# Learning Resembles Evolution – the Markov Case

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### Abstract

A learning system can be said to learn strings of actions. An evolving population can be said to evolve strings of genes. We show here that in a broad class of adaptive plans, the string frequencies change according to the same simple formula whether the strings are strings of actions in time or strings of genes in space, just as John Holland foresaw. The result is new. We have shown this by first analyzing the basic case where the Markov property holds in the learning system and then extending the analysis to cases where it doesn't. This paper analyzes the basic case, where an action is simply a state transition. In these adaptive plans, a transition's frequency increase is proportional to the product of its frequency and its total value. Its total value is the sum of its pre-value, which reflects payoff received in time steps before the transition, and its post-value, which reflects payoff received in time steps after the transition. Total value is time symmetric. Machine learning procedures are correctly based on post-values alone. In this paper we reframe that learning in terms of total values. Then in these plans, the formulae simplify and come to resemble those of population genetics and evolutionary computation. The procedures have not changed, only the analysis. It establishes a formal link between the process of learning and the process of evolution.

**Key Words:** adaptive systems, reinforcement learning, evolutionary computation, time symmetric values, undiscounted value, adaptive Markov chain, actor-critic, temporal difference.

# 1 Learning and Evolution

A brain learns. A population evolves. In his 1975 book, *Adaptation in Natural and Artificial Systems* [3], John Holland placed these adaptive systems and others in a common formal framework. He believed that learning and evolution are similar adaptive processes.

But a formal approach highlighted problems. Reinforcement Learning [5] deals with conditional probabilities of actions, whereas evolution deals with unconditional probabilities (frequencies) of genes and gene strings. These different probabilities seeemed to change and adapt differently. Learning and evolution seemed different. The fields of Reinforcement Learning and Evolutionary Computation drifted apart.

Our work shows that if we take a time symmetric aproach in the formal framework, then the probability changes are not really different. Learning and evolution are similar. Reinforcement Learning and Evolutionary Computation can now get back in touch. Holland was right.

Through interaction with the environment, a learning system learns what to do, which actions to take when and in what combinations. An evolving population, through interaction with the environment, learns which genes are appropriate when and in what combinations. A learning system can be said to learn strings of actions. An evolving population can be said to evolve strings of genes. Our work shows that in a broad class of adaptive plans, which we call Natural Plans, the string frequencies change according to the same simple formula whether the strings are strings of actions in time or strings of genes in space. We show this by first analyzing the basic case where the Markov property holds in the learning system and then extending the analysis to cases where it doesn't. This paper analyzes the basic case, where the Markov property holds and the system can distinguish the various states. An action is simply a Markov chain state transition.

Adaptive frequency change is based on value<sup>1</sup>, either explicitly or implicitly. In an evolving population of a haploid microorganism, the value  $v_{\sigma}$  of a gene  $\sigma$  is the average of the values of the individuals in the population that have that gene. The frequency  $\varphi_{\sigma}$  of the gene changes in this way.

$$\varphi_{\sigma}' = \varphi_{\sigma} K v_{\sigma} \tag{1}$$

<sup>&</sup>lt;sup>1</sup>In biology and Evolutionary Computation, the word "fitness" is often used to mean value. But sometimes it means reproductive rate, so I avoid the word.

In this paper, K is the adaptation rate constant, and ' is derivative with respect to time. So  $\varphi'_{\sigma}$  is the gene's frequency change rate.

Equation (1) holds roughly not only when  $\sigma$  is a single gene, but also when it is a string of several genes, and even when it is an entire genome.<sup>2</sup> This is the basis of the hierarchical adaptive structure of evolving populations. It is the basis of Evolutionary Computation. The frequencies of the more valuable strings increase.

This paper shows that equation (1) also holds in the basic reinforcement learning context, where  $\sigma$  is a string of successive state transitions. This result is new, and depends on the correct definition of string total value  $v_{\sigma}$ . The total value  $v_{ij}$  of state transition  $i \to j$  is the sum of its pre-value, which reflects payoff <sup>3</sup> received in time steps before the transition, and its post-value, which reflects payoff received in time steps after the transition. Total value is time symmetric.<sup>4</sup>

Machine Learning systems tend to ignore pre-values. They adjust the state transition conditional probabilities  $P_{ij}$  on the basis of the post-values alone. The broad class of what I call Natural Adaptive Plans do this. This makes good sense, since two alternative transitions coming from the same state have the same pre-value. Post-values are usually called simply values. But the resulting conditional probability change rates  $P'_{ij}$  do not follow equation (1), and the unconditional transition probabilities (frequencies)  $F_{ij}$  are a complicated function of the conditional probabilities  $P_{ij}$ , so learning and evolution looked different, until now

This paper shows that in any Natural Plan, the change in unconditional transition frequency  $F_{ij}$  does in fact follow the very simple formula  $F'_{ij} = F_{ij}Kv_{ij}$  based on total value  $v_{ij}$ . The system is not using pre-values. But using pre-values and total values in analysis allows us to describe the system's action simply. The changes in transition string frequencies follow the simple equation (1), just as in evolving populations.

The Actor-Critic architecture [1] in Reinforcement Learning conceptually separates the system into the critic, which calculates post-value estimates, and the actor, which uses these estimates to adjust the probabilities.<sup>5</sup> Generally speaking, the estimates are both noisy and biased,<sup>6</sup> but if the Markov property holds then the estimates are unbiased.

This paper deals with only the basic case, where the Markov property holds. We have an adaptive finite state Markov chain, with a fixed payoff number attached to each state. When the chain enters a state, the system receives payoff equal to the payoff number attached to that state. I write  $\bar{m}$  for the average payoff received per time step.

Each legal transition has an attached positive availability number  $s_{ij}$ . The transition probabilities  $P_{ij}$  are the normalized availabilities. The actor adjusts the availabilities in an attempt to increase  $\bar{m}$ . The actor and critic can distinguish the various states. In this basic case, the post-value estimates are unbiased. This paper deals only with the actor, and we assume that when we are in state i, the actor receives the correct post-value from the critic. This paper derives formulae for  $F'_{ij}$  and  $\varphi'_{\sigma}$  in this basic adaptive Markov chain situation.

We have extended these results to more general systems in which the Markov property does not hold. [7] In such systems a Temporal Difference Critic usually gives biased post-value estimates. Our analysis of these systems has already helped to make sense of the biases. The adaptive Markov chain results form the basis of all these extensions. This paper reports only the adaptive Markov chain results.

Section 2 is preparatory material. In it we introduce our adaptive Markov chain terminology and define the probabilities, the values, and  $\bar{m}$  as functions of the availabilities. We note that in fact they are all differentiable (in fact rational) functions of the availabilities. We then assume that the availabilities are differentiable functions of time, and this makes all the quantities differentiable functions of time. We exhibit seven needed equations that relate the time derivatives of the various quantities. Proof outlines are given for proofs that are not fairly obvious. Almost everything in section 2 is traditional time-asymmetric material. It is given here mainly to illustrate our notation. Only at the end of section 2 do we introduce the non-traditional time-symmetric quantities, the pre-values, total values, and string total values.

Section 3 proves the key equivalence (Lemma 6). It says that in an adaptive Markov chain, equation  $F'_{ij} = F_{ij}Kv_{ij}$  holds if and only if  $P'_{ij} = P_{ij}Kh_{ij}$  holds. The forward implication (Lemma 3)

<sup>&</sup>lt;sup>2</sup>Sexual recombination distorts this for the longer strings, and there are many complications.

<sup>&</sup>lt;sup>3</sup>In Reinforcement Learning literature, the word "reward" means payoff, whereas in Evolutionary Computation literature, "reward" usually means reinforcement.

<sup>&</sup>lt;sup>4</sup>The pre-value and post-value are both undiscounted.

<sup>&</sup>lt;sup>5</sup>The estimates can be implicit, but Temporal Difference critics use explicit estimates.

<sup>&</sup>lt;sup>6</sup>Temporal Difference estimates have less noise, but they are usually biased. For a simple example of the bias see [6].

<sup>&</sup>lt;sup>7</sup>They have separate parameters for each state and they know which state they are in.

is easy, but turning the implication around involves constructing what I call the derivative relation. The construction is in subsection 3.1.

From the key equivalence, the rest follows. Section 4 defines the Markov chain version of Natural Adaptive Plan and proves Theorem 1. Actually, you could think of the whole paper as a proof of Theorem 1. Theorem 1 gives three equivalent definitions of Natural Plan. It follows that transition string frequencies change as in the evolution formula (1).

### $\mathbf{2}$ Adaptive Markov Chains

All vectors in this paper are row vectors. Their transposes are column vectors. Each of our vectors will be a row of N complex numbers. A vector is non-negative if all its entries are non-negative real numbers. A vector is called stochastic if its entries are all non-negative real numbers and the entries sum to 1. Of course a vector is nonzero if it has a nonzero entry.

In most cases we will use the following notation. A vector will be a bold lower case letter, for example,  $\mathbf{v}$ . Each entry in the vector will be written using the corresponding italic letter thus,  $v_i$ . A matrix will be an upper case italic letter, for example, M. Each of its entries will be written using that same letter thus,  $M_{ij}$ .

The vector  $\mathbf{e}$  is the vector of all ones. The vector  $\mathbf{e}_i$  is the vector whose i'th entry is 1 and whose other entries are all 0.

Our matrices will be  $N \times N$  matrices of real numbers. A matrix is non-negative if all of its entries are non-negative real numbers. A matrix is row stochastic if each of its rows is a stochastic vector. So we see that a matrix A is row stochastic of and only if A is non-negative and  $A\mathbf{e}^{\top} = \mathbf{e}^{\top}$ . Of course a row is nonzero if it has a nonzero entry. Similarly for nonzero column.

To normalize a non-negative vector means to change its entries, dividing each entry by the sum of all the entries. So the normalized vector is stochastic. To row normalize a non-negative matrix means to normalize each of its rows, to divide each entry by the corresponding row sum.

If **v** is a vector, then  $\operatorname{diag}(\mathbf{v})$  is the diagonal matrix whose ii'th entry is  $v_i$ , for all i.

We will be discussing a Markov chain that has N states. (The states are numbered from 1 to N.) When I say Markov chain, I will mean a Markov chain with N states.  $(N \ge 2)$ 

Attached to each legal chain transition  $i \to j$  is a positive real number  $s_{ij}$  that I call its availability. If there is no legal transition from i to j then  $s_{ij}=0$ . The matrix S is the  $N\times N$  availabilities  $s_{ij}$ . Adaptation will change the availabilities.

The matrix P is the row normalized S . The number  $\bar{s}_i$  is the i'th row sum of S . So  $P_{ij} = s_{ij}\bar{s}_i^{-1}.$ 

The matrix P is the chain's transition probability matrix. If  $i \to j$  is a legal chain transition, then  $P_{ij}$  is the transition probability. By that I mean that  $P_{ij}$  is the conditional probability that the next state is j, given that the current state is i. If  $i \to j$  is illegal then of course  $P_{ij} = 0$ . The transition probability of every legal transition is positive. We see that P is row stochastic. We see that P is a rational function of S.

Our Markov chain will be strongly connected, which means that for any ordered pair of states  $\langle i,j \rangle$ , there is a sequence of legal transitions that takes the chain from state i to state j.

We write  $\tilde{p}_i$  for the probability the chain is in state i.

And  $\tilde{\mathbf{p}} \mathbf{e}^{\top} = 1$ . The state probability vector  $\tilde{\mathbf{p}}$  is a left eigenvector of P with eigenvalue 1. Since the chain is strongly connected, the Perron-Frobenius Theorem [2] tells us that:

The set of left eigenvectors of P that have eigenvalue 1 forms a one-dimensional subspace. The set of right eigenvectors of P that have eigenvalue 1 forms a one-dimensional subspace.

And it tells us that every  $\tilde{p}_i$  is positive.

We define  $F_{ij} = \tilde{p}_i P_{ij}$ , so  $F_{ij}$  is the *frequency* or unconditional probability of transition  $i \to j$ . We define the matrix  $\hat{P} = I - P + \mathbf{e}^{\top} \tilde{\mathbf{p}}$ . We note that  $\hat{P}$  is nonsingular.<sup>10</sup>

Attached to each state i is a fixed unchanging real number  $m_i$  called its payoff. As S changes, P changes, but the payoff vector  $\mathbf{m}$  remains the same.

<sup>&</sup>lt;sup>8</sup>The matrix S is the only matrix whose entries I write with a lower case letter,  $s_{ij}$ .

<sup>&</sup>lt;sup>9</sup>Since the chain is strongly connected, the state probabilities  $\tilde{p}_i$  are well defined. [4] <sup>10</sup>Suppose  $\mathbf{v}\hat{P} = 0$  for some non-zero vector  $\mathbf{v}$ . Since  $\hat{P}\mathbf{e}^{\top} = \mathbf{e}^{\top}$ , we have  $\mathbf{v}\mathbf{e}^{\top} = \mathbf{v}\hat{P}\mathbf{e}^{\top} = 0$ . Therefore,  $\mathbf{v}(I-P) = \mathbf{v}\hat{P} = 0$ , and  $\mathbf{v}$  is a left eigenvector of P with eigenvalue 1. So (2) tells us that  $\mathbf{v} = \lambda \tilde{\mathbf{p}}$  for some scalar  $\lambda$ . Therefore,  $\mathbf{v} = \lambda \tilde{\mathbf{p}} = \lambda \tilde{\mathbf{p}} \hat{P} = \mathbf{v} \hat{P} = 0$ . Contradiction.

When the chain visits state i, the system receives payoff equal to  $m_i$ . So in each time step, the chain changes state and the system receives payoff. I write  $\bar{m}$  for the average payoff received per time step. So  $\bar{m} = \tilde{\mathbf{p}} \mathbf{m}^{\perp}$ .

The actor adjusts S, and this changes the probabilities P and all the other quantities including  $\bar{m}$ . The hope is that  $\bar{m}$  will rise. I use the term excess payoff to mean payoff minus  $\bar{m}$ . The vector **a** is the state excess payoff vector, that is,  $a_i = m_i - \bar{m}$ .

The post-value  $c_i$  of state i is the expectation of the total excess payoff the system would receive on and after a visit to state i. That is,

$$c_i = \sum_{k=0}^{\infty} (\mathbf{e}_i P^k \mathbf{a}^\top)$$
 (I write  $\sum$  for Cesaro summation.)

We use Cesaro summation to iron out any periodicity in the chain.

We show below that the Cesaro sum converges and that  $c_i = \mathbf{e}_i \hat{P}^{-1} \mathbf{a}^{\top}$ .

We define  $h_{ij} = c_j - c_i + a_i$ . It says how much better  $i \to j$  is than the average transition from i . I call it the *choice value* of transition  $i \to j$  . We also define the correction factor  $q_i = \tilde{p}_i \bar{s}_i^{-1}$ . Our definitions are summarized in the table below.

$\underline{\operatorname{Symbol}}$	Meaning	Defining Equation
$ar{ar{s}_i}{ar{S}}$	availability row sum	$\bar{s}_i = \sum_j s_{ij}$ or $\bar{\mathbf{s}} = \mathbf{e} S^{\top}$
$ar{S}$		$\bar{S} = \operatorname{diag}(\bar{\mathbf{s}})$
$P_{ij}$	probability of $i \to j$	$P_{ij} = s_{ij}\bar{s}_i^{-1}$ or $P = \bar{S}^{-1}S$
$ ilde{p}_i$	probability of state $i$	
D		$D = \operatorname{diag}(\mathbf{\tilde{p}})$
$F_{ij}$ $\hat{P}$	frequency of $i \to j$	$F_{ij} = \tilde{p}_i P_{ij}$ or $F = DP$
$\hat{P}$		$\hat{P} = I - P + \mathbf{e}^{\top} \mathbf{\tilde{p}}$
$\bar{m}$	average payoff	$ar{m} = \tilde{\mathbf{p}} \mathbf{m}^{ op}$
$a_i$	excess payoff of state $i$	$a_i = m_i - \bar{m}$
$c_i$	post-value of state $i$	$\mathbf{c}^{\top} = \hat{P}^{-1}\mathbf{a}^{\top} = \sum_{k=0}^{\infty} (P^k \mathbf{a}^{\top})$
$h_{ij}$	choice value of $i \to j$	$h_{ij} = c_j - c_i + a_i$
$q_i$		$q_i = \tilde{p}_i \bar{s}_i^{-1}$

Since  $\hat{P}$  is nonsingular, the definition  $\mathbf{c}^{\top} = \hat{P}^{-1}\mathbf{a}^{\top}$ makes sense. Using that definition we have the following facts.

$$\tilde{\mathbf{p}} = \tilde{\mathbf{p}}P = \tilde{\mathbf{p}}\hat{P} = \tilde{\mathbf{p}}\hat{P}^{-1}$$
 and  $\mathbf{e}^{\top} = P\mathbf{e}^{\top} = \hat{P}\mathbf{e}^{\top} = \hat{P}^{-1}\mathbf{e}^{\top}$  (3)

$$\tilde{\mathbf{p}} \mathbf{a}^{\mathsf{T}} = 0 \quad \text{and} \quad \tilde{\mathbf{p}} \mathbf{c}^{\mathsf{T}} = 0$$
 (4)

$$\tilde{\mathbf{p}} = \tilde{\mathbf{p}}P = \tilde{\mathbf{p}}\hat{P} = \tilde{\mathbf{p}}\hat{P}^{-1} \quad \text{and} \quad \mathbf{e}^{\top} = P\mathbf{e}^{\top} = \hat{P}\mathbf{e}^{\top} = \hat{P}^{-1}\mathbf{e}^{\top}$$
(3)  

$$\tilde{\mathbf{p}}\mathbf{a}^{\top} = 0 \quad \text{and} \quad \tilde{\mathbf{p}}\mathbf{c}^{\top} = 0$$
(4)  

$$(I - P)\mathbf{c}^{\top} = \mathbf{a}^{\top} \quad \text{and} \quad c_{i} - a_{i} = \sum_{j} P_{ij}c_{j}$$
(5)  

$$\sum_{i} P_{ij}h_{ij} = 0$$
(6)

$$\sum_{i} P_{ij} h_{ij} = 0 (6)$$

Since  $(P^k - \mathbf{e}^{\top} \tilde{\mathbf{p}}) \hat{P} = P^k - P^{k+1}$  we have

$$\sum_{k=0}^{n-1} (P^k - \mathbf{e}^{\top} \tilde{\mathbf{p}}) = (I - P^n) \hat{P}^{-1}$$
 (7)

From this we have  $\lim_{n\to\infty} \frac{1}{n} \sum_{k=0}^{n-1} (P^k - \mathbf{e}^\top \tilde{\mathbf{p}}) = 0$ , which gives us

$$\lim_{n \to \infty} \frac{1}{n} \sum_{k=0}^{n-1} P^k = \mathbf{e}^\top \tilde{\mathbf{p}}$$
 (8)

 $\sum_{n=0}^{\infty} (P^n - \mathbf{e}^{\top} \tilde{\mathbf{p}}) = \lim_{\ell \to \infty} \frac{1}{\ell} \sum_{n=0}^{\ell-1} \sum_{k=0}^{n-1} (P^k - \mathbf{e}^{\top} \tilde{\mathbf{p}}) ,$ The definition of Cesaro sum gives us and then equations (7) and (8) give us this.

$$\sum_{n=0}^{\infty} (P^n - \mathbf{e}^{\top} \tilde{\mathbf{p}}) = \hat{P}^{-1} - \mathbf{e}^{\top} \tilde{\mathbf{p}}$$
(9)

Multiplying by  $\mathbf{a}^{\top}$  on the right gives us  $\sum_{n=0}^{\infty} (P^n \mathbf{a}^{\top}) = \hat{P}^{-1} \mathbf{a}^{\top}$ , so the Cesaro sum in the definition of  $c_i$  converges and is correct.

We said that P is a rational function of S.

In fact, the following quantities are all rational functions of S.

 $P, \ \bar{\mathbf{p}}, \ \bar{m}, \ \mathbf{a}, \ \hat{P}, \ \hat{P}^{-1}, \ F, \ \text{and} \ \mathbf{c}.$ 

The only tricky part of showing this is showing that  $\tilde{\mathbf{p}}$  is a rational function of P.

One way of doing this is via the adj of a matrix.<sup>11</sup> We define M = adj(I - P).

By (2), the transformation (I-P) is singular and has a one dimensional kernel. Hence it has a nonzero  $(N-1)\times (N-1)$  minor and a non-zero cofactor. So M is not the zero matrix.

Now for any square matrix A we have (adj(A)) A = A (adj(A)) = |A| I. M(I-P)=(I-P)M=0, and consequently we have MP=M and PM=M. So M has the property that any nonzero row is a left eigenvector of P with eigenvalue 1, and hence 12 is a scalar multiple of  $\,\tilde{\mathbf{p}}\,$  . And any nonzero column is a right eigenvector of  $\,P\,$  with eigenvalue 1, and hence is a scalar multiple of  $\mathbf{e}^{\top}$ . So every row is identical, and since M is not the zero matrix, every row is nonzero and is a multiple of  $\tilde{\mathbf{p}}$ . So  $\tilde{\mathbf{p}}$  is a rational function of P.

Note that if A is a nonsingular square matrix then  $A^{-1}$  is a rational function of A since it is  $|A|^{-1}(adj(A))$ .

The rest is obvious. All the quantities are rational functions of S.

We now suppose that each entry  $s_{ij}$  in S is a continuous and differentiable function of some real parameter t, which we can think of as time. It follows that all our quantities are continuous and differentiable functions of t. We write ' to mean derivative with respect to t. So the entries in the matrix S' are the derivatives  $s'_{ij}$ , and the entries in the vector  $\tilde{\mathbf{p}}'$  are the derivatives  $\tilde{p}'_i$ , and so forth. The following equations show how the derivatives  $S', \bar{S}', P', \tilde{\mathbf{p}}', F', \text{ and } \bar{m}'$  are related.

$$\bar{S}' = \operatorname{diag}(\mathbf{e} (S')^{\top}) .$$
 (10)

$$\tilde{\mathbf{p}}' = \mathbf{e}F' \qquad . \tag{11}$$

$$F' = D'P + DP' \tag{12}$$

$$P' = D^{-1}(F' - D'P) \tag{13}$$

$$P' = \bar{S}^{-1}(S' - \bar{S}'P) .$$

$$\tilde{\mathbf{p}}' = \tilde{\mathbf{p}}P'\hat{P}^{-1}$$
(15)

$$\tilde{\mathbf{p}}' = \tilde{\mathbf{p}}P'P^{-1} \tag{15}$$

$$\bar{m}' = \tilde{\mathbf{p}} \bar{S}^{-1} (S' - \bar{S}' P) \mathbf{c}^{\top} . \tag{16}$$

Equations (10) and (11) are obvious. Equations (12) and (13) are just the product rule applied to F = DP, and equation (14) is the product rule applied to  $\bar{S}P = S$ . To derive equation (15) we first note that since  $\tilde{\mathbf{p}} \mathbf{e}^{\top} = 1$ , we have  $\tilde{\mathbf{p}}' \mathbf{e}^{\top} = 0$ . Therefore if we use the product rule on  $\tilde{\mathbf{p}} = \tilde{\mathbf{p}} P$  we can obtain  $\tilde{\mathbf{p}}' = \tilde{\mathbf{p}}P' + \tilde{\mathbf{p}}'P = \tilde{\mathbf{p}}P' + \tilde{\mathbf{p}}'P - \tilde{\mathbf{p}}'\mathbf{e}^{\top}\tilde{\mathbf{p}}$ . Then transposing a couple of terms yields  $\tilde{\mathbf{p}}'\hat{P} = \tilde{\mathbf{p}}P'$  and then (15). Now  $\bar{m} = \tilde{\mathbf{p}}\mathbf{m}^{\top}$ , so  $\bar{m}' = \tilde{\mathbf{p}}'\mathbf{m}^{\top} = \tilde{\mathbf{p}}'(\mathbf{a}^{\top} + \bar{m}\mathbf{e}^{\top}) = \tilde{\mathbf{p}}'\mathbf{a}^{\top}$ . So multiplying (15) on the right by  $\mathbf{a}^{\top}$  gives us  $\bar{m}' = \tilde{\mathbf{p}}P'\mathbf{c}^{\top}$ . This and equation (14) give us equation

We said that  $\bar{m}$  is a differentiable function of the availabilities  $s_{ij}$ . We would like a formula for the partial derivative  $-\frac{\partial \bar{m}}{\partial s_{ij}}$  . We proceed as follows.

We choose any legal transition  $x \to y$ . In the availability matrix we keep all entries  $s_{ij}$  constant except for the xy'th entry. The xy'th entry will be equal to the time parameter t. So t determines the xy'th entry, which determines  $\bar{m}$  . The current time t is  $s_{xy}$ , so the current availability matrix is S. The current time derivative  $\bar{m}'$  is  $\frac{\partial \bar{m}}{\partial s_{xy}}$ . The time derivative S' is  $\mathbf{e}_x^{\top} \mathbf{e}_y$ , and the time derivative

We plug those values into equation (16) and obtain a formula for  $\frac{\partial \bar{m}}{\partial s_{xx}}$ .

$$\frac{\partial \bar{m}}{\partial s_{xy}} = (\tilde{\mathbf{p}} \bar{S}^{-1} \mathbf{e}_x^{\top}) (\mathbf{e}_y \mathbf{c}^{\top} - \mathbf{e}_x P \mathbf{c}^{\top})$$

We see that  $\tilde{\mathbf{p}} \, \bar{S}^{-1} \mathbf{e}_x^{\top} = q_x$ . And equation (5) tells us that  $P \, \mathbf{c}^{\top} = \mathbf{c}^{\top} - \mathbf{a}^{\top}$ . Therefore, our formula simplifies to  $\frac{\partial \bar{m}}{\partial s_{xy}} = q_x h_{xy}$ .

 $<sup>^{11}</sup>$ If A is a square matrix, then we get the ij'th co-factor of A by deleting the i'th row and j'th column, taking the determinant of what is left, and then changing its sign if i+j is odd. We get adj(A) as follows. We take A, and for each element we replace it with the corresponding co-factor. Thus the ij'th element is replaced by the ij'th co-factor. When we are all done, we transpose the matrix. Suppose we look at the  $(N-1)\times (N-1)$  minors of A. We see that the ij'th minor either equals the ij'th co-factor or equals its negation. So there is a non-zero  $(N-1)\times (N-1)$  minor if and only if there is a non-zero co-factor.

 $<sup>^{12}</sup>$ by (2)

The chosen transition could have been any legal transition.

Therefore, for any legal transition  $i \to j$  we have

$$\frac{\partial \bar{m}}{\partial s_{ij}} = q_i h_{ij} . {17}$$

### We now define the non-traditional time symmetric quantities.

We call a square matrix row-column compatible if every row sum equals the corresponding column sum. The matrix F is row-column compatible. The i'th row sum and the i'th column sum of F are both  $\tilde{p}_i$ . We note that P is the row normalized F. Let the matrix B be the row normalized  $F^{\top}$ . The entry  $B_{ij}$  is the conditional probability that the previous state was j, given that the current state is i. The matrix B is the transition probability matrix of a different chain. I call it the backward chain and call the original chain the forward chain. The state probabilities and state payoffs in the backward chain are the same as in the forward chain. (The backward chain is sometimes called the time reversed chain.)

The pre-value  $b_i$  of state i is the expectation of the total excess payoff the system receives on and before a visit to state i. Pre-value in the forward chain is post-value in the backward chain.  $b_i = \sum_{k=0}^{\infty} (\mathbf{e}_i B^k \mathbf{a}^\top)$ Total value is pre-value plus post-value.

So we have the following additional definitions.

Symbol	Meaning	Defining Equation
$egin{aligned} B_{ij} \ \hat{B} \end{aligned}$	backward probability	$B_{ij} = F_{ji} \tilde{p}_i^{-1}$ or $B = D^{-1} F^{\top}$
$\hat{B}$		$\hat{B} = I - B + \mathbf{e}^{T} \tilde{\mathbf{p}}$
$b_i$	pre-value of state $i$	$\mathbf{b}^{\top} = \hat{B}^{\text{-}1} \mathbf{a}^{\top} = \sum_{k=0}^{\infty} (B^k \mathbf{a}^{\top})$
$v_{ij}$	total value of $i \to j$	$v_{ij} = b_i + c_j$
$ar{v}_i$	total value of state $i$	$\bar{v}_i = b_i - a_i + c_i$

These quantities too are obviously rational functions of S . It is straightforward to show the following unsurprising facts.

$$(I - B) \mathbf{b}^{\top} = \mathbf{a}^{\top}$$
 and  $b_i - a_i = \sum_{i} B_{ij} b_j$  (18)

$$(I - B) \mathbf{b}^{\top} = \mathbf{a}^{\top} \quad \text{and} \quad b_i - a_i = \sum_j B_{ij} b_j$$

$$\sum_j F_{ij} v_{ij} = \tilde{p}_i \bar{v}_i \quad \text{and} \quad \sum_i F_{ij} v_{ij} = \tilde{p}_j \bar{v}_j$$

$$\sum_i \tilde{p}_i \bar{v}_i = 0 \quad \text{and} \quad \sum_{ij} F_{ij} v_{ij} = 0$$

$$(18)$$

$$\sum_{i} \tilde{p}_{i} \bar{v}_{i} = 0 \qquad \text{and} \qquad \sum_{ij} F_{ij} v_{ij} = 0 \tag{20}$$

We can extend the notion of the total value of a transition and define what we can call the total-value of a string of transitions. We write  $v_{\sigma}$  to mean the total-value of string  $\sigma$ . To avoid introducing unnecessary notation, I shall avoid giving a formal definition and proving the facts about it. I shall merely illustrate with an example and leave the proofs of the generalizations to the reader.

We choose an illustrative string  $\sigma$ .

$$\sigma = (\alpha \to \beta)(\beta \to i)(i \to j)(j \to \delta)(\delta \to \varepsilon) \tag{21}$$

The frequency  $\varphi_{\sigma}$  of string  $\sigma$  is this.

 $\varphi_{\sigma} = \tilde{p}_{\alpha} P_{\alpha\beta} P_{\beta i} P_{ij} P_{j\delta} P_{\delta\varepsilon} .$ 

The total value of  $\sigma$  is this.

 $v_{\sigma} = b_{\alpha} + a_{\beta} + a_i + a_j + a_{\delta} + c_{\varepsilon}$ 

The pre-value  $b_{\alpha}$  and the post-value  $c_{\varepsilon}$  embody the interaction of  $\sigma$  with the environment, with the preceding and following strings.

These definitions make sense. For example, suppose we select a random five transition string, selecting each string  $\sigma$  with probability  $\varphi_{\sigma}$ . Then  $F_{ij}$  is the probability that the third transition in the selected sequence is  $i \to j$  . To see that this is the case, note that in general we have  $\tilde{p}_i P_{ij} = F_{ij} = B_{ji} \tilde{p}_j$  , so if  $\sigma$  is the example sequence above, then we can write the string frequency  $\varphi_{\sigma}$  as  $B_{\beta\alpha}B_{i\beta}F_{ij}P_{j\delta}P_{\delta\varepsilon}$ .

Now summing over  $\alpha$ ,  $\beta$ ,  $\varepsilon$ , and  $\delta$  gives us  $F_{ij}$ . The transition frequency is the sum of the frequencies of the strings it is in, just as in population genetics.<sup>13</sup>

The string of the string is the average of the total values of the strings it is the average of the total values of the strings it is the average of the strings is in, just as in population genetics.

# 3 Adaptation

# 3.1 The Derivative Relation

Our task now is to show that the matrix P' determines F', and that conversely, F' determines P'. We do this by defining a relation from the possible P' matrices to the possible F' matrices and then showing it is one to one.

Select any availability matrix S. This matrix will remain fixed throughout section 3. We will examine various different S' matrices.

Since S is fixed throughout section 3, the following quantities are also fixed.

 $\bar{S}$ , P,  $\tilde{\mathbf{p}}$ ,  $\hat{P}$ ,  $\hat{P}^{-1}$ , D, F, B,  $c_i$ ,  $b_i$ ,  $h_{ij}$ ,  $v_{ij}$ .

Although those quantities are fixed, their derivatives can differ depending on what S' is. We are particularly interested in P' and F'.

Let  $\mathfrak S$  be the set of real  $N\times N$  matrices that have a zero in every entry that corresponds to an illegal transition. It is easy to see that any S' matrix must be a member of  $\mathfrak S$ . In fact, any member of  $\mathfrak S$  could be an S' matrix. The set  $\mathfrak S$  is the set of possible S' matrices.

Now suppose we select an S' from the set  $\mathfrak{S}$ . Our selected S' gives us a matrix P' and a matrix F' via equations (10), (14), (15), and (12). Let's investigate what that P' and F' might be.

Let  $\mathfrak P$  be the set of all real  $N\times N$  matrices in which every row sum is zero and in which every entry corresponding to an illegal transition is zero. Obviously any P' must be a member of  $\mathfrak P$ . We now show that any member of  $\mathfrak P$  might be P'.

## Lemma 1

If  $A \in \mathfrak{P}$  then there is an S' in  $\mathfrak{S}$  such that P' = A.

### **Proof:**

Let  $S' = \bar{S}A$ . We see that  $S' \in \mathfrak{S}$ .

Since  $A\mathbf{e}^{\top} = 0$ , we have  $\bar{S}'\mathbf{e}^{\top} = S'\mathbf{e}^{\top} = \bar{S}A\mathbf{e}^{\top} = 0$ . But  $\bar{S}'$  is diagonal, so  $\bar{S}' = 0$ .

Plugging this and  $S' = \bar{S}A$  into equation (14) gives us P' = A.

So we see that  $\mathfrak{P}$  is exactly the set of all possible matrices P'.

Let's be quite clear what we have said. Remember that S is fixed. We have said that if we take any member A of  $\mathfrak P$ , that A could be P'. By that I mean that there is an S' that gives us a P' equal to A with S having the value of our fixed S.

Now let  $\mathfrak{F}$  be the set of all real  $N \times N$  matrices that are row column compatible, whose entries all sum to zero, and in which every entry corresponding to an illegal transition is zero. It is easy to see that every possible F' matrix must be a member of  $\mathfrak{F}$ . We now show it could be any member.

### Lemma 2

If  $G \in \mathfrak{F}$  then there is an S' in  $\mathfrak{S}$  such that F' = G.

## **Proof:**

Given  $G \in \mathfrak{F}$ , let  $\bar{G}$  be the diagonal matrix whose diagonal entries are the row sums of G.

Since G is row column compatible, they are also the column sums.

So we have  $\bar{G}\mathbf{e}^{\top} = G\mathbf{e}^{\top}$  and  $\mathbf{e}\bar{G} = \mathbf{e}G$ , and we also have  $(G - \bar{G}P)\mathbf{e}^{\top} = 0$ .

Define  $S' = \bar{S}D^{-1}(G - \bar{G}P)$ . We see that  $S' \in \mathfrak{S}$ .

From the last two equations we have  $S'\mathbf{e}^{\top} = 0$ . But we have  $\bar{S}'\mathbf{e}^{\top} = S'\mathbf{e}^{\top}$ , so  $\bar{S}'\mathbf{e}^{\top} = 0$ . Since  $\bar{S}'$  is diagonal, this means that  $\bar{S}' = 0$ .

We now put our values for S' and  $\bar{S}'$  in equation (14). It becomes

$$P' = D^{-1}(G - \bar{G}P) .$$

So we have this.

$$\tilde{\mathbf{p}}P' = \mathbf{e}(G - \bar{G}P) = \mathbf{e}G - \mathbf{e}\bar{G}P = \mathbf{e}G - \mathbf{e}GP = \mathbf{e}G(I - P)$$

Since  $\mathbf{e}G\mathbf{e}^{\top} = 0$ , we can write

$$\tilde{\mathbf{p}}P' = \mathbf{e}G(I-P) = \mathbf{e}G(I-P) + (\mathbf{e}G\mathbf{e}^{\top})\tilde{\mathbf{p}} = \mathbf{e}G\hat{P}$$
.

$$\tilde{\mathbf{p}}P'\hat{P}^{-1} = \mathbf{e}G$$

By equation (15), this becomes  $\tilde{\mathbf{p}}' = \mathbf{e}G$ .

Now  $\mathbf{e}D' = \tilde{\mathbf{p}}'$  and  $\mathbf{e}\bar{G} = \mathbf{e}G$ , so we have  $\mathbf{e}D' = \mathbf{e}\bar{G}$ .

Since D' and  $\bar{G}$  are diagonal, we have

 $D' = \bar{G}$ .

We insert our values of P' and D' in equation (12).

$$F' = \bar{G}P + D(D^{-1}(G - \bar{G}P)) = G$$

So we see that  $\mathfrak{F}$  is exactly the set of all possible matrices F'.

Remember that we have a fixed S and we are investigating what P' and F' are for different matrices S' . We define a relation from  $\mathfrak P$  to  $\mathfrak F$  that I call the *derivative relation*.

Derivative Relation:

Suppose  $A \in \mathfrak{P}$  and  $G \in \mathfrak{F}$ .

Matrix A is related to matrix G if and only if there is an S' in  $\mathfrak{S}$  that

both gives us a P' equal to A and also gives us an F' equal to G.

In the above definition, when I said "if there is an S' in  $\mathfrak{S}$  that" I meant if there is at least one such S'. If there is one there are probably lots.

Lemmas 1 and 2 tell us that the domain of the derivative relation is the whole of  $\mathfrak{P}$  and that the range of the derivative relation is the whole of  $\mathfrak{F}$ .

Equations (15), (12), (11), and (13) tell us that whatever S' is, we have  $F'=(\operatorname{diag}(\mathbf{\tilde{p}}P'\hat{P}^{-1}))\,P+DP'$  and

 $P' = D^{-1}(F' - (\operatorname{diag}(\mathbf{e} F')) P) .$ 

So if A is related to G by the derivative relation, then we have

 $G = (\operatorname{diag}(\mathbf{\tilde{p}}A\hat{P}^{-1}))P + DA$ and

 $A = D^{-1}(G - (\operatorname{diag}(\mathbf{e} G)) P) .$ 

In other words, A determines G, and G determines A. The derivative relation is one to one.

The derivative relation is a function from  $\,\mathfrak{P}\,$  one to one and onto  $\,\mathfrak{F}\,$ .

If at the start of section 3 we had selected a different fixed S then we would probably have had a different derivative relation. The set  $\mathfrak P$  would have been the same, and the set  $\mathfrak F$  would have been the same, and the new different derivative relation would still have been a function from  $\mathfrak{P}$  one to one and onto  $\mathfrak{F}$ .

So in a sense we can say that the fixed matrix S determines the derivative relation. We selected a particular S at the start of this section and we are sticking with it. Our derivative relation is fixed and unchanging.

### 3.2The Key Equivalence

**Notation:** In this paper, K is a positive real number.

I call it the adaptation rate. It is constant. It might be any positive real.

Now at last we are ready to prove the Key Equivalence, Lemma 6.

We begin with the easy part, the forward implication.

Of course whatever S' is, it gives us a P' and F' such that

$$P'$$
 is related to  $F'$  by the derivative relation. (22)

We now show that whatever S' is, it gives us a P' and F' for which the following lemma holds.

## Lemma 3

If for all ij we have  $F'_{ij} = F_{ij}Kv_{ij}$ , then for all ij we have  $\tilde{p}'_i = \tilde{p}_iK\bar{v}_i$  and  $P'_{ij} = P_{ij}Kh_{ij}$ .

### Proof:

Assume for all ij we have  $F'_{ij} = F_{ij}Kv_{ij}$ . We know that  $\sum_j F_{ij} = \tilde{p}_i$ , so taking derivatives and using the assumption and equation (19) gives us  $\tilde{p}'_i = \sum_j F'_{ij} = \sum_j F_{ij}Kv_{ij} = K\sum_j F_{ij}v_{ij} = K\tilde{p}_i\bar{v}_i$ .

$$\tilde{p}_i' = \tilde{p}_i K \bar{v}_i \tag{23}$$

Now we derive an expression for  $P'_{ij}$  . Applying the product rule to  $F_{ij} = \tilde{p}_i P_{ij}$  $\begin{array}{lll} F'_{ij} = \tilde{p}'_i P_{ij} + \tilde{p}_i P'_{ij} \; . & \text{From this and the assumption and (23) we obtain} \\ \tilde{p}_i P'_{ij} = F'_{ij} - \tilde{p}'_i P_{ij} \; = \; F_{ij} K v_{ij} - \tilde{p}_i K \bar{v}_i P_{ij} \; = \; \tilde{p}_i P_{ij} K (v_{ij} - \bar{v}_i) \; = \; \tilde{p}_i P_{ij} K h_{ij} \; . \end{array}$ From this and the assumption and (23) we obtain

$$\tilde{p}_i P'_i = F'_i - \tilde{p}'_i P_{i\dot{\alpha}} = F_{i\dot{\alpha}} K v_{i\dot{\alpha}} - \tilde{p}_i K \bar{v}_i P_{i\dot{\alpha}} = \tilde{p}_i P_{i\dot{\alpha}} K (v_{i\dot{\alpha}} - \bar{v}_i) = \tilde{p}_i P_{i\dot{\alpha}} K h_{i\dot{\alpha}}$$

$$P'_{ij} = P_{ij}Kh_{ij} \quad . \tag{24}$$

Now what we are going to do is turn the implication in Lemma 3 round the other way and say that if  $P'_{ij} = P_{ij}Kh_{ij}$  for all ij then  $F'_{ij} = F_{ij}Kv_{ij}$  for all ij. In a sense, it's obvious that the reverse implication follows directly from the fact that the derivative relation is one to one, but because this reverse implication is central we are going to be pedantic about proving it.

```
Suppose we have a positive real number K and matrices P^* and F^*
for which the following two statements hold:
```

(statement 1)  $P_{ij}^* = P_{ij}Kh_{ij}$  for all ij. (statement 2)  $F_{ij}^* = F_{ij}Kv_{ij}$  for all ij. Then the following three things are true:

- (A)  $P^* \in \mathfrak{P}$
- (B)  $F^* \in \mathfrak{F}$
- (C)  $P^*$  is related to  $F^*$  by the derivative relation.

### **Proof:**

Suppose we have a K,  $P^*$ , and  $F^*$  such that the two statements in the lemma's supposition hold.

We note that in both  $P^*$  and  $F^*$ , every entry corresponding to an illegal transition is zero.

By equation (6), every row sum in  $P^*$  is zero.

Therefore,  $P^* \in \mathfrak{P}$ . (conclusion (A))

Equation (19) can be written  $\sum_{j} F_{ji} v_{ji} = \tilde{p}_{i} \bar{v}_{i} = \sum_{j} F_{ij} v_{ij}$ ,

so we see that  $F^*$  is row column compatible.

Equation (20) tells us that the entries in  $F^*$  all sum to zero.

Therefore,  $F^* \in \mathfrak{F}$ . (conclusion (B))

Now since  $F^* \in \mathfrak{F}$ , Lemma 2 tells us that there is some derivative matrix

S' in  $\mathfrak{S}$  such that  $F' = F^*$ .

We will use that derivative S' matrix. It gives us P' and F'.

 $F'_{ij} = F_{ij}Kv_{ij}$  for all ij. We have  $F' = F^*$ , so by supposition (statement 2) we have

Lemma 3 then tells us that we have  $P'_{ij} = P_{ij}Kh_{ij}$  for all ij. Comparing this with supposition (statement 1) tells us that  $P' = P^*$ .

So S' gives us a P' equal to  $P^*$  and also gives us an F' equal to  $F^*$ 

This means by definition that  $P^*$  is related to  $F^*$  by the derivative relation. (conclusion (C))

Whatever S' is, it gives us a P' and F' for which the following lemma holds.

### Lemma 5

If for all ij we have  $P'_{ij} = P_{ij}Kh_{ij}$ , then for all ij we have  $F'_{ij} = F_{ij}Kv_{ij}$ .

Suppose we have an S' such that  $P'_{ij}=P_{ij}Kh_{ij}$  for all ij. We use that same K to define the matrix  $F^*$  such that

$$F_{ij}^* = F_{ij}Kv_{ij}$$
 for all  $ij$ .

And we define the matrix  $P^*$  by simply setting  $P^* = P'$ .

So now, looking at  $P^*$  and  $F^*$ , we see that both statements in the Lemma 4 supposition hold.

So Lemma 4 tells us that  $P^*$  is related to  $F^*$  by the derivative relation.

And of course P' is related to F' by the derivative relation. (See (22).)

 $P^* = P'$ Since and the derivative relation is one to one, it follows that  $F^* = F'$ .

Therefore we have

$$\underline{F}'_{ij} \ = \ F^*_{ij} \ = \ F_{ij}Kv_{ij} \quad \text{ for all } \ ij \ .$$

This is Lemma 3 reversed.

In a sense Lemma 5 is obvious, but in another sense it's astonishing.

Let's re-write it using the definitions of  $h_{ij}$  and  $v_{ij}$ .

If for all 
$$ij$$
 we have  $P'_{ij} = P_{ij}K(c_j - c_i + a_i)$ , then for all  $ij$  we have  $F'_{ij} = F_{ij}K(b_i + c_j)$ .

The astonishing part is the pre-values  $b_i$ , which appear in the implication's consequent but not in the antecedent.

In Lemma 3 the implication is the other way round, and all the proof of Lemma 3 has to do is find a way of getting rid of the pre-values by having them cancel one another. But in Lemma 5 the pre-values pop into existence, created out of thin air.

We can now sum up the results of this subsection.

Whatever S' is, it gives us a P' and F' for which the following lemma holds.

### The Key Equivalence Lemma 6

The equation 
$$F'_{ij} = F_{ij}Kv_{ij}$$
 holds for all  $ij$  if and only if the equation  $P'_{ij} = P_{ij}Kh_{ij}$  holds for all  $ij$ .

### **Proof:**

The forward implication is Lemma 3.

The backward implication is Lemma 5.

Let's look at Lemma 6. It holds whatever S' is. At the start of section 3 we selected an arbitrary matrix S. That S determines each  $F_{ij}$ ,  $v_{ij}$ ,  $P_{ij}$ , and  $h_{ij}$ , so it determines the right hand sides of the equations in the lemma. It also determines the derivative relation.

If at the start of section 3 we had selected a different S, then we would have had different  $F_{ij}$ ,  $v_{ij}$ ,  $P_{ij}$ , and  $h_{ij}$ . Sets  $\mathfrak{P}$  and  $\mathfrak{F}$  would have been the same, but the derivative relation would have been different. But Lemma 6 would still hold whatever S' is.

So whatever S we select, Lemma 6 holds whatever S' is. In other words, whatever S and S' are, Lemma 6 holds. We can now forget about the derivative relation. Lemma 6 always holds.

# Natural Adaptive Plans

We now define a class of adaptive plans that I call Natural Plans. 14

## Natural Adaptive Plan

There are numbers 
$$\beta_1, \beta_2, \beta_3, ...., \beta_N$$
 such that for all  $ij$  we have  $s'_{ij} = s_{ij}K(\beta_i + c_j)$ .

Plan  $s'_{ij} = s_{ij}Kc_j$  and plan  $s'_{ij} = s_{ij}Kh_{ij}$  are both Natural Plans. 15 We first show that Natural Plans tend to increase payoff.

### Lemma 7

In any Natural Plan,  

$$\bar{m}' = K \sum_{ij} F_{ij} h_{ij}^2$$
.

### **Proof:**

If we write  $\sum_{ij}$  to mean sum over all legal transitions  $i \to j$ , then we have  $\bar{m}' = \sum_{ij} \frac{\partial \bar{m}}{\partial s_{ij}} s'_{ij}$ . Using equation (17) and the definition of Natural Plan, this becomes

$$\bar{m}' = \sum_{ij} q_i h_{ij} s_{ij} K(\beta_i + c_j)$$
.

If there is no legal transition from i to j, then  $s_{ij} = 0$ ,

so we see that the last equation holds if the sum is over all ij .

$$\bar{m}' = K \sum_{i} \tilde{p}_{i} P_{i,i} h_{i,i} (h_{i,i} + c_{i} - a_{i} + \beta_{i})$$

We now use 
$$q_i s_{ij} = \tilde{p}_i P_{ij}$$
 and  $c_j = h_{ij} + c_i - a_i$ .  
 $\bar{m}' = K \sum_{ij} \tilde{p}_i P_{ij} h_{ij} (h_{ij} + c_i - a_i + \beta_i)$   
 $\bar{m}' = K \sum_{ij} \tilde{p}_i P_{ij} h_{ij}^2 + K \sum_i \tilde{p}_i (c_i - a_i + \beta_i) \sum_j P_{ij} h_{ij}$ 

Equation (6) tells us that the second term on the right is zero.

Lemma 7 is an analog of Fisher's Fundamental Theorem of Natural Selection.

We see that  $\bar{m}'$  can be zero only if  $h_{ij}$  is zero for every legal transition  $i \to j$ . Equation (17) says that this can happen only if the ground is level.

 $<sup>^{14}\</sup>mathrm{Natural}$  in the sense of a natural population.

<sup>&</sup>lt;sup>15</sup>This paper does not discuss plan implementation. There are various implementations of these Natural Plans, but it doesn't work to simply add  $Kc_j$  to the availability  $s_{ij}$  of the current transition  $i \to j$ . That implements the plan  $s'_{ij} = F_{ij}Kc_j$ , which is not a Natural Plan.

So in a Natural Plan, the climb rate  $\bar{m}'$  is positive unless the ground is level. The quantity  $\bar{m}$  is a function of S, and we are heading uphill on that function unless the ground is level.

We now show that it is the Natural Plans for which the equations in the Key Equivalence hold.

### Lemma 8

If there are numbers  $\beta_1, \beta_2, \beta_3, ..., \beta_N$  such that for all ij we have  $s'_{ij} = s_{ij}K(\beta_i + c_j)$ , then for all ij we have  $P'_{ij} = P_{ij}Kh_{ij}$ .

Assume for all ij we have  $s'_{ij} = s_{ij}K(\beta_i + c_j)$ . Now we have  $\bar{s}_i = \sum_j s_{ij}$ , so using equation (5) gives us this.  $\bar{s}'_i = \sum_j s'_{ij} = \sum_j s_{ij}K(\beta_i + c_j) = \bar{s}_iK\sum_j P_{ij}(\beta_i + c_j) = \bar{s}_iK(\beta_i + \sum_j P_{ij}c_j) = \bar{s}_iK(\beta_i + c_i - a_i)$ We have  $s_{ij} = \bar{s}_iP_{ij}$ , so  $s'_{ij} = \bar{s}'_iP_{ij} + \bar{s}_iP'_{ij}$ . Substituting for  $s'_{ij}$  and  $\bar{s}'_i$  gives us  $s_{ij}K(\beta_i + c_j) = \bar{s}_iK(\beta_i + c_i - a_i)P_{ij} + \bar{s}_iP'_{ij}$ . Dividing by  $\bar{s}_i$  gives us  $P_{ij}K(\beta_i + c_j) = P_{ij}K(\beta_i + c_i - a_i) + P'_{ij}$ , which simplifies to  $P_{ij}Kh_{ij} = P'_{ij}$ .

### Lemma 9

If for all ij we have  $P'_{ij} = P_{ij}Kh_{ij}$ , then there are numbers  $\beta_1, \beta_2, \beta_3, ..., \beta_N$  such that for all ij we have  $s'_{ij} = s_{ij}K(\beta_i + c_j)$ .

Assume for all ij we have  $P'_{ij} = P_{ij}Kh_{ij}$ . For each i, we define  $\beta_i = K^{-1}\bar{s}_i'\bar{s}_i^{-1} - c_i + a_i$ . Then  $K(\beta_i + c_j) = \bar{s}_i'\bar{s}_i^{-1} + Kh_{ij}$ . Since  $s_{ij} = \bar{s}_i P_{ij}$ , we have  $s'_{ij} = \bar{s}'_i P_{ij} + \bar{s}_i P'_{ij} = \bar{s}'_i \bar{s}_i^{-1} s_{ij} + \bar{s}_i P_{ij} K h_{ij} = s_{ij} (\bar{s}'_i \bar{s}_i^{-1} + K h_{ij}) = s_{ij} K (\beta_i + c_j)$ 

From Lemmas 8, 9, and 6, we see that we have

## Theorem 1

The following three conditions are equivalent. Either all three conditions hold or none of them do.

- $F'_{ij} = F_{ij}Kv_{ij}$  for all ij.  $P'_{ij} = P_{ij}Kh_{ij}$  for all ij. There are numbers  $\beta_1, \beta_2, \beta_3, ...., \beta_N$  such that  $s'_{ij} = s_{ij}K(\beta_i + c_j)$  for all ij.

Theorem 1 gives us three equivalent definitions of Natural Plan.

Lemma 3 tells us that in any Natural Plan we have  $\tilde{p}'_i = \tilde{p}_i K \bar{v}_i$ .

Now let's look at string frequencies.

Suppose  $\sigma$  is the example string we gave in (21). There we gave the expressions for the string's frequency  $\varphi_{\sigma}$  and total value  $v_{\sigma}$ . We have the following.

$$\varphi_{\sigma} = \tilde{p}_{\alpha} P_{\alpha\beta} P_{\beta i} P_{ij} P_{j\delta} P_{\delta\varepsilon} \log(\varphi_{\sigma}) = \log(\tilde{p}_{\alpha}) + \log(P_{\alpha\beta}) + \log(P_{\beta i}) + \log(P_{ij}) + \log(P_{j\delta}) + \log(P_{\delta\varepsilon})$$

$$\frac{\varphi_{\sigma}'}{\varphi_{\sigma}} = \frac{\tilde{p}_{\alpha}'}{\tilde{p}_{\alpha}} + \frac{P_{\alpha\beta}'}{P_{\alpha\beta}} + \frac{P_{\beta i}'}{P_{\beta i}} + \frac{P_{ij}'}{P_{ij}} + \frac{P_{j\delta}'}{P_{j\delta}} + \frac{P_{\delta\varepsilon}'}{P_{\delta\varepsilon}}$$

Now suppose we are using a Natural Plan. Then the last equation becomes

$$\begin{split} \varphi_{\sigma}^{-1}\varphi_{\sigma}' &= K\bar{v}_{\alpha} + Kh_{\alpha\beta} + Kh_{\beta i} + Kh_{ij} + Kh_{j\delta} + Kh_{\delta\varepsilon} \\ K^{-1}\varphi_{\sigma}^{-1}\varphi_{\sigma}' &= \bar{v}_{\alpha} + h_{\alpha\beta} + h_{\beta i} + h_{ij} + h_{j\delta} + h_{\delta\varepsilon} \\ &= (b_{\alpha} - a_{\alpha} + c_{\alpha}) + (c_{\beta} - c_{\alpha} + a_{\alpha}) + (c_{i} - c_{\beta} + a_{\beta}) + (c_{j} - c_{i} + a_{i}) + (c_{\delta} - c_{j} + a_{j}) + (c_{\varepsilon} - c_{\delta} + a_{\delta}) \\ &= b_{\alpha} + a_{\beta} + a_{i} + a_{j} + a_{\delta} + c_{\varepsilon} \\ &= v_{\sigma} \end{split}$$

$$\varphi_{\sigma}' = \varphi_{\sigma} K v_{\sigma} \tag{25}$$

It is easy to see that if we are using a Natural Plan, then Equation (25) holds in general for any string  $\sigma$  of any length.

The converse is also true. If equation (25) holds in general for any string  $\sigma$  then the plan we are using must be Natural since equation  $F'_{ij} = F_{ij}Kv_{ij}$  is a special case of equation (25). So we have:

### Corollary 1

```
An adaptive plan is Natural if and only if \varphi'_{\sigma} = \varphi_{\sigma} K v_{\sigma} \quad \text{for every transition string } \sigma.
```

Corollary 1 amounts to a fourth definition of Natural Plan.

Equation (25) is the same as equation (1).

Strings of transitions are strings in time, and strings of genes are strings in space, but their frequencies here are changing in the same way. Learning and evolution are similar processes.

# 5 Time Symmetry

This paper analyses only the cases where the Markov property holds. The results form the basis of analysis of more complicated cases, but that is beyond the scope of this paper. This paper can be thought of as a proof of Theorem 1 and Corollary 1.

In retrospect, Theorem 1 looks almost obvious, but it long eluded us. To compare changes in transition frequencies with changes in gene frequencies we needed a usable formula for  $F'_{ij}$ , the change in unconditional transition frequency. All our formulae for  $F'_{ij}$  were terribly complicated until we realized we should include pre-values in the analysis. Then everything simplified. The time-symmetric approach works.

This paper shows that in the basic case, where the Markov property holds, string frequencies change according to the same simple formula whether the strings are strings of actions in time or strings of genes in space.

Learning and Evolution are similar processes.

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