenerate populations, as we will see in:

Proposition 5 (Immortality with mutation)**.** *Suppose that the number of initial population of any behavior* $f \in \{f_1, f_2, \cdots, f_{K+1}\}$ *is* n_0*,*

(i) Consider the model without mutation. Under Assumptions 1-2, any behavior f *with* $\mu(f) < 0$ *is extinct with probability 1, and any behavior* f *with* $\mu(f) > 0$ *is immortal.*

(ii) Consider the model with mutation rate $\epsilon > 0$*. Under Assumptions 1-3, all behaviors* $f \in \{f_1, f_2, \ldots, f_{K+1}\}$ *are immortal if* μ_ϵ *in Proposition 3 is positive. In particular, if there exists a behavior* $f \in \{f_1, f_2, \cdots, f_{K+1}\}$ *such that* $\mu(f) > |\log(1-\epsilon)|$ *without mutation, then all behaviors are immortal.*

Proposition 5 asserts that positive mutation rates make all behaviors in the population immortal, and help preserve all behaviors even if some of them are inferior in the current environment. In other words, mutation provides robustness to evolution by avoiding extinction.

So far we have considered stationary environments generating IID fecundities across time. In this case, mutation does not help increase the speed of population growth (Corollary 1). This brings us to the next topic, where non-stationary environments are considered and mutation can indeed speed up growth.

3 Results: Optimal Degree of Irrationality

The binary choice model with mutation provides a framework of evolution of behaviors. Given a particular environment $\Phi(x_a, x_b)$, we define *rational behavior* as the evolutionarily optimal behavior f^* that achieves the maximum log-geometric-average growth rate. We would like to emphasize that the rational behavior depends on the particular environment, and therefore rational behaviors might change over time because the environment $\Phi(x_a, x_b)$ could change. In contrast to the rational behavior f^*, all the other sub-optimal behaviors with slower growth rates are *irrational.*

Mutation provides the link between rational and irrational behaviors. Positive mutation rates and irrational behaviors are necessary because environmental shocks could happen unexpectedly. In this sense, a population with irrational behaviors is favored in order to maintain robust growth under possible environmental shocks. We further elaborate this idea by considering a simple example with one-time environmental change.

Following the binary choice model with mutation, suppose that the fecundity is specified by the joint distribution $\Phi^1(x_a, x_b)$ before generation T^1, and after generation T^1 the environment suddenly changes and the distribution becomes $\Phi^2(x_a, x_b)$. To be more precise, let $\Phi_t(x_a, x_b)$ be the joint distribution of (x_a, x_b) in generation t, and

$$\Phi_t(x_a, x_b) = \begin{cases} \Phi^1(x_a, x_b) & \text{if } t = 1, 2, \cdots, T^1 \\ \Phi^2(x_a, x_b) & \text{if } t = T^1 + 1, T^1 + 2, \cdots . \end{cases}$$

Denote by $\mu^1(\cdot)$ and $\mu^2(\cdot)$ the log-geometric-average growth rate without mutation for Φ^1 and Φ^2 respectively. Furthermore, denote by f_1^* and f_2^* the optimal behavior under Φ^1 and Φ^2 respectively. Suppose that the optimal behavior in a given environment is extinct almost surely in the other. More specifically,

$$\mu^1(f_1^*) > |\log(1-\epsilon)|, \quad \mu^1(f_2^*) < 0; \quad \mu^2(f_2^*) > |\log(1-\epsilon)|, \quad \mu^2(f_1^*) < 0$$

for some fixed mutation rate $\epsilon > 0$.

Without mutation, f_2^* is extinct with probability 1 as the number of generations before the shock T^1 increases without bound. After the shock, the long-term optimal behavior and optimal growth rate are therefore given by $\max_{\{f|\mu^1(f)>0\}} \mu^2(f)$.

On the other hand, with mutation rate $\epsilon > 0$, as a direct corollary of Proposition 5 and Corollary 1, all behaviors are immortal under both Φ^1 and Φ^2. The long-term optimal behavior is f_2^*, and optimal growth rate is at least $\mu^2(f_2^*) - |\log(1-\epsilon)|$, which is greater than the optimal growth rate without mutation as long as the mutation rate ϵ is sufficiently small.

In this simple example, irrational behaviors and positive mutation rates are seemingly inefficient because they slow down the growth rate of the individually rational behavior. However, as long as the environment $\Phi(x_a, x_b)$ and rational behavior f^* change, it is the irrational behaviors that provide a variety of diversified possibilities in the population, so that new rational behaviors can emerge and thrive. In other words, certain behaviors that are growth-optimal under Φ^2 might become extinct under Φ^1 in the absence of mutation. Mutation ensures a constant flow of new entrants into the population each generation; hence when the regime shifts to Φ^2, these new entrants reproduce more quickly than others, and f_2^* emerges as the new dominant behavior. As a result, the very notion of "optimality" is ill-defined in isolation, and must be interpreted with respect to a given environment. This is consistent with Simon's notion of bounded rationality (Simon, 1955). Note that the individuals are mindless and need not know whether they are behaving optimally or not—natural selection is sufficient for determining what is optimal for a given environment.

3.1 Regime-switching environments

As a generalization of the example of one-time environmental change, a more realistic world has multiple environmental changes and possibly cycles. In this case, not only the irrational behaviors are necessary in terms of providing robustness, but also the degree of irrationality in the population is determined by how often the environment changes. In other words, the degree of mutation is selected by the nature, and there is an optimal degree of irrationality in the entire population. We formalize this idea by considering the following regime-switching environments.

Suppose that the nature switches randomly between two regimes, in which the fecundities are specified by $\Phi^1(x_a, x_b)$ and $\Phi^2(x_a, x_b)$ respectively. The lengths of regime 1 and regime 2 are positive integer random variables T^1 and T^2 specified by some well-behaved probability distribution function $F(T^1, T^2)$. The nature draws IID samples from $F(T^1, T^2)$ to generate lengths of consecutive regimes $T_1^1, T_1^2, T_2^1, T_2^2, \cdots$. Note that the superscript denotes the regime number and the subscript indicates the number of cycle, where a cycle is defined as the two consecutive changes of regime:

$$0 \xrightarrow{\Phi^1} T_1^1 \xrightarrow{\Phi^2} T_1^2 \xrightarrow{\Phi^1} T_2^1 \xrightarrow{\Phi^2} T_2^2 \cdots .$$

We would like to emphasize that the environment within each regime is still stochastic, this is an important distinction to the existing literature where the environment is usually assumed to be approximately constant between changes or within a period (Ishii, H., Iwasa, and Sasaki, 1989; Acar, Mettetal, and van Oudenaarden, 2008; Kussell and Leibler, 2005; Gaal, Pitchford, and Wood, 2010). For general $\Phi^1(x_a, x_b)$ and $\Phi^2(x_a, x_b)$, the exact population dynamics is hardly computable after a few regime switches. However, a simple example suffices to illustrate the optimal degree of irrationality in the population.

3.2 An example of two behaviors

For simplicity, we consider a world with only two behaviors $f \in \{0, 1\}$. Suppose that the fecundities in the two regimes are given by $\Phi^1(x_a, x_b)$ and $\Phi^2(x_a, x_b)$ that satisfy the following condition:

$$\mathbb{P}_{\Phi^1}(x_b = 0) = \mathbb{P}_{\Phi^2}(x_a = 0) = 1.$$

That is, one choice in each regime results in no offspring for sure. Note that in regime 1, x_a is still a random variable; in regime 2, x_b is still a random variable. In this world, during regime 1, only action a generates positive offspring; during regime 2, only action b generates positive offspring. Therefore, both behaviors die out without mutation after a few regime switches.

A positive mutation rate ϵ helps preserve the irrational behaviors in the current environment to prepare for possible environmental shocks, at the cost of slowing down the growth of the rational behavior. In other words, a positive mutation rate implies that there is always a fixed positive fraction of new entrants into the population in each generation, even if their behavior may be suboptimal with respect to the current environment.

Proposition 6. *With a positive mutation rate* $\epsilon > 0$*, let* $n_k^{\epsilon, Total}$ *be the total number of individuals in the entire population at the end of k-th cycle. Under Assumptions 1-3 and the regime-switching model described above where the fecundities* $\Phi^1(x_a, x_b)$ *and* $\Phi^2(x_a, x_b)$ *satisfy*

$$\mathbb{P}_{\Phi^1}(x_b = 0) = \mathbb{P}_{\Phi^2}(x_a = 0) = 1,$$

as k *increases without bound,* $k^{-1} \log n_k^{\epsilon, Total}$ *converges almost surely to*

$$\pi(\epsilon) = 2 \log \frac{\epsilon}{1-\epsilon} + \mathbb{E}[T^1 + T^2] \log(1-\epsilon) + \mathbb{E}[T^1]\mathbb{E}_{\Phi^1}[\log x_a] + \mathbb{E}[T^2]\mathbb{E}_{\Phi^2}[\log x_b] \tag{9}$$

for $0 < \epsilon < 1$*. The growth optimal mutation rate* ϵ^* *that maximizes (9) is*

$$\epsilon^* = \frac{2}{\mathbb{E}[T^1 + T^2]}.$$

As a special case of Proposition 6, we have the following result when the lengths of each regime are all IID.

Corollary 2. *Under the assumptions of Proposition 6, if in addition the lengths of both regime 1 and regime 2 are drawn IID from a single distribution $F(T)$, then the growth optimal behavior that maximizes (9) is*

$$\epsilon^* = \frac{1}{\mathbb{E}[T]}.$$

By Proposition 6 and Corollary 2, the optimal mutation rate is simply the reciprocal of the expected length of a regime. In the long run, the more stable the environment is, the less irrational behaviors are present in the population; the more frequently environmental changes happen, the more irrational behaviors prevail in the population. The mutation rate and the amount of irrational behaviors are not exogenous variables given by the nature. They are not only necessary, but also important quantities that are selected by the nature in evolution to match the degree of environmental instability. In this sense, natural selection shapes the degree of irrationality in the population.

This also implies that the optimal amount of new entrants into the population is determined by the degree of environmental stability. For example, one would expect relatively small amount of new entrants in areas with relatively stable market conditions, such as the automobile industry; and relatively high turnover rates in areas with relatively volatile market conditions such as the hedge fund industry.

3.3 Generalization and simulation experiments

The implications from the above two-behavior example with a special fecundity structure can be generalized to any number of types and any fecundity structures. We use simulation to demonstrate the generality of the optimal degree of mutation and irrationality. In this section, we consider eight different pairs of environments and different lengths of regimes. We calculate the optimal degree of mutation for each of them.

In the following experiments, the lengths of regimes T^1 and T^2 are independent random variables with expectation $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$ respectively, ranging from 10 to 37. For a given expectation $\mathbb{E}[T^1]$, T^1 is uniformly distributed in the interval $\left[0.8 \times \mathbb{E}[T^1], 1.2 \times \mathbb{E}[T^1]\right]$, rounding to the nearest integer. T^2 is distributed in the same way.

For a given pair of $(\mathbb{E}[T^1], \mathbb{E}[T^2])$, 11 types of behavior from $\{0, \frac{1}{10}, \frac{2}{10}, \cdots, 1\}$ starting with one individual each evolve for 700 to 1000 generations. The optimal degree of mutation in each pair of environment is calculated by taking the average over 200 to 500 simulation paths.

Table 1 gives eight different environmental conditions, for which we plot the optimal degree of mutation and the optimal log-geometric-average growth rate as a function of $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$ in Fig. 1. In these figures, the colored plane with colorbar shows the optimal mutation rates; the transparent surface of which the height is indicated by the z-axis shows the optimal log-geometric-average growth rate associated with that optimal mutation rate.

Table 1: Probability table for the simulation of optimal mutation rates: environment 1-8

(a) Environment 1

	Regime 1			Regime 2		
Prob.	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$
x_a	3	2	1	0	0	0
x_b	0	0	0	3	2	1

(b) Environment 2

	Regime 1			Regime 2		
Prob.	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$
x_a	3	2	1	1	1	1
x_b	1	1	1	3	2	1

(c) Environment 3

	Regime 1		Regime 2	
Prob.	0.8	0.2	0.8	0.2
x_a	3	0	0	3
x_b	0	3	3	0

(d) Environment 4

	Regime 1		Regime 2	
Prob.	0.8	0.2	0.8	0.2
x_a	3	1	1	3
x_b	1	3	3	1

(e) Environment 5

	Regime 1		Regime 2	
Prob.	0.8	0.2	0.8	0.2
x_a	3	0	1	3
x_b	0	3	3	1

(f) Environment 6

	Regime 1		Regime 2		
Prob.	0.8	0.2	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$
x_a	3	1	1	1	0
x_b	1	3	3	2	1

(g) Environment 7

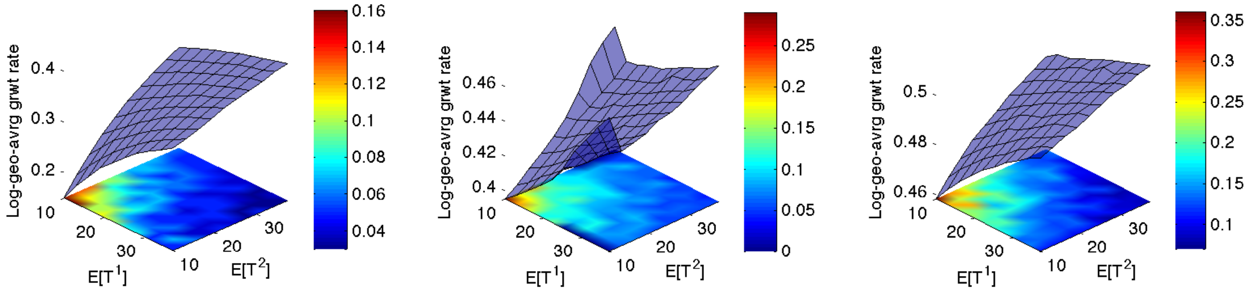
	Regime 1		Regime 2	
Prob.	0.8	0.2	0.8	0.2
x_a	3	0	3	1
x_b	0	3	1	3

(h) Environment 8

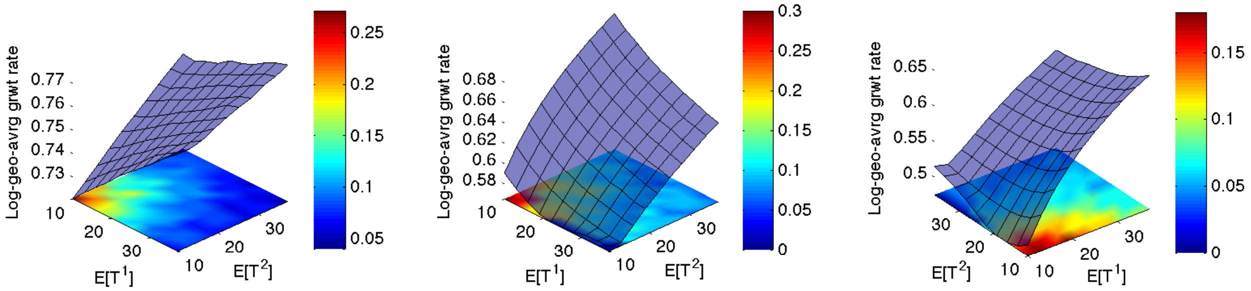
	Regime 1		Regime 2		
Prob.	0.8	0.2	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$
x_a	3	1	3	2	1
x_b	1	3	1	1	0

Symmetric regimes. Environment 1 assumes that one of the actions in each regime leads to no offspring. Results are consistent with the example of two behaviors: the optimal degree of mutation is inversely proportional to $\mathbb{E}[T^1] + \mathbb{E}[T^2]$. However, the growth rate is proportional to $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$: the longer the length of a regime is, the faster the population grows.

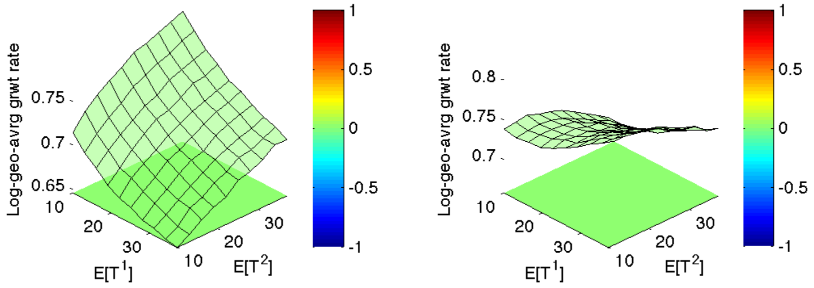
Environment 2 considers the case where both action a and b produce positive number of off-



(a) environment 1 (b) environment 2 (c) environment 3



(d) environment 4 (e) environment 5 (f) environment 6



(g) environment 7 (h) environment 8

Figure 1: Optimal degree of mutation and optimal log-geometric-average growth rate as a function of regime lengths $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$. Eight subfigures show simulation results of eight different environments in Table 1. The colored plain with the colorbar shows the optimal mutation rates; the transparent surface of which the height is indicated by the z-axis shows the optimal log-geometric-average growth rate associated with that optimal mutation rate.

spring. As expected, the growth rates are much higher than those in environment 1. The optimal degree of mutation is inversely proportional to the length of a regime, except for two regions where the length of one regime is much larger than that of the other (the region $\mathbb{E}[T^1] > 25, \mathbb{E}[T^2] < 12$, and the region $\mathbb{E}[T^1] < 12, \mathbb{E}[T^2] > 25$). In these two regions, the optimal degree of mutation drops to nearly 0 because one regime is significantly shorter than the other and therefore it is not worth sacrificing growth in one regime for the other by mutation, as long as the inferior behavior does not die out in the shorter regime.

Environment 3 adds dependence of x_a and x_b in each regime. In this case the optimal behavior in each regime is the perfect probability matching behavior: $f_1^* = 0.8, f_2^* = 0.2$. Simulation results are similar to environment 1.

Environment 4 considers a different kind of dependence of x_a and x_b in each regime. In this case the optimal behavior in each regime is deterministic: $f_1^* = 1, f_2^* = 0$. Simulation results are similar to environment 1.

Asymmetric regimes. The four experiments considered so far are all symmetric in terms of the two regimes. In other words, the second regime is simply a copy of the first regime with x_a and x_b reversed. As a consequence, all results are expected to be symmetric with respect to the line $\mathbb{E}[T^1] = \mathbb{E}[T^2]$. In this part we consider asymmetric regimes and investigate how this changes the optimal mutation rates and growth rates.

Environment 5 is a mixture of environment 3 and 4 in the symmetric regime case: regime 1 is from environment 3 and regime 2 is from environment 4. In this case the optimal behavior is $f_1^* = 0.8$ in regime 1 and $f_2^* = 0$ in regime 2. There are several interesting observations. First of all, both the optimal degree of mutation and the growth rate are no longer symmetric with respect to $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$. Secondly, the growth rate increases as $\mathbb{E}[T^2]$ increases; decreases as $\mathbb{E}[T^1]$ increases. This is because regime 2 has a larger geometric-mean fitness than regime 1, and the growth rate increases as the proportion of generations in regime 2 increases. Thirdly, similar phenomenon to environment 2 of zero-mutation appears when $\mathbb{E}[T^1]$ is large and $\mathbb{E}[T^2]$ is small.

Environment 6 makes the two regimes more asymmetric. The optimal behavior is $f_1^* = 1$ in regime 1 and $f_2^* = 0$ in regime 2. This time regime 1 has an edge in terms of geometric-mean fitness. Results are similar to environment 5 except that $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$ are reversed.

When mutation is not desirable. Mutation is desirable because the environment is unstationarily stochastic and the two regimes favor different actions. When these conditions change, mutation is no longer desirable.

Environment 7 reverses action a and b in the second regime of environment 5. The shape of the transparent surface indicating growth rates is similar to environment 5. However, the optimal degree of mutation is 0 for any combination of $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$, because the optimal behavior is $f_1^* = 0.8$ in regime 1 and $f_2^* = 1$ in regime 2. They are close to each other, and both of them grow relatively fast in both regimes.

Environment 8 reverses action a and b in the second regime of environment 6. The shape of the transparent surface indicating growth rates is similar to environment 6, and the optimal degree of mutation is 0 for the same reason as in environment 7. The optimal behavior is $f^* = 1$ in both regime 1 and regime 2.

3.4 Optimal degree of irrationality

It is clear that there exists a balance between growth without mutation and robustness with mutation. The simulation results confirm the inverse relation between the optimal degree of mutation and expected lengths of regimes derived analytically in the simple two-behavior model with special fecundity structure (Proposition 6 and Corollary 2). The relation is robust across a variety of environmental conditions.

For symmetric regimes, the optimal degree of mutation is inversely proportional to $\mathbb{E}[T^1]+\mathbb{E}[T^2]$; the growth rate is proportional to both $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$. For asymmetric regimes, the growth rate increases as the proportion of the regime that has a larger geometric-mean fitness increases. The relative magnitude of the two regimes matters.

The optimal degree of mutation could be zero if one regime is significantly shorter than the other, because it is not worth sacrificing growth in one regime for the other as long as the inferior behavior does not die out in the shorter regime. The optimal degree of mutation could also be zero if the optimal behaviors in two regimes are similar to each other, and both of them grow relatively fast in both regimes.

The length of regime, or equivalently the frequency of change, is one aspect of the nature of environmental change. The intensity of each environmental change is another aspect. In our framework, the intensity of environmental change is reflected by the difference in optimal behaviors in the two regimes: $|f_1^* - f_2^*|$. When the optimal behaviors in the two regimes are similar to each other, the optimal degree of mutation is relatively low; when the optimal behaviors in the two regimes are wildly different, the optimal degree of mutation must be high to compensate for the slow growth of the suboptimal behaviors in each regime.

In general, the evolutionarily optimal degree of irrationality in the population is influenced by both the frequency and intensity of environmental change. A higher frequency or intensity of change would imply a higher degree of irrationality. Equivalently, markets and industries with more volatile environments should attract more entrants over time.

4 Discussion

Evolutionary models of behavior are important for understanding the conflicts between individual rationality and human behavior. The binary choice model (Brennan and Lo, 2011) provides a framework for explanations of the deviations from the neoclassic utility-based economic theory. Building on the binary choice model, we investigate the evolution of irrational behaviors in this article. Mutation is the key because it provides the link between rational and irrational behaviors in an evolutionary context. Because the rational behavior is the evolutionarily optimal behavior given a particular environment, it is subject to change when the environment changes. As a result, irrational behavior is necessary to provide robustness for population growth. Furthermore, we have shown that there is an evolutionarily optimal degree of irrationality in the entire population. More unstable environments imply more irrational behaviors in the population and more new entry over time.

The evolutionary origins of strategic behavior have also been considered (Robson, 1996b; Skyrms, 2000; Skyrms, 2014), and natural selection can also produce more sophisticated behaviors such as overconfidence (Johnson and Fowler, 2011), altruism and self-deception (Trivers, 1971; Becker, 1976), and state-dependent strategies like the Hawk-Dove game (Maynard Smith, 1984), which emerge as a result of more complex environmental conditions. In our framework, if we assume that one individual's action is correlated with the reproductive success of another individual, individuals engaging in strategic behavior will reproduce more quickly than those with simpler behaviors such as probability matching. If the actions of individuals in the current generation can affect the reproductive success of individuals in future generations, even more complex dynamics are likely to emerge as in the well-known overlapping generations model (Samuelson, 1958). In a resource-constrained environment in which one individual's choice can affect another individual's reproductive success, strategic interactions such as reciprocity and cooperation will likely emerge within and across generations (Trivers, 1971; Nowak and Highfield, 2011).

In contrast, the model considered in this article does not require any strategic interactions, and individual decision-making is deliberately mindless, allowing us to determine the most primitive and fundamental links between stochastic environments and adaptive behavior. Even in such a simple setting, we find a range of behaviors—behaviors that do not always conform to common economic intuition about rationality—can arise and persist via natural selection. Simon (Simon, 1981) illustrated this principle vividly with the example of a single ant traversing a mixed terrain of sand, rocks, and grass. The ant's path seems highly complex, but the complexity is due more to the environment than the ant's navigational algorithm.

Much of the rationality debate among economists and psychologists focuses on whether the rational models can help people make better inferences and decisions in the real world (McKenzie, 2003). Instead, our framework provides an evolutionary explanation of irrational behaviors and different degrees of irrationality in the population. The results suggest that irrational behaviors are necessary even if they are seemingly inefficient in the current environment, and the nature of stochastic environment determines the degree of irrationality, and the amount of new entrants into the population.

From a policy perspective, our results underscore the importance of addressing different human behaviors in different environments. For example, the financial market is considered to be efficient most of the time (Samuelson, 1965; Fama, 1970), and participants with irrational beliefs constitutes a minimum part in the market. However, in periods of economic turbulence and financial crisis, irrational behaviors are much more prevalent than usual. Our results also highlight the importance of entry of new actors into the market even if they appear suboptimal in the current context, and suggest that the optimal amount of new entrants depends on the degree of environmental stability. On the other hand, if not properly managed, volatile environments can lead to increases in the degree of irrationality, implying higher social costs and lower economic growth. However, our results also highlight the potential dangers of sustained government intervention, which can become a source of systematic risk and cause volatile environments in its own right (Acharya, Richardso, Van Nieuwerburgh, and White, 2011; Lucas, 2011).

A Appendix

In this Appendix, we provide additional technical details and proofs for the main results of the paper.

A.1 Birkhoff's contraction coefficient

The definition and properties of the Birkhoff's contraction coefficient can be found in Caswell (2001) p.370-372 or Ipsen and Selee (2011) p.159. Let $\mathbf{x}$ and $\mathbf{y}$ be positive vectors. The Hilbert pseudo-metric distance between $\mathbf{x}$ and $\mathbf{y}$ is defined as:

$$d(\mathbf{x}, \mathbf{y}) := \log\left(\frac{\max_i \frac{x_i}{y_i}}{\min_i \frac{x_i}{y_i}}\right) = \max_{i,j} \log\left(\frac{x_i y_j}{x_j y_i}\right).$$

It measures the distance between two vectors in a way that depends only on their proportional composition, independent of their absolute size. It satisfies the following conditions:

$$\begin{aligned}
&d(\mathbf{x}, \mathbf{y}) \geq 0 \\
&d(\mathbf{x}, \mathbf{y}) = d(\mathbf{y}, \mathbf{x}) \\
&d(\mathbf{x}, \mathbf{y}) \leq d(\mathbf{x}, \mathbf{z}) + d(\mathbf{z}, \mathbf{y}) \\
&d(\mathbf{x}, \mathbf{y}) = 0 \quad \text{iff} \quad \mathbf{x} = a\mathbf{y} \\
&d(\mathbf{x}, \mathbf{y}) = d(a\mathbf{x}, b\mathbf{y}) \quad \text{for} \quad a, b > 0.
\end{aligned}$$

The Birkhoff's contraction coefficient of a non-negative matrix $\mathbf{A}$ is defined as:

$$\tau(\mathbf{A}) = \sup \frac{d(\mathbf{A}\mathbf{x}, \mathbf{A}\mathbf{y})}{d(\mathbf{x}, \mathbf{y})} \tag{A.1}$$

where the supremum is taken over all vectors $\mathbf{x} > 0$ and $\mathbf{y} > 0$ that are not multiples of each other. Note that because d is invariant with respect to the absolute magnitude of vectors, the supremum can be taken over a compact subset equivalently, say $||\mathbf{x}||_1 = ||\mathbf{y}||_1 = 1$.

If $\mathbf{A}$ is a strictly positive matrix, then $\tau(\mathbf{A}) < 1$ (see Caswell (2001) p.372 for example). Under Assumptions 1-3, the matrix $\mathbf{A}_t$ might not be strictly positive. However, there is at least one positive entry in each row of $\mathbf{A}_t$, so $\tau(\mathbf{A}_t) \leq 1$ (see Hajnal (1976) discussion on "row allowable" matrices). We will prove in Lemma 1 that $\tau(\mathbf{A}_t)$ is indeed strictly less than 1.

Lemma 1 (Contraction properties of $\mathbf{A}_t$)**.** *Under Assumptions 1-3, the Birkhoff's contraction* *coefficient τ of $\mathbf{A}_t$ is strictly less than 1 almost surely:*

$$\mathbb{P}\left(\tau(\mathbf{A}_t) < 1\right) = 1.$$

Because of Assumption 1, there are only finitely many possible random matrices $\mathbf{A}_t$ if x_a and x_b are integers. Therefore, the Birkhoff's contraction coefficient $\tau(\mathbf{A}_t)$ is uniformly less than some positive constant $\delta < 1$. But Lemma 1 is enough for the analysis henceforth.

A.2 Additional results for population dynamics

Lemma 2 (Decomposition of population vector)**.** *Under Assumptions 1-3, starting from $\mathbf{n}_0 = \mathbf{1}$ to be a $(K+1)$-dimensional column vector of 1's. Write $P_t = \mathbf{1}'\mathbf{n}_t$ for total population size at time t. Then the population vector at time t can be written as:*

$$\mathbf{n}_t = \widetilde{\mathbf{F}}_t\widetilde{\mathbf{F}}_{t-1}\cdots\widetilde{\mathbf{F}}_1\mathbf{n}_0 + \frac{\epsilon}{K}\left(\widetilde{\mathbf{F}}_t\cdots\widetilde{\mathbf{F}}_2 P_1\mathbf{1} + \widetilde{\mathbf{F}}_t\cdots\widetilde{\mathbf{F}}_3 P_2\mathbf{1} + \cdots + \widetilde{\mathbf{F}}_t P_{t-1}\mathbf{1} + P_t\mathbf{1}\right)$$

almost surely, where $\widetilde{\mathbf{F}}_t = \left(1 - \left(1 + \frac{1}{K}\right)\epsilon\right)\mathbf{F}_t$ is the "mutation-adjusted" fecundity matrix.

Lemma 2 provides a decomposition of the population vector $\mathbf{n}_t$ into a linear combination of non-mutation vector and t vectors for shorter generational spans, each of which is weighted by $\frac{\epsilon}{K}$ and stands for evolution starting from a certain time in evolution.

Proposition 7 (Asymptotic population distribution)**.** *Under Assumptions 1-3, there exists some σ such that the total population size $P_t = \mathbf{1}'\mathbf{n}_t$ at time t satisfies:*

$$\frac{\log P_t - t\mu_\epsilon}{\sigma\sqrt{t}} \Longrightarrow Normal(0,1)$$

in distribution as $t \to \infty$.

By Proposition 7, the asymptotic distribution of total population is lognormal, and the mean and variance of $\log P_t$ both increase linearly with time.

Proposition 8 (Rate of convergence)**.** *Under Assumptions 1-3, the Markov chain $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is uniformly ergodic if the support of $\mathscr{L}(\cdot)$ has nonempty interior*[1]*. By uniformly ergodic we mean that $\mathscr{L}_T$ converges to the stationary distribution $\mathscr{L}$ geometrically fast:*

$$||\mathscr{L}_T(\cdot) - \mathscr{L}(\cdot)||_{TV} \le M\rho^T,\ T = 1, 2, 3, \cdots$$

---

[1] The support of $\mathscr{L}(\cdot)$ is defined to be the set of all points $\mathbf{y} \in \mathscr{Y}$ for which every open neighborhood of $\mathbf{y}$ has positive measure.

for some $\rho < 1$ and $M < \infty$, where $|| \cdot ||_{TV}$ is the total variation distance between two probability measures.

Proposition 8 asserts that the rate of convergence in Proposition 4 is exponential. Therefore, one would expect that the convergence of $\mathscr{L}_T(\cdot)$ to the stationary distribution $\mathscr{L}(\cdot)$ is very fast in evolution.

Proposition 9 (Selection of the optimal behavior (Robson, 1996a))**.** *Suppose the optimal behavior without mutation is f^* and $\mu(f^*) > 0$ (see Proposition 1). Under Assumptions 1-3, suppose the corresponding element of f^* in the vector $\mathbf{y}_t$ is y^*. For any all small probability $\bar{p} > 0$, positive constant $\bar{\delta} > 0$, there exists $\bar{\epsilon} \in (0,1)$ such that, for all mutation rates $\epsilon \in (0, \bar{\epsilon})$, we have:*

$$\mathbb{P}_{\mathscr{L}}\left(y^* \geq 1 - \bar{\delta}\right) > 1 - \bar{p}$$

with respect to the limit distribution $\mathscr{L}$.

Proposition 9 asserts an important property of $\mathscr{L}$: f^* without mutation again dominates the population in evolution with mutation with arbitrarily high probability, provided that the mutation rate is small enough. However, explicit calculation of the stationary distribution is difficult. Section A.3 discusses a simulation experiment to understand the limit stationary distribution $\mathscr{L}$.

A.3 Simulation for the limit distribution of population proportions

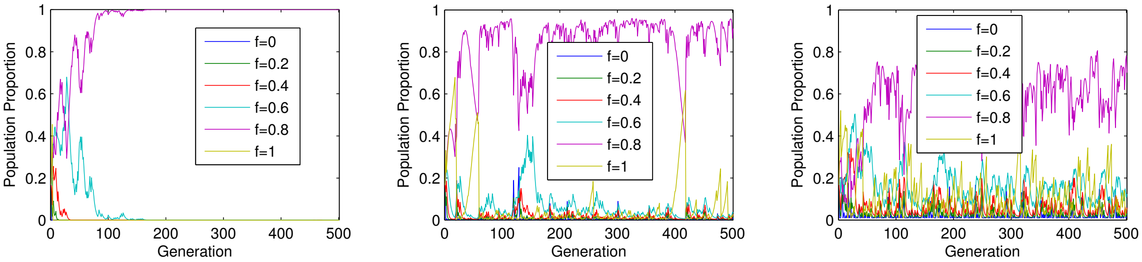
Let's consider an example to show how the limit distribution of population proportions behaves. Let $\Phi(x_a, x_b)$ be given in Table A.1 and we study a system with 6 behaviors $f \in \{0, \frac{1}{5}, \frac{2}{5}, \cdots, 1\}$.

Table A.1: Probability table for the simulation of asymptotic population dynamics

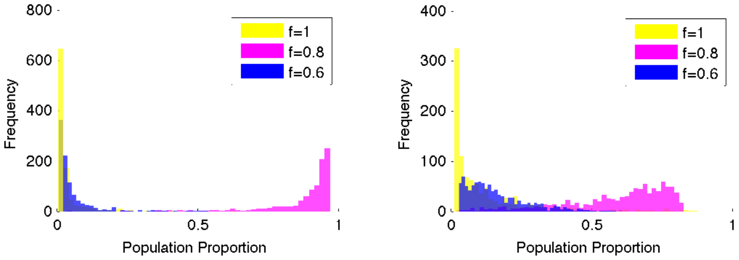
	State 1	State 2
Action	prob. $p = 0.8$	prob. $1 - p = 0.2$
a	$x_a = 3$	$x_a = 0$
b	$x_b = 0$	$x_b = 3$

Figure 1a 1b and 1c show the proportion of each behavior in the entire population as the number of generation increases in one simulation. Without mutation, the proportion of different behaviors converges almost surely. With positive mutation rates, the population proportion vector is stochastic even in the long run.

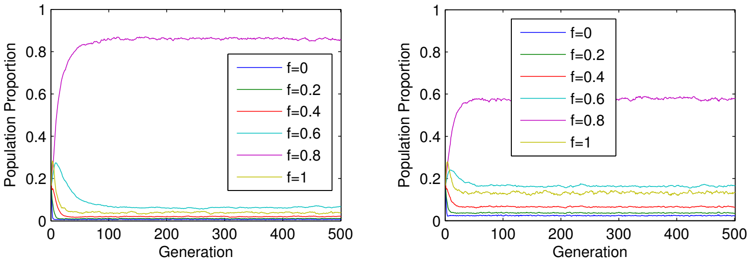
Figure 1d and 1e show the limit distribution of population proportions for mutation rates $\epsilon = 0.01$ and 0.05. Each subplot shows the histogram of three behaviors in the last generation $T = 500$ with 1000 simulation paths: the optimal behavior $f^* = 0.8$, and two suboptimal behaviors $f = 0.6, f = 1$. We only plot three representative behaviors for simplicity. From the histogram, it is clear that $f^* = 0.8$ (purple bar) corresponds to the optimal behavior. As the mutation rate gets smaller, the probability that $f^* = 0.8$ dominates the entire population gets closer to 1.



(a) 1 path, $\epsilon = 0$ (b) 1 path, $\epsilon = 0.01$ (c) 1 path, $\epsilon = 0.05$



(d) limit distribution, $\epsilon = 0.01$ (e) limit distribution, $\epsilon = 0.05$



(f) average path, $\epsilon = 0.01$ (g) average path, $\epsilon = 0.05$

Figure 1: Simulation for the limit distribution of population proportions. (1a): simulation of one evolution path without mutation. (1b): simulation of one evolution path with mutation $\epsilon = 0.01$. (1c): simulation of one evolution path with mutation $\epsilon = 0.05$. (1d): simulation of limit distribution of 1000 evolution paths with mutation $\epsilon = 0.01$; only $f = 0.6, 0.8, 1$ are shown. (1e): simulation of limit distribution of 1000 evolution paths with mutation $\epsilon = 0.05$; only $f = 0.6, 0.8, 1$ are shown. 1f): sample paths averaged over 1000 simulation with mutation $\epsilon = 0.01$. 1g): sample paths averaged over 1000 simulation with mutation $\epsilon = 0.05$.

Furthermore, the final stationary distribution does not behave like normal because of the heavy-tailness observed in simulation. In particular, a Kolmogorov-Smirnov test of normality on the distribution of $f^* = 0.8$ proportion gives p-value $= 1.08 \times 10^{-50}$, rejecting the normality hypothesis.

Finally, although it is hard to show the evolution of the complete distribution of normalized population vector (5) in one figure, Figure 1f and 1g show the proportion of each behavior in the entire population averaged over 1000 simulation paths. It is clear that the expectation of the distribution converges quickly, and the optimal behavior without mutation again dominates the population in expectation. This supports our results in Proposition 8 and 9.

A.4 Proofs

Lemma 1. The proof generalizes the discussion in Caswell (2001) p.371-372. Let $\mathbf{A} = (a_{ij})_{(K+1)\times(K+1)}$ be any matrix drawn under Assumptions 1-3. If $\mathbf{A}$ is strictly positive, then $\tau(\mathbf{A}) < 1$. If $\mathbf{A}$ is not strictly positive, because $\mathbf{P}(x_a > 0 \text{ or } x_b > 0) = 1$, $\mathbf{A}$ must be a strictly positive matrix except for the 1st column or the $(K+1)$-th column (but not both). Suppose without loss of generality that the 1st column of $\mathbf{A}$ is 0 and the rest is strictly positive, and it suffices to prove $\tau(\mathbf{A}) < 1$ in this case.

Now let $\mathbf{x}(t) = (x_i(t+1))_{i=1}^{K+1}$ and $\mathbf{y}(t) = (y_i(t+1))_{i=1}^{K+1}$ be positive vectors that are not proportional to each other, and $\mathbf{x}(t+1) = \mathbf{A}\cdot\mathbf{x}(t)$ and $\mathbf{y}(t+1) = \mathbf{A}\cdot\mathbf{y}(t)$. Then

$$\frac{x_i(t+1)}{y_i(t+1)} = \frac{\sum_j a_{ij}x_j(t)}{\sum_k a_{ik}y_k(t)} = \sum_j \left(\frac{a_{ij}y_j(t)}{\sum_k a_{ik}y_k(t)}\right)\frac{x_j(t)}{y_j(t)} = \sum_j p_{ij}\frac{x_j(t)}{y_j(t)}$$

where $\sum_j p_{ij} = 1$. A careful examination of p_{ij} yields that for any i,

$$p_{i1} = 0, \quad \text{and} \quad p_{ij} > 0 \text{ for } j = 2, 3, \cdots, K+1.$$

Therefore, $\frac{x_i(t+1)}{y_i(t+1)}$ is a positive weighted average of $\{\frac{x_j(t)}{y_j(t)}\}_{j=2}^{K+1}$, and this is true for all i. Because $\mathbf{x}(t)$ and $\mathbf{y}(t)$ are not proportional to each other, there are two possibilities:

(1) The ratios in $\{\frac{x_j(t)}{y_j(t)}\}_{j=2}^{K+1}$ are all the same, but different from $\frac{x_1(t)}{y_1(t)}$. In this case exactly one of the following must be true:

$$\min_j \frac{x_j(t)}{y_j(t)} < \frac{x_i(t+1)}{y_i(t+1)} \le \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i,$$

or

$$\min_j \frac{x_j(t)}{y_j(t)} \le \frac{x_i(t+1)}{y_i(t+1)} < \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i.$$

(2) The ratios in $\{\frac{x_j(t)}{y_j(t)}\}_{j=2}^{K+1}$ are not all the same. In this case we have

$$\min_j \frac{x_j(t)}{y_j(t)} < \frac{x_i(t+1)}{y_i(t+1)} < \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i.$$

In both (1) and (2) we have

$$d\left(\mathbf{x}(t+1), \mathbf{y}(t+1)\right) < d\left(\mathbf{x}(t), \mathbf{y}(t)\right).$$

That is, each multiplication by $\mathbf{A}$ contracts the distance between the two vectors. Because the supremum in Birkhoff's contraction coefficient (A.1) can be taken over a compact set, we have $\tau(\mathbf{A}) < 1$ with probability 1. □

Lemma 2. The mutation matrix $\mathbf{M}$ can be written as

$$\mathbf{M} = \left(1 - \left(1 + \frac{1}{K}\right)\epsilon\right)\mathbf{I}_{K+1} + \frac{\epsilon}{K}\mathbf{1}_{K+1}\mathbf{1}'_{K+1},$$

where $\mathbf{I}_{K+1}$ is the identity matrix of dimension $(K+1)\times(K+1)$. Plugging into (4) in Proposition 2 we get

$$\mathbf{n}_t \overset{\text{a.s.}}{=} \mathbf{M}\mathbf{F}_t\mathbf{n}_{t-1} = \left(1 - \left(1 + \frac{1}{K}\right)\epsilon\right)\mathbf{F}_t\mathbf{n}_{t-1} + \frac{\epsilon}{K}P_t\mathbf{1}_{K+1}. \tag{A.2}$$

Note that the identity

$$\mathbf{1}'\mathbf{F}_t\mathbf{n}_{t-1} = \mathbf{1}'\mathbf{M}\mathbf{F}_t\mathbf{n}_{t-1} = P_t$$

was used in order to obtain (A.2). Proceeding inductively from (A.2), we have the desired result. □

Proposition 1. See Brennan and Lo (2011) Proposition 1. Strong Law of Large Numbers implies almost sure convergence (see also Brennan and Lo (2011) Proof of Corollary 1). □

Proposition 2. The proof is a simple generalization of Brennan and Lo (2011). Let I^f be a Bernoulli variable defined same as in Brennan and Lo (2011), which equals 1 with probability f and 0 otherwise. Define "not mutation" indicator N and "mutation from g to f" indicator $M^{g\to f}$:

$$N = \begin{cases} 1 & \text{with prob } 1-\epsilon \\ 0 & \text{with prob } \epsilon, \end{cases} \qquad M^{g\to f} = \begin{cases} 1 & \text{with prob } \frac{\epsilon}{K} \\ 0 & \text{with prob } 1-\frac{\epsilon}{K}. \end{cases}$$

In generation t, type f individuals come from type f individuals without mutation and type

$g(\neq f)$ individuals with mutation in generation $t-1$. Consider them separately. From type f:

$$\begin{aligned}\sum_{i=1}^{n_{t-1}^f} x_{i,t}^{f\to f} &= \left(\sum_{i=1}^{n_{t-1}^f} N_{i,t} I_{i,t}^f\right) x_{a,t} + \left(\sum_{i=1}^{n_{t-1}^f} N_{i,t}(1-I_{i,t}^f)\right) x_{b,t} \\ &\overset{\text{a.s.}}{=} (1-\epsilon) n_{t-1}^f \left(f x_{a,t} + (1-f) x_{b,t}\right)\end{aligned}$$

as n_{t-1}^f increases without bound. From type $g(\neq f)$:

$$\begin{aligned}\sum_{g\neq f}\sum_{i=1}^{n_{t-1}^g} x_{i,t}^{g\to f} &= \sum_{g\neq f}\left[\left(\sum_{i=1}^{n_{t-1}^g} M_{i,t}^{g\to f} I_{i,t}^g\right) x_{a,t} + \left(\sum_{i=1}^{n_{t-1}^g} M_{i,t}^{g\to f}(1-I_{i,t}^g)\right) x_{b,t}\right] \\ &\overset{\text{a.s.}}{=} \frac{\epsilon}{K}\sum_{g\neq f} n_{t-1}^g \left(g x_{a,t} + (1-g) x_{b,t}\right)\end{aligned}$$

as n_{t-1}^g increases without bound. Note that

$$\begin{aligned}n_t^f &= \sum_{i=1}^{n_{t-1}^f} x_{i,t}^{f\to f} + \sum_{g\neq f}\sum_{i=1}^{n_{t-1}^g} x_{i,t}^{g\to f} \\ &\overset{\text{a.s.}}{=} (1-\epsilon) n_{t-1}^f (f x_{a,t} + (1-f) x_{b,t}) + \frac{\epsilon}{K}\sum_{g\neq f} n_{t-1}^g (g x_{a,t} + (1-g) x_{b,t}).\end{aligned}$$

(4) simply rewrites the above equation in matrix form. ☐

Proposition 3. By Lemma 1 and Caswell (2001, p. 386, 14.22), demographic weak ergodicity[2] holds. In addition, $\mathbb{E}\log_+ ||\mathbf{A}_1|| < \infty$ because x_a and x_b are bounded, where $\log_+ ||\mathbf{A}_1|| = \max\{0, \log ||\mathbf{A}_1||\}$. Therefore, assumption 4.2.1 in Tuljapurkar (1990) is satisfied, and Proposition 3 follows from Tuljapurkar (1990, p. 26, (A)). ☐

Proposition 4. Because the random matrices $\mathbf{A}_t$ are IID, assumption 4.2.1, 4.2.3, and 4.2.6 in Tuljapurkar (1990) are satisfied, and the conclusion follows directly from Tuljapurkar (1990) p.29 (J). ☐

Proposition 5. Part (i) is standard result for single type branching process in random environments (see Smith and Wilkinson (1969) Theorem 3.1 for example). Part (ii) follows from Proposition 3 and Corollary 1. ☐

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[2] The definition of demographic weak ergodicity is given in Caswell (2001, p. 383) and Tuljapurkar (1990, p. 17). Essentially it means that the difference between the probability distributions of normalized population vectors resulting from any two initial populations, exposed to independent sample paths of the stochastic environment, decays to zero.

Proposition 6. To clarify notation, let $x_{a,j}^1$ be the number of offspring generated by Φ^1 for action a in the j-th generation; $x_{b,j}^2$ the number of offspring generated by Φ^2 for action b in the j-th generation. Table A.2 calculates the number of individuals of both behaviors along evolution, starting with 1 individual of each type. From the last line of Table A.2 we have:

$$n_k^{\epsilon,\text{Total}} = \epsilon^{2k-1}(1-\epsilon)^{\sum_{i=1}^k (T_i^1+T_i^2)-2k} \prod_{j=1}^{\sum_{i=1}^k T_i^1} x_{a,j}^1 \prod_{j=1}^{\sum_{i=1}^k T_i^2} x_{b,j}^2.$$

Therefore,

$$\begin{aligned}
\frac{1}{k}\log n_k^{\epsilon,\text{Total}} &= \frac{2k-1}{k}\log\epsilon + \left(\frac{1}{k}\sum_{i=1}^k (T_i^1+T_i^2) - 2\right)\log(1-\epsilon) + \frac{1}{k}\sum_{j=1}^{\sum_{i=1}^k T_i^1}\log x_{a,j}^1 + \frac{1}{k}\sum_{j=1}^{\sum_{i=1}^k T_i^2}\log x_{b,j}^2 \\
&\overset{\text{a.s.}}{\to} 2\log\epsilon + \big(\mathbb{E}[T^1+T^2]-2\big)\log(1-\epsilon) + \mathbb{E}[T^1]\mathbb{E}[\log x_a^1] + \mathbb{E}[T^2]\mathbb{E}[\log x_b^2] \\
&= 2\log\frac{\epsilon}{1-\epsilon} + \mathbb{E}[T^1+T^2]\log(1-\epsilon) + \mathbb{E}[T^1]\mathbb{E}[\log x_a^1] + \mathbb{E}[T^2]\mathbb{E}[\log x_b^2]
\end{aligned}$$

where "$\overset{\text{a.s.}}{\to}$" denotes almost sure convergence and follows from Strong Law of Large Numbers as k increases without bound. Since the value of ϵ that maximizes the population size $n_k^{\epsilon,\text{Total}}$ is also the value of ϵ that maximizes $k^{-1}\log n_k^{\epsilon,\text{Total}}$, the above analysis implies that this maximum converges in probability to the maximum of

$$\pi(\epsilon) = 2\log\frac{\epsilon}{1-\epsilon} + \mathbb{E}[T^1+T^2]\log(1-\epsilon) + \mathbb{E}[T^1]\mathbb{E}_{\Phi^1}[\log x_a] + \mathbb{E}[T^2]\mathbb{E}_{\Phi^2}[\log x_b]$$

where $0 < \epsilon < 1$. Take the first and second derivatives of the above equation:

$$\begin{aligned}
\pi'(\epsilon) &= \frac{2}{\epsilon} - \frac{\mathbb{E}[T^1+T^2]-2}{1-\epsilon}, \\
\pi''(\epsilon) &= -\frac{2}{\epsilon^2} - \frac{\mathbb{E}[T^1+T^2]-2}{(1-\epsilon)^2}.
\end{aligned}$$

Note that T^1 and T^2 are positive integers, so $\mathbb{E}[T^1+T^2] \geq 2$. Therefore, the second derivative is always negative for $0 < \epsilon < 1$. In addition, $\pi'(0^+) > 0, \pi'(1^-) < 0$, which implies that $\pi(\epsilon)$ has a unique maximum in $(0,1)$ at $\pi'(\epsilon) = 0$. Solve for ϵ we get the desired result. $\square$

Proposition 7. Because the random matrices $\mathbf{A}_t$ are IID, assumption 4.2.1 and 4.2.3 in Tuljapurkar (1990) are satisfied, and the conclusion follows directly from Tuljapurkar (1990, p. 27,(F)). $\square$

Proposition 8. We utilize Meyn and Tweedie (2009, p. 411, Theorem 16.2.5):

If $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is a ψ-irreducible[3] and aperiodic T-chain[4], and if the state space $\mathscr{Y}$ is compact, then $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is uniformly ergodic.

The uniqueness of the stationary distribution $\mathscr{L}$ in Proposition 4 implies that $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is aperiodic, so it suffices to prove that $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is a ψ-irreducible T-chain.

Take $\psi = \mathscr{L}$ to be the stationary distribution of $\{\mathbf{y}_t\}_{t=0}^{\infty}$, then for all $\mathbf{y} \in \mathscr{Y}$ and $B \subseteq \mathscr{Y}$, whenever $\psi(B) > 0$, there exists some $n > 0$, possibly depending on both $\mathbf{y}$ and B, such that the n-step transition probability $p_n(\mathbf{y}, B) > 0$. Then it follows from Meyn and Tweedie (2009, p. 82, Proposition 4.2.1(ii)) that $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is ψ-irreducible.

Furthermore, the 1-step transition probability $p_1(\cdot, O)$ is a lower semicontinuous function for any open set $O \subseteq \mathscr{Y}$. Remember that the support of ψ is assumed to have non-empty interior. Then it follows from Meyn and Tweedie (2009, p. 124, Theorem 6.0.1(iii)) that $\{\mathbf{y}_t\}_{t=0}^{\infty}$ is a T-chain.

Finally, the uniform ergodicity of the Markov chain $\{\mathbf{y}_t\}_{t=0}^{\infty}$ follows from Meyn and Tweedie (2009, p. 411, Theorem 16.2.5). $\square$

Proposition 9. This Proposition is essentially due to Robson (1996a, p. 413, Theorem 2(iii)). $\square$

Corollary 1. The lower bound is obvious by simply considering the growth of non-mutated type f^* individuals. To prove the upper bound, first note that

$$\begin{aligned}
\mathbf{1}'\mathbf{F}_t\mathbf{y}_{t-1} &= \mathbf{1}' \begin{pmatrix} f_1 x_{a,t} + (1-f_1)x_{b,t} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & f_{K+1}x_{a,t} + (1-f_{K+1})x_{b,t} \end{pmatrix} \begin{pmatrix} y_{t-1}(1) \\ \vdots \\ y_{t-1}(K+1) \end{pmatrix} \\
&= \sum_{i=1}^{K+1} y_{t-1}(i)\left(f_i x_{a,t} + (1-f_i)x_{b,t}\right) = \left(\alpha_{t-1}x_{a,t} + \beta_{t-1}x_{b,t}\right)
\end{aligned}$$

where

$$\alpha_{t-1} = \sum_{i=1}^{K+1} y_{t-1}(i) f_i, \quad \beta_{t-1} = \sum_{i=1}^{K+1} y_{t-1}(i)(1-f_i),$$

and $\alpha_{t-1} + \beta_{t-1} = 1$. Note that $\mathbf{F}_t$ and $\mathbf{y}_{t-1}$ are independent in (7), and α_{t-1} and β_{t-1} are constants conditioning on $\mathbf{y}_{t-1}$, so one have:

$$\begin{aligned}
\mu_\epsilon = \mathbb{E}_{\mathscr{L}}\left\{\mathbb{E}_\Phi\left[\log(\mathbf{1}'\mathbf{F}_t\mathbf{y}_{t-1})\right]\middle|\mathbf{y}_{t-1}\right\} &= \mathbb{E}_{\mathscr{L}}\left\{\mathbb{E}_\Phi\left[\log\left(\alpha_{t-1}x_{a,t} + \beta_{t-1}x_{b,t}\right)\right]\middle|\mathbf{y}_{t-1}\right\} \\
\leq \mathbb{E}_{\mathscr{L}}\left\{\mathbb{E}_\Phi\left[\log\left(f^* x_{a,t} + (1-f^*)x_{b,t}\right)\right]\middle|\mathbf{y}_{t-1}\right\} &= \mathbb{E}_{\mathscr{L}}\left\{\mu(f^*)\middle|\mathbf{y}_{t-1}\right\} = \mu(f^*)
\end{aligned}$$

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[3] The definition of ψ-irreducibility can be found in Meyn and Tweedie (2009, p. 82).

[4] The definition of T-chains can be found in Meyn and Tweedie (2009, p. 124).

where the following fact is used for the inequality:

$$f^* = \arg\max_{0 \le f \le 1} \mathbb{E}_\Phi \left[\log \left(f x_{a,t} + (1-f) x_{b,t} \right) \right].$$

$\square$

Corollary 2. The conclusion follows immediately from Proposition 6 by replacing $\mathbb{E}[T^1 + T^2]$ by $2 \cdot \mathbb{E}[T]$. $\square$

Table A.2: Population dynamics for the two-behavior regime-switching model

Cycle	Regime	Generation	# of individuals $f = 0$	# of individuals $f = 1$
		0	1	1
		1	$q \cdot x^1_{a,1}$	$\epsilon \cdot x^1_{a,1}$
1	Φ^1	$\vdots$	$\vdots$	$\vdots$
		T^1_1	$q^{T^1_1} \prod_{j=1}^{T^1_1} x^1_{a,j}$	$\epsilon q^{T^1_1 - 1} \prod_{j=1}^{T^1_1} x^1_{a,j}$
		$T^1_1 + 1$	$\epsilon^2 q^{T^1_1 - 1} \prod_{j=1}^{T^1_1} x^1_{a,j} \cdot x^2_{b,1}$	$\epsilon q^{T^1_1} \prod_{j=1}^{T^1_1} x^1_{a,j} \cdot x^2_{b,1}$
1	Φ^2	$\vdots$	$\vdots$	$\vdots$
		$T^1_1 + T^2_1$	$\epsilon^2 q^{T^1_1 + T^2_1 - 2} \prod_{j=1}^{T^1_1} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j}$	$\epsilon q^{T^1_1 + T^2_1 - 1} \prod_{j=1}^{T^1_1} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j}$
		$T^1_1 + T^2_1 + 1$	$\epsilon^2 q^{T^1_1 + T^2_1 - 1} \prod_{j=1}^{T^1_1} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j} \cdot x^1_{a,T^1_1+1}$	$\epsilon^3 q^{T^1_1 + T^2_1 - 2} \prod_{j=1}^{T^1_1} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j} \cdot x^1_{a,T^1_1+1}$
2	Φ^1	$\vdots$	$\vdots$	$\vdots$
		$T^1_1 + T^2_1 + T^1_2$	$\epsilon^2 q^{T^1_1 + T^2_1 + T^1_2 - 2} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j}$	$\epsilon^3 q^{T^1_1 + T^2_1 + T^1_2 - 3} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j}$
		$T^1_1 + T^2_1 + T^1_2 + 1$	$\epsilon^4 q^{T^1_1 + T^2_1 + T^1_2 - 3} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j} \cdot x^2_{b,T^2_1+1}$	$\epsilon^3 q^{T^1_1 + T^2_1 + T^1_2 - 2} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1} x^2_{b,j} \cdot x^2_{b,T^2_1+1}$
2	Φ^2	$\vdots$	$\vdots$	$\vdots$
		$T^1_1 + T^2_1 + T^1_2 + T^2_2$	$\epsilon^4 q^{T^1_1 + T^2_1 + T^1_2 + T^2_2 - 4} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1 + T^2_2} x^2_{b,j}$	$\epsilon^3 q^{T^1_1 + T^2_1 + T^1_2 + T^2_2 - 3} \prod_{j=1}^{T^1_1 + T^1_2} x^1_{a,j} \prod_{j=1}^{T^2_1 + T^2_2} x^2_{b,j}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
k	Φ^2	$\sum_{i=1}^k (T^1_i + T^2_i)$	$\epsilon^{2k} q^{\sum_{i=1}^k (T^1_i + T^2_i) - 2k} \prod_{j=1}^{\sum_{i=1}^k T^1_i} x^1_{a,j} \prod_{j=1}^{\sum_{i=1}^k T^2_i} x^2_{b,j}$	$\epsilon^{2k-1} q^{\sum_{i=1}^k (T^1_i + T^2_i) - (2k-1)} \prod_{j=1}^{\sum_{i=1}^k T^1_i} x^1_{a,j} \prod_{j=1}^{\sum_{i=1}^k T^2_i} x^2_{b,j}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$

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