

# The nature of the mutation process matters\*

## Bergin and Lipman [1996] revisited

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### Abstract

The incorporation of small mutation rates has significantly improved the predictive capacity of evolutionary models. Bergin and Lipman [1996], however, demonstrate that this improvement depends entirely on the nature of the mutation process. We provide a *constructive* corroboration of their result: we derive matching mutation rates for each desired set of stochastic stable states.

KEYWORDS: Evolution; Mutation.

## 1 Introduction

In evolutionary game theory, ‘finite memory’ is a standard assumption: players’ actions are based on a limited sample of past actions. Therefore, Markov processes naturally suit the analysis. The limiting distribution of such a Markov process defines the distribution over the steady states of the evolutionary model. The steady states with strict positive limiting distribution are called ‘stable’ states.

The inherent path dependence of these evolutionary models is viewed as a serious weakness but is overcome by introducing, besides the deterministic evolution, ‘mutation’ as a second equilibrium–selection driving force, where states are ‘stochastically stable’ if they have a positive limiting distribution as the mutation rates converge to zero (Kandori et al.

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[1993], Young [1993]). Interestingly, stochastic stability is a refinement of the deterministic evolutionary process: each stochastic stable state is also a stable state in the model without mutation.

As Bergin and Lipman [1996] (henceforth BL) convincingly prove, however, the predictive power of the latter models crucially depends on the assumption that mutation rates are constant across states and agents and over time. In a non-constructive manner, by using the Kakutani fixed point theorem, BL show that once this assumption is (partially) dropped, “with state-dependent [but time-invariant] mutation rates, any invariant distribution of the mutationless process is achievable with any mutation model” (p. 951).

Evidently, this landmark result has spurred an interesting debate on modeling the mutation process. By endogenizing the mutation process, Blume [2003], van Damme and Weibull [2002], Baron et al. [2003], to name but a few, have certainly contributed to understanding the restrictions on mutation models. We believe, however, that more work needs to be done. For instance, although BL show that the function, which maps the mutation rates to the corresponding stable states, is surjective on the set of deterministic stable states, the general shape of this function remains vague: e.g. what is the range of mutation rates that leads to a same set of stable states? Therefore, our constructive corroboration of the BL result not only stresses its pertinence, it will also, we hope, allow us to see more transparently how specifics of the mutation process select outcomes.

By allowing mutation rates to differ *between* absorbing sets (we keep mutation rates constant *within* absorbing sets), we show that, for suitably adjusted mutation rates, any set of stable states of a deterministic evolutionary process can also be reached as the set of *stochastic* stable states. Our proof is constructive in the sense that for each desired set of stochastic stable states, we derive matching mutation rates.

## 2 The Model

An extensive but necessary section on notation, definitions and assumptions precedes the central theorem of the paper, which is elaborated in section 2.2.

### 2.1 Definitions and Assumptions

Let  $S = \{1, 2, \dots, n\}$  be a finite set of states. A Markov process  $P$  on the set  $S$  is a set of elements  $\{P(x, y)\}_{x, y \in S}$  such that for all  $x, y \in S$ ,  $P(x, y) \geq 0$  and for all  $x \in S$ ,  $\sum_{y \in S} P(x, y) = 1$ . The element  $P(x, y)$  is the transition probability from state  $x$  to state  $y$ . We denote by  $\mathcal{P}$  the set of all Markov processes on the set  $S$ . Henceforth,  $P$  denotes a Markov process on the set  $S$ :  $P \in \mathcal{P}$ .

An invariant distribution of  $P$  is a real vector  $q = (q(1), \dots, q(n))$  such that for all  $x \in S$ ,  $q(x) \geq 0$ ,  $\sum_{x \in S} q(x) = 1$  and  $\sum_{y \in S} q(y) P(y, x) = q(x)$ .

For each  $P$  we can define a binary relation,  $R_P$ , on the set  $S$ :

$$(x, y) \in R_P \text{ if } P(x, y) > 0.$$

The transitive closure of  $R_P$  is denoted by  $T(R_P)$  and is defined as  $(x, y) \in R_P$  if there is a finite sequence  $s = x_1, \dots, x_m$  of elements in  $S$  such that  $x = x_1, y = x_m$  and for all  $t = 1, \dots, m - 1$ ,  $(x_t, x_{t+1}) \in R_P$ .

A Markov process is irreducible if for all  $x, y \in S$ ,  $(x, y) \in T(R_P)$ . Moreover, a subset  $A$  of  $S$  is absorbing in  $P$  if for all  $x, y \in A$ ,  $(x, y) \in T(R_P)$  and for all  $x \in A, y \notin A$ ,  $(x, y) \notin R_P$ .

**Fact 1.** If  $A$  and  $A'$  are two absorbing sets of  $P$ , then  $A \neq A'$  implies  $C \cap C' = \emptyset$ .

Fact 1. states that two absorbing sets are either equal or disjoint. Let  $A_1, \dots, A_k$  be the finite number of disjoint absorbing sets of  $P$ . The following facts concern invariant distributions:

**Fact 2.** If  $P$  is irreducible, it has a unique invariant distribution.

**Fact 3.** If  $P$  has absorbing sets  $A_1, \dots, A_k$ , and if  $q$  is an invariant distribution of  $P$ , then  $q(x) > 0$  only if for some  $i, x \in A_i$ . Further if  $y \in A_i$ , then also  $q(y) > 0$ .

Consider a function  $\Sigma$  from the set  $[0, 1]^n$  to the set  $\mathcal{P}$  (where  $n$  is the cardinality of the set  $S$ ). The function  $\Sigma$  is a perturbation of  $P$  if:

- (i)  $\Sigma(0) = P$ ;
- (ii)  $\Sigma(\epsilon)$  is irreducible for all  $\epsilon \gg 0$ ;
- (iii)  $\Sigma(\epsilon)$  is continuous in  $\epsilon$ ; and
- (iv)  $\forall x, y \in S$ , the transition rate from  $x$  to  $y$  in the Markov process  $\Sigma(\epsilon)$  only depends on  $\epsilon_x$ .

Here,  $\epsilon_x$  is the  $x$ -th element of the vector  $\epsilon$ .

The element in row  $x$  and column  $y$  of  $\Sigma(\epsilon)$  is denoted by  $P(\epsilon_x, x, y)$ . The  $x$ -th element of the invariant distribution of  $\Sigma(\epsilon)$ , which is unique by Fact 2, is denoted by  $q(\epsilon, x)$ .

We say that the state  $x$  is a *stochastic stable state* if:

$$\lim_{\epsilon \rightarrow 0} q(\epsilon, x) > 0.$$

As the Markov process  $\Sigma(\epsilon)$  is continuous, the set of stochastic stable states is necessarily the support of some invariant distribution of  $P$ . By Fact 3, this invariant distribution has positive support for some  $x \in S$  only if  $x$  is in some absorbing set of  $P$ .

Our aim is to show the reverse: given an element  $x \in S$  from an absorbing set  $A_i$  of  $P$ , and a state dependent mutation process  $\Sigma(\epsilon)$ , there exist mutation rates such that  $x$  is a stochastic stable state of this mutation process.

In order to compute the stochastic stable states of a given mutation process, we use the Markov chain tree theorem of Freidlin and Weitzell. For  $x \in S$ , and Markov chain  $P$  and a mutation process  $\Sigma(\epsilon)$ , an  $x$ -tree is a subset  $t_x$  of  $R_{\Sigma(\epsilon)}$  such that:

- (i)  $\forall y \in S$  and  $y \neq x, (y, x) \in T(t_x)$ .
- (ii)  $\forall y \in S, (x, y) \notin t_x$
- (iii)  $\forall y, z, w \in S, (y, z) \in t_x$  and  $(y, w) \in t_x$  implies  $w = z$

Let  $\mathcal{T}_x$  be the set of all  $x$ -trees. For an  $x$ -tree  $t_x$ , we denote the value  $v(t_x, \epsilon)$  as:

$$v(t_x, \epsilon) = \prod_{(z,w) \in t_x} P(\epsilon_z, z, w).$$

**Theorem 1.** *Given a Markov chain  $P$ , a mutation process  $\Sigma(\epsilon)$  and a mutation rate  $\epsilon \gg 0$ :*

$$\frac{q(\epsilon, x)}{q(\epsilon, y)} = \frac{\sum_{t_x \in \mathcal{T}_x} v(\epsilon, t_x)}{\sum_{t_y \in \mathcal{T}_y} v(\epsilon, t_y)}.$$

In order to show that  $x$  is stochastic stable, we have to show that for all  $y \in S$

$$\lim_{\epsilon \rightarrow 0} \frac{q(\epsilon, x)}{q(\epsilon, y)} > 0.$$

## 2.2 Result

**Theorem 2.** *Consider a Markov chain  $P$ , a mutation process  $\Sigma(\cdot)$  and an element  $x \in S$  in a stable state  $A_i$  of  $P$ . Then there exist mutation rates  $\epsilon$  such that  $x$  is a stochastic stable state of  $\Sigma(\epsilon)$ .*

*Proof.* To begin we first provide two lemmas on properties of  $x$ -trees.

**Lemma 1.** For all  $y \in S$ , there is an  $y$ -tree  $t_y \in \mathcal{T}_y$  such that for all  $t'_x \in \mathcal{T}_y$

$$\lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t'_y)}{v(\epsilon, t_y)} < \infty.$$

*Proof.* Assume on the contrary that for all  $t_y \in \mathcal{T}_y$ , there exist a  $t'_y \in \mathcal{T}_y$  such that  $\lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t'_y)}{v(\epsilon, t_y)} = \infty$ . As such, from finiteness of the set  $\mathcal{T}_y$ , there exist a sequence of  $y$ -trees  $t_y^1, \dots, t_y^m$  such that  $\lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^i)}{v(\epsilon, t_y^{i+1})} = \infty$  for all  $i = 1, \dots, m-1$  and  $\lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^m)}{v(\epsilon, t_y^1)} = \infty$ . This gives:

$$1 = \lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^1)}{v(\epsilon, t_y^2)} \frac{v(\epsilon, t_y^2)}{v(\epsilon, t_y^3)} \dots \frac{v(\epsilon, t_y^m)}{v(\epsilon, t_y^1)} = \lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^1)}{v(\epsilon, t_y^2)} \lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^2)}{v(\epsilon, t_y^3)} \dots \lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_y^m)}{v(\epsilon, t_y^1)} = \infty$$

... a contradiction □

An  $y$ -tree for which the above holds is called a minimal tree for  $y$ . Now let  $t_y$  be a minimal tree for  $y$  and let  $t_x$  be a minimal tree for  $x$ . We have,

$$\lim_{\epsilon \rightarrow 0} \frac{q(\epsilon, x)}{q(\epsilon, y)} = \lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t_x)}{v(\epsilon, t_y)} \lim_{\epsilon \rightarrow 0} \frac{\sum_{t'_x \in \mathcal{T}_x - \{t_x\}} \frac{v(\epsilon, t'_x)}{v(\epsilon, t_x)} + 1}{\underbrace{\sum_{t'_y \in \mathcal{T}_y - \{t_y\}} \frac{v(\epsilon, t'_y)}{v(\epsilon, t_y)} + 1}_{B(\epsilon)}}$$

The second limiting term on the rhs,  $B(\epsilon)$ , converges to a strict positive number. Therefore, for stochastic stability, we only have to look at the ratios of the values of the minimal trees.

**Lemma 2.** If  $t_y$  is a minimal tree for  $y \in A_j$ , then:

- $(z, w) \in t_y - R_P$  implies that  $z \notin A_j$ .
- $(z, w)$  and  $(k, l) \in t_x - R_P$  implies that  $z$  and  $k$  are not in the same absorbing set.

*Proof.* Assume that  $(z, w) \in t_x - R_P$  and  $z \in A_j$ . Assume without loss of generality that there are no other elements  $k \in A_j$  such that there is a  $v \in S$  for which  $(k, v) \in t_y - R_P$  and  $(k, z) \in T(t_x)$ . Consider an element  $l$  in  $A_j$  for which  $(z, l) \in R_P$ . (such an element exist due to the definition of absorbing sets and the assumption that  $y \in A_j$ ). Now consider the tree  $t'_x = t_x - \{(z, w)\} \cup \{z, l\}$ . This is also an  $x$ -tree and has value:

$$v'(\epsilon, t'_x) = v(\epsilon, t_x) \frac{P(\epsilon, z, l)}{P(\epsilon, z, w)}.$$

Now,

$$\lim_{\epsilon \rightarrow 0} \frac{v(\epsilon, t'_x)}{v(\epsilon, t_x)} = P(z, l) \lim_{\epsilon \rightarrow 0} \frac{1}{P(\epsilon, z, w)} = \infty.$$

The second part of the proof is analogous. □

For all  $y \in S$ , we consider two continuous and strictly increasing functions  $f_m(\epsilon_y, y)$  and  $f_M(\epsilon_y, y)$ , such that  $f_m(0, y) = f_M(0, y) = 0$  and for all  $z \in S$  for which  $(y, z) \in R_{\Sigma(\epsilon)} - R_P$  for all  $\epsilon \gg 0$ :

$$f_m(\epsilon_y, y) \leq P(\epsilon_y, y, z) \leq f_M(\epsilon_y, y).$$

The existence of such functions is shown in appendix A. For each  $y \in S - A_i$  and  $\beta_y \in \mathbb{R}_0^+$ , we define the function  $\epsilon_y(\sigma, \beta_y)$  as:

$$f_m(\epsilon_y(\sigma, \beta_y), y) = f_m(1, y) \sigma^{\beta_y}.$$

For all  $x \in A_i$  and  $\beta_x \in \mathbb{R}_0^+$ , we define the function  $\epsilon_x(\sigma, \beta_x)$  as:

$$f_M(\epsilon_x(\sigma, \beta_x), x) = f_M(1, x) \sigma^{\beta_x}.$$

For all  $y \in S$ , the functions  $\epsilon_y(\cdot, \beta_y)$  are functions from  $[0, 1]$  to  $[0, 1]$  which are continuous and strictly increasing. By choosing the values of  $\beta_y$ , we fix the mutation rates  $\epsilon_y$ . We do this in the following way:

- For all absorbing sets  $A_j$  we construct a number  $\beta_{A_j} > 0$  and put for all  $y \in A_j$ ,  $\beta_y = \beta_{A_j}$ .
- For  $A_i$ , set  $\beta_{A_i} > \sum_{A_j, j \neq i} \beta_{A_j} + \sum_{y \notin A_j, j=1, \dots, k} \beta_y$ .

Consider a minimal  $x$ -tree  $t_x$ . From Lemma 2 and the definition of  $f_m$ , we have that there exist a function  $a(\epsilon)$  for which  $\lim_{\epsilon \rightarrow 0} a(\epsilon) \in \mathbb{R}_0^+$  such that for  $\epsilon \gg 0$  small enough:

$$v(\epsilon, t_x) \geq a(\epsilon) \prod_{A_j, j \neq i} \sigma^{\beta_{A_j}} \prod_{y \notin A_j, j=1, \dots, k} \sigma^{\beta_y}.$$

For a minimal  $y$ -tree, we have from Lemma 2 and the definition of  $f_M$  that there exist a function  $b(\epsilon)$  such that  $\lim_{\epsilon \rightarrow 0} b(\epsilon) \in \mathbb{R}_0^+$  and for  $\epsilon \gg 0$  small enough:

$$v(\epsilon, t_y) \leq b(\epsilon) \sigma^{\beta_{A_i}}.$$

From this, we have that

$$\lim_{\epsilon \rightarrow 0} \frac{q(\epsilon, x)}{q(\epsilon, y)} \geq c \lim_{\sigma \rightarrow 0} \left( \sigma^{\sum_{A_j, j \neq i} \beta_{A_j} + \sum_{y \notin A_j, j=1, \dots, k} \beta_y - \beta_{A_i}} \right) > 0.$$

□

Theorem 2 states the main result of the paper: given a Markov chain  $P$  and a mutation process  $\Sigma(\epsilon)$ , any element in an absorbing set can be a stochastic stable states of the mutation process by suitable adjustment of the mutation rates.

### 3 Conclusion

Bergin and Lipman [1996] showed that the predictive power of evolutionary models which incorporate *mutation* as an equilibrium selection device, crucially depends on the nature of the mutation process, i.e. they prove that a suitably defined mutation process allows to achieve any stable distribution of the process without mutation with a model that incorporates mutation.

By allowing mutation rates to differ between absorbing sets, we show that, any element in an absorbing set of a deterministic evolutionary process can also be reached as the set of stochastic stable states for any mutation process. Our result is an intuitive and constructive corroboration of their – non-constructive – result, which stresses its pertinence: the nature of the mutation process matters, and “must be analyzed more carefully to derive some economically justifiable restrictions” (Bergin and Lipman [1996], p. 956).

We hope that the constructive argument in this note adds some transparency to, and spurs further research into, the modeling of mutation processes.

### 4 Appendix

#### Construction of $f_m$ and $f_M$

Construction of  $f_M(\epsilon_x, x)$ . Let  $\delta > 0$  and construct following functions.

- i  $P_M(\epsilon_y, y) = \arg \max_z \{ P(\epsilon_y, y, z) \mid z \in S, (y, z) \in R_{\Sigma(\epsilon)} - R_P \}$
- ii  $P'_M(\epsilon_y, y) = \arg \max_{\epsilon \in [0, \epsilon_y]} P_M(\epsilon, y)$

$$\text{iii } f_M(\varepsilon_y, y) = P'_M(\varepsilon_y, y) + \delta\varepsilon_y$$

The function  $P_M(\varepsilon_y, y)$  is a continuous function such that for all  $z \in S$ :  $(y, z) \in R_{\Sigma(\varepsilon)} - R_P$ :  $P_M(\varepsilon_y, y) \geq P(\varepsilon_y, y, z)$ . The function  $P'(\varepsilon_y, y)$  is a continuous increasing function with  $P'_M(\varepsilon_y, y) \geq P_M(\varepsilon_y, y)$ . The function  $f_M$  is a continuous strictly increasing function such that  $f_M(\varepsilon_y, y) \geq P'_M(\varepsilon_y, y)$ .

Construction of  $f_m(\varepsilon_x, x)$ .

$$\text{i } P_m(\varepsilon_y, y) = \arg \min_z \{P(\varepsilon_y, y, z) \mid z \in S, (y, z) \in R_{\Sigma(\varepsilon)} - R_P\}$$

$$\text{ii } P'_m(\varepsilon_y, y) = \arg \min_{\varepsilon \in [\varepsilon_y, 1]} P_M(\varepsilon_y, y)$$

The function  $P_m(\varepsilon_y, y)$  is such that for all  $z \in S, (y, z) \in R_{\Sigma(\varepsilon)} - R_P$ :  $P_m(\varepsilon_y, y) \leq P(\varepsilon_y, y, z)$ . The function  $P'_m$  is an increasing function such that  $P'_m(\varepsilon_y, y) \leq P_m(\varepsilon_y, y)$ . Consider the set:

$$C_y = \left\{ (P, \theta) \in R \times [0, 1] \mid \begin{array}{l} \exists \alpha \in [0, 1], \varepsilon_1, \varepsilon_2 \in [0, 1] : \\ \theta = \alpha\varepsilon_1 + (1 - \alpha)\varepsilon_2 \\ P = \alpha P'_m(\varepsilon_1, y) + (1 - \alpha) P'_m(\varepsilon_2, y) \end{array} \right\}.$$

This set collects the convex combinations of all elements  $(P'_m(\varepsilon_y, y), \varepsilon)$ . Now define the function:

$$\text{iii } f_m(\varepsilon_y, y) = \arg \min_{(P, \varepsilon_y) \in C_y} P$$

This function selects the lower contour of the set  $C_y$ . It is continuous and  $f_m(\varepsilon_y, y) \leq P'_m(\varepsilon_y, y)$ . To see that it is strictly increasing, we show that every slope of the lower contour of  $C_y$  is strictly positive. The slope is positive there

$$\frac{P'_m(\varepsilon_1, y) - P'_m(\varepsilon_2, y)}{(\varepsilon_1 - \varepsilon_2)} \geq 0$$

for all  $\varepsilon_1$  and  $\varepsilon_2$ . Now assume that there is a part of the lower contour set which has slope 0, which implies that there are two elements  $\varepsilon_1, \varepsilon_2$  such that:  $\frac{P'_m(\varepsilon_1, y) - P'_m(\varepsilon_2, y)}{(\varepsilon_1 - \varepsilon_2)} = 0$

and an element  $\alpha\varepsilon_2 + (1 - \alpha)\varepsilon_1$  which is at the lower part of  $C_y$  with value  $\alpha P'_m(\varepsilon_2, y) + (1 - \alpha) P'_m(\varepsilon_1, y)$ .

Notice that  $P'_m(\varepsilon_1, y) = P'_m(\varepsilon_2, y)$ . Now let  $\alpha\varepsilon_2 + (1 - \alpha)\varepsilon_1 = \beta\varepsilon_2$ . We have that:



$$\alpha P'_m(\varepsilon_2, y) + (1 - \alpha) P'_m(\varepsilon_1, y) = P'_m(\varepsilon_2, y) > \beta P'_m(\varepsilon_2, y) + (1 - \beta) P'_m(0, y)$$

Therefore,  $(P'_m(\varepsilon_2, y), \alpha\varepsilon_2 + (1 - \alpha)\varepsilon_1)$  is not part of the lower contour of  $C_y$ .

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