

# Mutual Information for a Replicator System: the Role of Mutation

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# Mutual Information for a Replicator System: the Role of Mutation

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## Abstract

What does an evolving population remember about the environments it has experienced? This fundamental question connects adaptation, information theory, and the reconstruction of environmental history. We study a multispecies replicator–mutator system in a fluctuating environment, focusing on the information that population composition contains about the latest environment and the preceding sequence of environments. Without mutation, we prove that for independently sampled environments, mutual information about the latest environment vanishes with an  $O(1/n)$  upper bound as the number of epochs increases and is independent of epoch duration under exact observation. Nevertheless, a necessary and sufficient rational-independence condition allows exact recovery of environmental visit counts, although their order is lost. With strictly positive mutation, a strikingly different picture emerges: when environment-specific equilibria are distinct and epochs are sufficiently long, composition identifies the latest environment even in the presence of some noise. Moreover, in the noiseless case, decoding and inverting successive evolutionary flows recovers the entire ordered history at every known finite horizon. Thus mutation, intuitively associated with information loss and the erasure of memory, can enable an ordered environmental record that mutation-free dynamics cannot retain. Our results distinguish exact historical encoding from practically accessible memory and reveal how mutation can fundamentally alter the information retained by an evolving population.

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# 1 Introduction

Evolution by natural selection has long been viewed not only as a process of adaptation, but also as a process through which populations acquire and store information about their environments. As environmental conditions favor some heritable variants over others, the genetic and phenotypic composition of a population changes in ways that reflect the selective pressures it has experienced. From this perspective, an evolving population can be regarded as a system that learns from its environment, with natural selection providing a mechanism for updating information and heredity allowing that information to persist across generations. This viewpoint has been developed in several complementary directions: information-theoretic approaches interpret adaptation as the accumulation of environmental information in genomes [Adami \[2002, 2012\]](#); connections between natural selection, Bayesian inference, and learning theory describe evolutionary dynamics as a form of information updating [Frank \[2012\]](#); [Czégel et al. \[2022\]](#); [Vanchurin et al. \[2022\]](#); and studies of populations in fluctuating environments quantify the relationship between environmental information and long-term reproductive success [Donaldson-Matasci et al. \[2010\]](#); [Rivoire and Leibler \[2011\]](#); [Mafessoni et al. \[2021\]](#); [Piñero et al. \[2026\]](#). All these perspectives suggest that the state of an evolving population may encode a record of its environmental experience. Yet this raises a fundamental question: what information about the environment is actually retained in the population, and to what extent can that information be recovered from its present composition?

The idea that evolving populations retain information about their environmental history has been investigated in several different settings. [Guttenberg \[2019\]](#) studied the acquisition and loss of environmental information in simulated evolving populations, examining how mutation and environmental fluctuations affect the timescales of evolutionary memory. This work demonstrates the importance of distinguishing information about newly encountered environments from information retained about earlier ones. [Marzen and Crutchfield \[2018\]](#) investigate a different aspect of memory: its usefulness for prediction. In their analysis of bacterial bet-hedging, epigenetic memories improve growth by retaining information relevant to future environmental conditions; efficient memories are connected to minimal sufficient statistics for prediction, or approximations to them. From a complementary perspective, [Czégel et al. \[2022\]](#) established mathematical connections between evolutionary dynamics and Bayesian inference, including an interpretation of mutation–selection dynamics in terms of filtering hidden environmental states. These studies suggest that population composition may be viewed as a record of environmental experience, whose informational content evolves over time. However, the precise nature of this record, and in particular which aspects of the

environmental history can be inferred from the present population composition, remain questions that depend on the underlying evolutionary dynamics.

In this paper, we investigate what population composition reveals about environmental experience in a replicating population evolving in a fluctuating environment. We consider a quasispecies model in which the reproductive rates of different types depend on the environment, and environmental conditions change between successive epochs. Our main object of study is the mutual information between the environment experienced during an epoch and the population composition at its endpoint. We also ask a more general question: to what extent does the present population composition retain information about the entire sequence of environments encountered during its evolution? Particular attention is given to the role of mutation, which, as we show, can fundamentally alter the way environmental information is represented and retained.

Our results reveal a striking contrast between evolution with and without mutation. In the absence of mutation, the mutual information between the most recent environment and the resulting population composition vanishes asymptotically when the environments are independently sampled. Nevertheless, under suitable conditions, the population retains an exact record of how many times each environment has occurred, although not of their temporal order. In contrast, when mutation is present, with a strictly positive mutation matrix and distinguishable environment-specific equilibria, sufficiently long environmental epochs guarantee that the most recent environment can be identified exactly from the population composition, independently of the preceding history. Moreover, under these conditions, exact observation of the population at any finite time horizon allows reconstruction of the entire ordered environmental history. This reconstruction, however, can become increasingly sensitive to observational errors as the history grows longer.

These findings illustrate a subtle and somewhat counterintuitive relationship between evolution and environmental information. In particular, we show that mutation, usually regarded as a source of genetic variation and a mechanism that can erode inherited information, can also enable the population composition to distinguish environmental histories that would otherwise be indistinguishable. Our analysis thus provides a concrete information-theoretic characterization of evolutionary memory and clarifies the role of mutation in determining what an evolving population can reveal about its environmental experience.

Our results below distinguish information about the latest environment from memory of the accumulated environmental history. Without mutation, Theorem 3.2 shows that the mutual information between an epoch’s environment and its endpoint composition is independent of epoch duration and vanishes with an  $O(1/n)$  upper bound under iid environmental sampling. Nevertheless, Theorem 3.3 gives a necessary and sufficient rational-independence condition for exact recovery of environmental visit counts at every known finite horizon; Corollary 3.5 expresses this count memory in information-theoretic terms, and Section 3.3 provides a reconstruction algorithm. With strictly positive mutation, Lemma 4.1 establishes contraction in Hilbert’s projective distance, which underlies the sufficient epoch duration for complete identification of the latest environment in Theorem 4.6. Under the same separation assumptions, Corollary 4.10 establishes exact recovery of the full ordered environmental history, implemented by the backward reconstruction algorithm in Section 4.6. Finally, Corollary 4.11 guarantees identification of the latest environment under sufficiently small bounded observation error, while the analysis of historical reconstruction explains why recovering earlier environments can become increasingly sensitive to finite precision.

## 2 Setup and notations

### 2.1 The quasi-species model

We consider a population of  $S \geq 2$  species in one of  $M \geq 2$  environments, labelled  $\mathcal{E} = \{\varepsilon_1, \dots, \varepsilon_M\}$ . In environment  $\varepsilon_r$ , species  $j$  reproduces at a constant rate  $f_{jr} > 0$ , independent of the population composition. Let  $Q_{ij}$  be the probability that a species- $j$  parent produces a species- $i$  offspring. The mutation matrix  $Q$  is fixed across environments and satisfies

$$Q_{ij} \geq 0, \quad \sum_{i=1}^S Q_{ij} = 1. \quad (2.1)$$

Thus each column of  $Q$  describes the possible offspring types of one parental species. When mutation is symmetric, we have

$$Q_{ii}(u) = 1 - u, \quad Q_{ij}(u) = \frac{u}{S-1} \quad (i \neq j), \quad 0 \leq u \leq 1. \quad (2.2)$$

where  $u$  is the total probability of mutation at a reproduction event.

Next, we will give a short derivation of the quasi-species model, which is the ODE model used in this paper, see [Eigen \[1971\]](#); [Eigen and Schuster \[2012\]](#). Let  $z_i(t)$  denote the abundance of species  $i$ . Species- $j$  parents produce species- $i$  offspring at rate  $Q_{ij}f_{jr}z_j$ . Summing over parental species gives

$$\dot{z}_i = \sum_{j=1}^S Q_{ij}f_{jr}z_j, \quad (2.3)$$

where dot denotes the time derivative. In matrix form, that is

$$\dot{\mathbf{z}} = W_r \mathbf{z}, \quad (2.4)$$

where  $W_r := Q \operatorname{diag}(\mathbf{f}_r)$ ,  $\mathbf{f}_r = (f_{1r}, \dots, f_{Sr})^\top$ .

Instead of the absolute abundance, let us focus on the population composition, characterized by the population frequencies  $x_i = z_i/Z$ , where  $Z = \sum_j z_j$  is the total abundance. Writing  $\mathbf{x} = (x_1, \dots, x_S)^\top$ , we notice that

$$\dot{Z} = \sum_{i=1}^S \sum_{j=1}^S Q_{ij}f_{jr}z_j = \sum_{j=1}^S f_{jr}z_j = Z \bar{f}_r(\mathbf{x}), \quad \bar{f}_r(\mathbf{x}) := \mathbf{f}_r^\top \mathbf{x}. \quad (2.5)$$

The quotient rule now gives

$$\begin{aligned} \dot{x}_i &= \frac{\dot{z}_i}{Z} - \frac{z_i \dot{Z}}{Z^2} = \sum_{j=1}^S Q_{ij}f_{jr}x_j - \bar{f}_r(\mathbf{x})x_i, \\ \dot{\mathbf{x}} &= W_r \mathbf{x} - \bar{f}_r(\mathbf{x})\mathbf{x}. \end{aligned} \quad (2.6)$$

This ODE ensures that  $\sum_i x_i = 1$  is preserved. When there is no mutation,  $Q = I_S$ , the equation reduces to  $\dot{x}_i = (f_{ir} - \bar{f}_r(\mathbf{x}))x_i$ : a species increases in frequency when its reproduction rate exceeds the population average.

For a fixed environment,  $W_r$  is constant, so the abundance equation has the solution

$$\mathbf{z}(t) = \exp(tW_r)\mathbf{z}(0).$$

Given an initial composition  $\mathbf{x}(0)$ , normalizing the solution therefore gives the explicit flow map

$$\Phi_r^t(\mathbf{x}(0)) = \frac{\exp(tW_r)\mathbf{x}(0)}{\mathbf{1}^\top \exp(tW_r)\mathbf{x}(0)}. \quad (2.7)$$

## 2.2 Fitness seascape

To describe environmental changes, we allow the fitness values to depend on the environments as well, hence the notation  $f_{jr}$ . We assume environment changes in epochs of fixed duration. Denote this duration  $T$ . During epoch  $n$  or  $[nT, (n+1)T)$ , its environment  $E_n$  is chosen iid from  $\mathcal{E} = \{\varepsilon_1, \dots, \varepsilon_M\}$ :

$$\mathbb{P}(E_n = \varepsilon_r) = p_r > 0, \quad \sum_{r=1}^M p_r = 1. \quad (2.8)$$

The population then carries its composition from one epoch to the next:

$$\mathbf{X}_n := \mathbf{X}(nT), \quad \mathbf{X}_{n+1} = \Phi_r^T(\mathbf{X}_n) \quad \text{when } E_n = \varepsilon_r. \quad (2.9)$$

Here we use  $\mathbf{X}$  to indicate that it is a random variable, unlike the  $\mathbf{x}$  in an ODE. Thus each epoch allows the system to evolve from the result of the previous epoch, the dynamics of which depends on the environment drawn randomly.

## 2.3 Mutual Information

For a discrete random variable  $A$  taking values in a finite set  $\mathcal{A}$ , its Shannon entropy is

$$H(A) := - \sum_{a \in \mathcal{A}} \mathbb{P}(A = a) \log_2 \mathbb{P}(A = a),$$

with the convention  $0 \log_2 0 := 0$ . Using base-two logarithms, entropy is measured in bits.

For two random variables  $A$  and  $Z$ , their mutual information (MI) is defined as

$$I(A; Z) := H(A) - H(A | Z).$$

which is also in bits.

The main quantity that will be of interest to us is the mutual information between the species frequency composition and the current environment, which we denote  $I(E_n; \mathbf{X}_{n+1})$  for the  $n$ th epoch. This is an information-theoretic tool that measures how much the current environment can tell us about the frequencies, and vice-versa.

Observations are exact unless an error bound is explicitly given. No differential entropy of the population is required. At each fixed finite horizon with a deterministic initial state and a finite environmental alphabet, the population endpoint in fact has finite support. Under iid sampling, the next environment  $E_{n+1}$  is independent of  $\mathbf{X}_{n+1}$ ; this independence is not asserted for correlated environments.

## 3 Without mutation: cumulative memory and vanishing matched information

Throughout this section, the algebraic identities below hold for every fixed environmental history, regardless of how the environments are selected. We assume iid environmental sampling without needing to specify a specific distribution.

### 3.1 Log-ratio coordinates

It is convenient to use log-ratio coordinates, which we will establish below.

Use species  $S$  as a reference. Define the coordinate map

$$\ell : \Delta_S^\circ \longrightarrow \mathbb{R}^{S-1}, \quad y_i = \ln \frac{x_i}{x_S}, \quad i = 1, \dots, S-1, \quad (3.1)$$

where

$$\Delta_S^\circ := \left\{ \mathbf{x} \in (0, 1)^S : \sum_{i=1}^S x_i = 1 \right\} \quad (3.2)$$

is the set of all possible frequency compositions.

It is a smooth bijection, which performs a change of variables on our ODE. The bijection also means that

$$I(E_n; \mathbf{X}_{n+1}) = I(E_n; \mathbf{Y}_{n+1}). \quad (3.3)$$

The map  $\ell$  has inverse

$$x_i = \frac{\exp(y_i)}{1 + \sum_{k=1}^{S-1} \exp(y_k)} \quad (i < S), \quad x_S = \frac{1}{1 + \sum_{k=1}^{S-1} \exp(y_k)}. \quad (3.4)$$

Notice that it is actually the softmax function, hence  $y_S = 0$ . Write  $\mathbf{Y}(t) = \ell(\mathbf{X}(t))$ ,  $\mathbf{Y}_n = \ell(\mathbf{X}_n)$ , and  $\mathbf{y}_0 = \ell(\mathbf{x}_0)$ . The mean-fitness terms cancel, yielding

$$\dot{y}_i = \frac{(W_r \mathbf{x})_i}{x_i} - \frac{(W_r \mathbf{x})_S}{x_S} = \sum_{j=1}^S (W_r)_{ij} \exp(y_j - y_i) - \sum_{j=1}^S (W_r)_{Sj} \exp(y_j), \quad i < S. \quad (3.5)$$

For  $S > 2$  this is generally a coupled ODE system. This change of variable will be useful later.

### 3.2 A vector-valued random walk

When there is no mutation,  $Q$  is the identity matrix, and as a result,  $W_r$  is a diagonal matrix for each environment  $r$ . Thus, equation (3.5) reduces to  $\dot{y}_i = f_{ir} - f_{Sr}$ . Define

$$\mathbf{s}_r = (f_{1r} - f_{Sr}, \dots, f_{S-1,r} - f_{Sr})^\top \in \mathbb{R}^{S-1}, \quad \mathbf{s}(\varepsilon_r) = \mathbf{s}_r. \quad (3.6)$$

For an epoch-horizon  $L \geq 1$ , meaning that we stop at the  $L$ th epochs, let

$$C_r^{(L)} := \sum_{k=0}^{L-1} \mathbf{1}_{\{E_k = \varepsilon_r\}}, \quad \mathbf{C}^{(L)} = (C_1^{(L)}, \dots, C_M^{(L)}) \quad (3.7)$$

be the count vector. Integrating the constant velocity in each epoch gives

$$\mathbf{Y}_L = \mathbf{y}_0 + T \mathbf{A}_L, \quad \mathbf{A}_L := \sum_{k=0}^{L-1} \mathbf{s}(E_k) = \sum_{r=1}^M C_r^{(L)} \mathbf{s}_r, \quad (3.8)$$

where  $\mathbf{Y}_L$  denotes the random vector-valued variable representing the frequency composition after epoch  $L$ , under the log-ratio coordinate.

Under iid environments, the increments  $T \mathbf{s}(E_k)$  are iid, so  $\mathbf{Y}_L$  is a vector-valued random walk. For every  $T > 0$ , exact knowledge of  $\mathbf{X}_L$  is equivalent to exact knowledge of  $\mathbf{Y}_L$  (since they are bijective), which is also equivalent to exact knowledge of  $\mathbf{A}_L$ . Consequently

$$I(E_{L-1}; \mathbf{X}_L) = I(E_{L-1}; \mathbf{A}_L) \quad (3.9)$$

is independent of  $T > 0$ . This is an exact-observation statement: a change of  $T$  can change distinguishability when observational errors are considered.

### 3.3 Matched information vanishes

The following lemma expresses the information about one environmental draw contained in the empirical count vector. Its upper bound is equivalent to the bound on the bias of the empirical entropy estimator established by Paninski [2003]. We include a short proof to make the application self-contained. Define the KL-divergence between two distributions  $a, b$  with  $b_r > 0$  as

$$D_{\text{KL}}(a||b) = \sum_{r:a_r>0} a_r \log_2 \frac{a_r}{b_r}.$$

**Lemma 3.1** (Information in iid counts). *Assume (2.8) and let  $\hat{p}_r = C_r^{(L)}/L$ . For every  $k \in \{0, \dots, L-1\}$ ,*

$$I(E_k; \mathbf{C}^{(L)}) = \mathbb{E} D_{\text{KL}}(\hat{p}||p) \leq \log_2 \left( 1 + \frac{M-1}{L} \right). \quad (3.10)$$

*Proof.* Conditional on a given count vector, all arrangements of those counts have the same probability  $\prod_r p_r^{C_r^{(L)}}$ . Therefore, we have  $\mathbb{P}(E_k = \varepsilon_r | \mathbf{C}^{(L)}) = \hat{p}_r$ .

Mutual information can equivalently be written as the expected KL divergence between the conditional and marginal distributions:

$$I(A; B) = \sum_{b:\mathbb{P}(B=b)>0} \mathbb{P}(B=b) D_{\text{KL}}(P_{A|B=b}||P_A) = \mathbb{E}_B \left[ D_{\text{KL}}(P_{A|B}||P_A) \right],$$

where

$$D_{\text{KL}}(P_{A|B=b}||P_A) := \sum_{a:\mathbb{P}(A=a|B=b)>0} \mathbb{P}(A=a | B=b) \log_2 \frac{\mathbb{P}(A=a | B=b)}{\mathbb{P}(A=a)}.$$

In our setting,  $P_{E_k} = p$  and  $P_{E_k|\mathbf{C}^{(L)}} = \hat{p}$ , so

$$I(E_k; \mathbf{C}^{(L)}) = \mathbb{E} D_{\text{KL}}(\hat{p}||p).$$

For any probability vector  $a$ , concavity of  $\log_2$  gives (using Jensen's inequality)

$$D_{\text{KL}}(a||p) = \sum_{r:a_r>0} a_r \log_2 \frac{a_r}{p_r} \leq \log_2 \left( \sum_{r=1}^M \frac{a_r^2}{p_r} \right).$$

Apply this to  $\hat{p}$  and use concavity (Jensen's inequality) once more:

$$\mathbb{E} D_{\text{KL}}(\hat{p}||p) \leq \log_2 \left( \sum_{r=1}^M \frac{\mathbb{E} \hat{p}_r^2}{p_r} \right).$$

The marginal count  $C_r^{(L)}$  is binomial, so

$$\mathbb{E} \hat{p}_r^2 = p_r^2 + \frac{p_r(1-p_r)}{L}.$$

Thus the sum inside the logarithm is  $\sum_r [p_r + (1-p_r)/L] = 1 + (M-1)/L$ , proving the bound. Independence of the different counts is not needed.  $\square$

**Theorem 3.2** (Mutation-free matched information vanishes). *Assume positive reproduction rates, a deterministic initial composition, iid environments satisfying (2.8), and  $Q = I_S$  (no mutation). For every  $T > 0$  and  $n \geq 0$ ,*

$$0 \leq I(E_n, \mathbf{X}_{n+1}) \leq \log_2 \left( 1 + \frac{M-1}{n+1} \right) \rightarrow 0 \quad (n \rightarrow \infty). \quad (3.11)$$

*The actual information is independent of  $T > 0$ . No requirement on the fitness vectors is needed.*

*Proof.* For  $L = n + 1$ , equation (3.8) and equation (3.4) makes  $\mathbf{X}_L$  a deterministic function of  $\mathbf{C}^{(L)}$ . The Data Processing Theorem thus gives  $I(E_{L-1}; \mathbf{X}_L) \leq I(E_{L-1}; \mathbf{C}^{(L)})$ . The rest of the inequality follows from Lemma 3.1.

The fact that actual information is independent of  $T$  follows from Equation (3.9).  $\square$

Note that this quantitative bound is valid for every  $S$  and for every iid environment probability vector with positive entries.

This theorem shows that with no mutation, matched mutual information between the species frequencies and the immediately preceding environment vanishes as the epoch number  $n$  progresses. In other words, the environments and the resulting frequency carry less and less mutual information, and asymptotically share no mutual information at all as the epochs go to infinity.

### 3.4 Memory of the entire history, but only in counts

The quantity  $I_n = I(E_n; \mathbf{X}_{n+1})$  can be interpreted as a memory of the current environment. Theorem 3.2 shows that as the number of epochs increases, observing the endpoint composition provides progressively vanishing information about which environment acted during the most recent epoch. In this section we show that, somewhat surprisingly, the population composition actually “remembers” the entire environmental history under certain conditions, up to reordering.

To develop some intuition, consider equation (3.8). The sum in the expression for  $\mathbf{Y}_L$  depends only on the counts, and reordering a history leaves its endpoint unchanged. Therefore, whenever multiple orderings are possible, no method using only that endpoint can distinguish them. Thus, recovering the complete count vector retains all historical information that this observation can possibly distinguish, making it the best kind of history-remembrance that one could hope to achieve. Here we show that the  $\mu = 0$  system has this memory property.

To show this rigorously, let

$$\mathcal{C}_L = \left\{ c \in \mathbb{Z}_{\geq 0}^M : \sum_{r=1}^M c_r = L \right\}.$$

be the count vector for all the  $M$  possible environments at horizon  $L$ . At a known horizon, counts have the additional known constraint  $\sum_r C_r^{(L)} = L$ . This is why differences relative to one environmental selection vector appear in the criterion below.

**Theorem 3.3** (Exact count memory: a necessary and sufficient condition). *Assume no mutation and known  $\mathbf{y}_0$ ,  $T > 0$ , and horizon  $L$ . The endpoint depends on the history only through its count vector. The following statements are equivalent:*

1. *The vectors  $\mathbf{s}_1 - \mathbf{s}_M, \dots, \mathbf{s}_{M-1} - \mathbf{s}_M$  are linearly independent over  $\mathbb{Q}$ .*

2. For every  $L \geq 1$ , the endpoint map

$$\Theta_L : \mathcal{C}_L \rightarrow \mathbb{R}^{S-1}, \quad \Theta_L(c) = \mathbf{y}_0 + T \sum_{r=1}^M c_r \mathbf{s}_r$$

is injective.

Under these conditions, exact observation of  $\mathbf{X}_L$ , or of  $\mathbf{Y}_L$ , determines the history up to reordering at every known finite horizon. If the independence condition fails, there exists  $L_0 \geq 1$  such that the endpoint map is noninjective for every  $L \geq L_0$ .

*Proof.* First we show that condition (1) implies condition (2). If  $c, c' \in \mathcal{C}_L$  have equal endpoints, their integer difference  $a = c - c'$  satisfies

$$\sum_{r=1}^M a_r = 0, \quad \sum_{r=1}^M a_r \mathbf{s}_r = \mathbf{0}. \quad (3.12)$$

The first equality comes from the fact that  $\sum_{r=1}^M c_r = \sum_{r=1}^M c'_r = L$ . The second equality comes from (3.8). Then, subtracting  $a_M \mathbf{s}_M$  from the second equality and substituting  $a_M$  using the first equality gives

$$\sum_{r=1}^{M-1} a_r (\mathbf{s}_r - \mathbf{s}_M) = \mathbf{0}. \quad (3.13)$$

Rational linear independence forces  $a_r = 0$  for  $r < M$ , and the zero-sum constraint then forces  $a_M = 0$ . Thus the endpoint map is injective for every horizon.

Conversely, if condition (1) is not satisfied, we can find rational numbers  $a_1, \dots, a_{M-1}$ , not all zero, satisfying (3.13). Multiplying by their common denominator would actually allow us to have integer-valued  $a_1, \dots, a_{M-1}$ .

Set  $a_M = -\sum_{r=1}^{M-1} a_r$ . Define  $c_r = \max\{a_r, 0\}$  and  $c'_r = \max\{-a_r, 0\}$ , counting the absolute values of only the positives and the negatives, respectively. The first equality in equation 3.12 then implies

$$L_0 := \sum_r c_r = \sum_r c'_r \geq 1.$$

These are distinct count vectors in  $\mathcal{C}_{L_0}$  with equal endpoints after substituting to equation 3.8, by construction. Further, adding  $L - L_0$  occurrences of the same label to both vectors preserves the collision at every  $L \geq L_0$ . Thus, the endpoint map is not injective.  $\square$

*Remark 3.4.* The condition is independence over  $\mathbb{Q}$ , not over  $\mathbb{R}$ . This arises because the count vector takes integer values, not real values. We do not assume anything about  $M$  and  $S$ . We do, however, assume exact observations; at finite measurement precision requires different analysis.

Next, we will establish the result above using information-theoretic terms. For finite-valued discrete random variables  $A$  and  $B$ , the conditional entropy of  $A$  given  $B$  is

$$H(A | B) := \sum_{b: \mathbb{P}(B=b) > 0} \mathbb{P}(B=b) H(A | B=b),$$

where

$$H(A | B=b) := - \sum_{a \in \mathcal{A}} \mathbb{P}(A=a | B=b) \log_2 \mathbb{P}(A=a | B=b),$$

and  $0 \log_2 0 := 0$ . It measures the uncertainty remaining about  $A$  after observing  $B$ , averaged over the possible values of  $B$ . Other equivalent definitions include

$$\begin{aligned} H(A | B) &= H(A, B) - H(B) \\ &= H(A) - I(A; B). \end{aligned}$$

Therefore, when the conditional entropy is 0, the entropy of  $A$  has no additional “surprise” compared to the mutual information between  $A$  and  $B$ .

**Corollary 3.5** (Exact count memory in information-theoretic terms). *Assume the iid law (2.8), and write the entire environmental history as  $\mathcal{H}_L = (E_0, \dots, E_{L-1})$ . The rational-independence condition in Theorem 3.3 (condition 1) holds if and only if*

$$H(\mathbf{C}^{(L)} | \mathbf{X}_L) = 0 \quad \text{for every } L \geq 1.$$

where  $H(\mathbf{C}^{(L)} | \mathbf{X}_L)$  is the conditional entropy. When it holds,

$$I(\mathcal{H}_L; \mathbf{X}_L) = H(\mathbf{C}^{(L)}), \tag{3.14}$$

$$H(\mathcal{H}_L | \mathbf{X}_L) = \mathbb{E} \log_2 \frac{L!}{\prod_{r=1}^M C_r^{(L)}!}. \tag{3.15}$$

Without that condition, the endpoint still determines cumulative selection, and

$$I(\mathcal{H}_L; \mathbf{X}_L) = H(\mathbf{A}_L) \leq H(\mathbf{C}^{(L)}). \tag{3.16}$$

where  $\mathbf{A}_L$  is the summed fitness differences defined in equation 3.8.

*Proof.* By theorem 3.3, the mapping from the  $\mathbf{C}^{(L)}$  to  $\mathbf{Y}_L$  is injective. By equation (3.4), the mapping from  $\mathbf{Y}_L$  to  $\mathbf{X}_L$  is injective. Therefore, the mapping from  $\mathbf{C}^{(L)}$  to  $\mathbf{X}_L$  is injective, and it is in fact a bijection over all such possible frequencies. Thus,  $H(\mathbf{C}^{(L)} | \mathbf{X}_L) = 0$ .

Next, since  $\mathbf{X}_L$  is a deterministic function of  $\mathbf{C}^{(L)}$ , the data processing inequality gives

$$I(\mathcal{H}_L; \mathbf{X}_L) \leq I(\mathcal{H}_L; \mathbf{C}^{(L)}).$$

Conversely, injectivity allows us to recover  $\mathbf{C}^{(L)}$  from  $\mathbf{X}_L$ , so the same inequality gives

$$I(\mathcal{H}_L; \mathbf{C}^{(L)}) \leq I(\mathcal{H}_L; \mathbf{X}_L).$$

Combining these inequalities yields

$$I(\mathcal{H}_L; \mathbf{X}_L) = I(\mathcal{H}_L; \mathbf{C}^{(L)}).$$

Finally, the entire history determines its count vector, so

$$I(\mathcal{H}_L; \mathbf{C}^{(L)}) = H(\mathbf{C}^{(L)}) - \underbrace{H(\mathbf{C}^{(L)} | \mathcal{H}_L)}_0 = H(\mathbf{C}^{(L)}).$$

This proves (3.14).

To prove (3.15), by (3.14),

$$H(\mathcal{H}_L | \mathbf{X}_L) = H(\mathcal{H}_L) - I(\mathcal{H}_L; \mathbf{X}_L) = H(\mathcal{H}_L) - H(\mathbf{C}^{(L)}).$$

Since the environments are iid,

$$H(\mathcal{H}_L) = LH(p), \quad H(p) := - \sum_{r=1}^M p_r \log_2 p_r.$$

The count vector has multinomial distribution:

$$\mathbb{P}(\mathbf{C}^{(L)} = c) = \frac{L!}{\prod_{r=1}^M c_r!} \prod_{r=1}^M p_r^{c_r}.$$

Taking minus the expected logarithm of this probability gives

$$\begin{aligned} H(\mathbf{C}^{(L)}) &= -\mathbb{E} \left[ \log_2 \frac{L!}{\prod_{r=1}^M C_r^{(L)}!} + \sum_{r=1}^M C_r^{(L)} \log_2 p_r \right] \\ &= -\mathbb{E} \log_2 \frac{L!}{\prod_{r=1}^M C_r^{(L)}!} - L \sum_{r=1}^M p_r \log_2 p_r \\ &= LH(p) - \mathbb{E} \log_2 \frac{L!}{\prod_{r=1}^M C_r^{(L)}!}, \end{aligned}$$

where we used  $\mathbb{E} C_r^{(L)} = Lp_r$ . Substituting this expression into the entropy difference yields

$$H(\mathcal{H}_L | \mathbf{X}_L) = \mathbb{E} \log_2 \frac{L!}{\prod_{r=1}^M C_r^{(L)}!},$$

which proves (3.15).

Lastly, to prove (3.16), note that since  $\mathbf{X}_L$  and  $\mathbf{A}_L$  determine each other, we have

$$I(\mathcal{H}_L; \mathbf{X}_L) = I(\mathcal{H}_L; \mathbf{A}_L).$$

Moreover, the history determines its cumulative selection, so

$$I(\mathcal{H}_L; \mathbf{A}_L) = H(\mathbf{A}_L) - \underbrace{H(\mathbf{A}_L | \mathcal{H}_L)}_0 = H(\mathbf{A}_L).$$

This proves the equality in (3.16). The equality follows from data processing inequality again. All entropies here are ordinary discrete entropies at a fixed finite horizon.  $\square$

Thus complete count memory and vanishing information about the latest environment are compatible. They answer different questions: how often each environment occurred, and which environment acted most recently.

**An algorithm of recovering environmental visit counts from an exact endpoint.** Based on this theory, the procedure of recovery is algorithmic. The inputs are: the initial composition  $x_0$ , the observed endpoint  $x_L$ , the known number of epochs  $L$ , the epoch duration  $T > 0$ , and the fitness vectors  $f_r$ , for  $r = 1, \dots, M$ . Both compositions are assumed to have strictly positive coordinates.

1. Compute the cumulative selection vector  $a \in \mathbb{R}^{S-1}$ :

$$a_i = \frac{1}{T} \ln \left( \frac{x_{i,L} x_{S,0}}{x_{S,L} x_{i,0}} \right), \quad i = 1, \dots, S-1.$$

2. Form the selection vectors:

$$s_r = (f_{1r} - f_{Sr}, \dots, f_{S-1,r} - f_{Sr})^\top, \quad r = 1, \dots, M.$$

3. Enumerate all nonnegative integer vectors  $c = (c_1, \dots, c_M)$  satisfying

$$\sum_{r=1}^M c_r = L,$$

and retain those satisfying

$$\sum_{r=1}^M c_r s_r = a.$$

4. Return the unique matching vector. Under the rational-independence condition of Theorem 3.3 and with exact, model-consistent inputs, exactly one matching vector exists.

This procedure returns the number of visits to each environment, without their temporal order.

This is a finite exact-recovery algorithm. Theorem 3.3 guarantees uniqueness, but does not discuss computational efficiency or numerical robustness, when enumerating

$$\binom{L + M - 1}{M - 1}$$

candidate count vectors.

### 3.5 No mutation: numerical illustrations

We illustrate the theoretical results using a two-species system evolving under two discrete environments. The fitness vectors are  $f_1 = (1.00, 0.98)$  and  $f_2 = (0.97, 0.99)$ , with each environment independently sampled with probability 0.5. The initial composition is  $x_0 = (0.5, 0.5)$ . We consider epoch durations  $T = 1, 5, 10, 20, 50, 100, 200, 500$ .

We first investigate the mutual information between the current environment and the population composition at the end of the corresponding epoch,  $I(E_n; X_{n+1})$ . For each epoch duration, 10,000 independent environmental trajectories are simulated over 100 epochs. The first species frequency is rounded to the nearest 0.001 and treated as a discrete random variable, allowing mutual information to be estimated directly from empirical joint frequencies. Given the two-species simplex, it suffices to consider the first species frequency. The fixed rounding resolution prevents tiny floating-point differences between theoretically identical population states from being treated as distinct observational categories.

As predicted by Theorem 3.2, the estimated mutual information decreases rapidly with the number of environmental epochs, see figure 1. The curves for different epoch durations exhibit similar decay, approaching values close to zero over the simulated horizon. The log-log inset emphasizes the power-law decay at later epochs. The residual differences across  $T$  reflect finite observation resolution and sampling.

We next examine the recovery of environmental visit counts from the endpoint composition, as described in Section 3.4. For each known total number of epoch  $N$ , the count vector is inferred from cumulative selection in log-ratio coordinates. We sweep  $N \in \{10, 100, 1000, 10000, 100000\}$  and the same eight epoch durations  $T$  as in mutual information simulation. For each  $(T, N)$  combination,

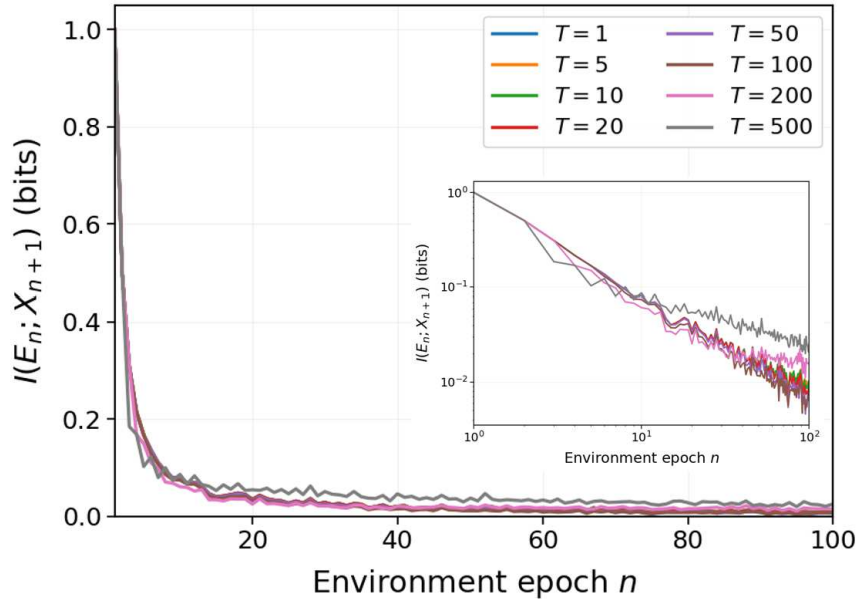


Figure 1: **Mutation-free mutual information.** Empirical  $I(E_n; X_{n+1})$  in bits versus environmental epoch  $n$  for eight epoch durations  $T$ , using population frequencies rounded to 0.001. The inset displays the same estimates on logarithmic axes. The decay supports Theorem 3.2; small between-curve discrepancies arise from finite-resolution estimation.

the heatmaps in figure 2 report the fraction of trajectories whose inferred counts agree with the generating history.

To minimize interference of numerical errors, this experiment uses the exact mutation-free flow map given by Eq. 2.7 instead of repeatedly integrating the ODE numerically. This removes time-discretization and solver-error accumulation, but the flow map is not an exact-arithmetic oracle: evaluating exponential, normalizing frequencies, and representing values close to 0 or 1 can still discard information. Therefore, the log-ratio reference is added. It directly implemented the additive identity of Section 3.2 and thus provides a more faithful numerical check of the exact-recovery claim in Section 3.4.

Figure 2a shows that floating endpoint recovery remains accurate over much of the parameter grid but deteriorates at long horizons and large  $T$ . By contrast, the log-ratio reference in figure 2b recovers the counts in every tested configuration. These results support the algebraic recovery criterion while illustrating why its exact-observation hypothesis matters for numerical representations.

## 4 With mutation: Saturated matched information under large intervals

Now we will study the system with mutation. Mathematically, assume

$$Q_{ij} > 0 \quad \text{for all } i, j, \quad (4.1)$$

in addition to column-stochasticity and positive reproduction rates. The environmental sequence is otherwise unrestricted.

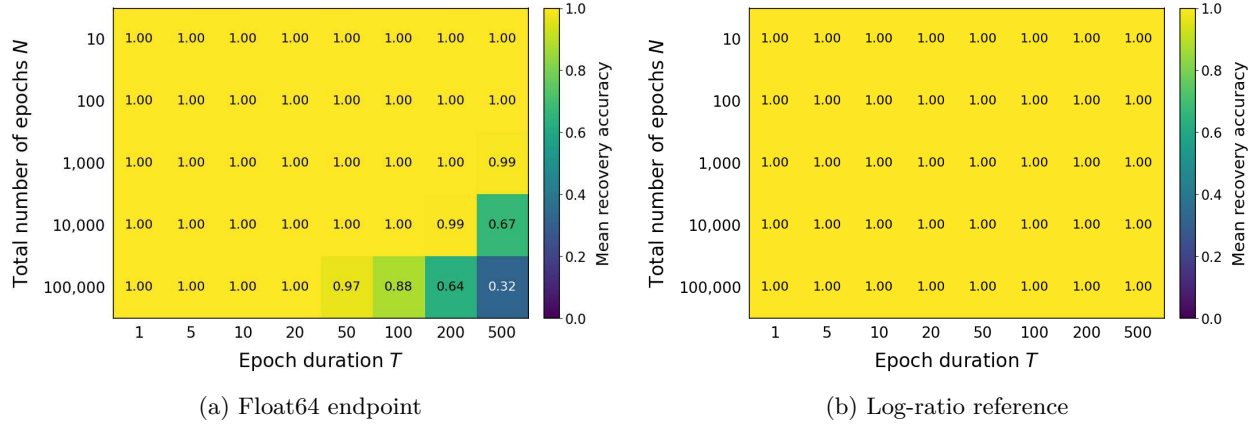


Figure 2: **Mutation-free visit-count recovery.** (a) Mean recovery accuracy across epoch duration  $T$  and total number of epochs  $N$ , using the exact flow map with the final composition represented in ordinary double-precision frequencies. Decreased accuracy at large  $T$  and  $N$  reflects finite-precision loss rather than failure of count identifiability. (b) Mean recovery accuracy for the same  $(T, N)$  grid, using directly accumulated log-ratio selection as the numerical reference. Perfect recovery throughout the tested grid supports the exact count-recovery construction of Section 3.4.

#### 4.1 Hilbert's projective distance

Recall that all frequency vectors live inside the simplex  $\Delta_S^\circ$  defined in (3.2). For  $\mathbf{x}, \mathbf{z} \in \Delta_S^\circ$ , define

$$d_H(\mathbf{x}, \mathbf{z}) := \max_i \ln \frac{x_i}{z_i} - \min_i \ln \frac{x_i}{z_i}. \quad (4.2)$$

This is a metric on the normalized positive simplex. Nonnegativity and symmetry follow directly; zero distance means proportional vectors, hence equal vectors after normalization. The triangle inequality follows from  $\text{osc}(a+b) \leq \text{osc}(a) + \text{osc}(b)$ , where  $\text{osc}(a) = \max_i a_i - \min_i a_i$ .

If  $\mathbf{y} = \ell(\mathbf{x})$  and  $\tilde{\mathbf{y}} = \ell(\mathbf{z})$ , then

$$d_H(\mathbf{x}, \mathbf{z}) = \max_{1 \leq i \leq S} (y_i - \tilde{y}_i) - \min_{1 \leq i \leq S} (y_i - \tilde{y}_i), \quad y_S = \tilde{y}_S = 0. \quad (4.3)$$

For  $S = 2$ , this is exactly the absolute difference of the two logits.

#### 4.2 A global contraction estimate under fixed environment

**Lemma 4.1** (Environmental projective contraction). *For each environment, define*

$$\kappa_r := 2 \min_{i \neq j} \sqrt{(W_r)_{ij}(W_r)_{ji}} > 0. \quad (4.4)$$

*Then, for all  $\mathbf{x}, \mathbf{z} \in \Delta_S^\circ$  and all  $t \geq 0$ ,*

$$d_H(\Phi_r^t(\mathbf{x}), \Phi_r^t(\mathbf{z})) \leq \exp(-\kappa_r t) d_H(\mathbf{x}, \mathbf{z}). \quad (4.5)$$

*where  $\Phi_r^t(\mathbf{x})$  is the flow-map of the ODE defined in (2.7).*

*When the mutation matrix  $Q$  is symmetric,*

$$\kappa_r = \frac{2u}{S-1} \min_{i \neq j} \sqrt{f_{ir} f_{jr}}. \quad (4.6)$$

*Proof.* Fix  $\mathbf{x}, \mathbf{z} \in \Delta_S^\circ$  and define

$$h_i(t) := \ln \frac{[\Phi_r^t(\mathbf{x})]_i}{[\Phi_r^t(\mathbf{z})]_i}, \quad \mathcal{D}(t) := \max_i h_i(t) - \min_i h_i(t).$$

Then

$$\mathcal{D}(t) = d_H(\Phi_r^t(\mathbf{x}), \Phi_r^t(\mathbf{z})).$$

is the Hilbert's projective distance. Differentiation on  $h_i(t)$  gives

$$\dot{h}_i = \sum_{k=1}^S (W_r)_{ik} \frac{z_k}{z_i} (\exp(h_k - h_i) - 1) - (\bar{f}_r(\mathbf{x}) - \bar{f}_r(\mathbf{z})).$$

First, if  $\mathcal{D} = 0$  for some  $t$ , this means two trajectories collide. But by uniqueness of solutions to an ODE, this means they started from the same initial condition, and thus the Lemma is trivially true.

Fix an arbitrary  $t$ . If  $\mathcal{D}(t) > 0$ , let  $i$  be the index that maximizes  $h(t)$  and let  $j$  be the index that minimizes  $h(t)$ . Consider  $\dot{h}_i - \dot{h}_j$ . The mean-fitness terms cancel. Every summand in the sum for  $i$  is nonpositive; every summand in the sum for  $j$  is nonnegative. Keeping only the two terms linking  $i$  and  $j$  gives

$$\dot{h}_i - \dot{h}_j \leq -A(1 - \exp(-\mathcal{D})) - B(\exp(\mathcal{D}) - 1), \quad A = (W_r)_{ij} \frac{z_j}{z_i}, \quad B = (W_r)_{ji} \frac{z_i}{z_j}.$$

Since  $AB = (W_r)_{ij}(W_r)_{ji}$ , the arithmetic-geometric mean inequality yields

$$\begin{aligned} A(1 - \exp(-\mathcal{D})) + B(\exp(\mathcal{D}) - 1) &\geq 2\sqrt{AB(1 - \exp(-\mathcal{D}))(\exp(\mathcal{D}) - 1)} \\ &= 4\sqrt{AB} \sinh(\mathcal{D}/2) \\ &\geq 2\sqrt{AB} \mathcal{D} \geq \kappa_r \mathcal{D}. \end{aligned}$$

The second-to-last inequality is true because  $\sinh s \geq s$  for all  $s \geq 0$ . Thus we have

$$\dot{h}_i(t) - \dot{h}_j(t) \leq -\kappa_r \mathcal{D}(t).$$

Now we try to bound the variation of  $\mathcal{D}$ . Since each  $h_i(t)$  is smooth, the function  $\mathcal{D}$  is locally smooth, and corners can only occur when the maximizing or minimizing index changes. Define the upper right Dini derivative of  $\mathcal{D}$  as:

$$D^+ \mathcal{D}(t) := \limsup_{\epsilon \downarrow 0} \frac{\mathcal{D}(t + \epsilon) - \mathcal{D}(t)}{\epsilon}.$$

which captures the largest limiting slope to the right. Let  $I_+(t)$  and  $I_-(t)$  be the sets of indices attaining the maximum and minimum of  $h_i(t)$ , respectively. For a finite collection of smooth functions,

$$D^+ \mathcal{D}(t) = \max_{\substack{i \in I_+(t) \\ j \in I_-(t)}} (\dot{h}_i(t) - \dot{h}_j(t)).$$

When several indices tie, this selects the pair producing the largest right-hand slope. But the preceding calculation established, for every  $t$  when  $\mathcal{D}(t) > 0$ ,

$$\dot{h}_i(t) - \dot{h}_j(t) \leq -\kappa_r \mathcal{D}(t).$$

Taking the maximum over those pairs therefore preserves the bound:

$$D^+ \mathcal{D}(t) \leq -\kappa_r \mathcal{D}(t).$$

Finally, by Grönwall's inequality,

$$\mathcal{D}(t) \leq e^{-\kappa_r t} \mathcal{D}(0) \quad (t \geq 0).$$

which is (4.5). Formula (4.6) follows by substituting the off-diagonal entries of  $Q(u)$ .  $\square$

This contraction estimate is an instance of Hilbert projective contraction for positive evolution operators. A corresponding continuous-time estimate, with rate  $2 \min_{i \neq j} \sqrt{A_{ij} A_{ji}}$  for a Markov generator  $A$ , is given by Cohen and Fausti [2023] (Appendix A, Proposition A.2). Lemma 4.1 gives a direct proof for the normalized reproduction–mutation dynamics used here.

### 4.3 Equilibria and a common invariant set under different environments

Since  $W_r$  has strictly positive entries, the Perron–Frobenius theorem gives a simple dominant eigenvalue  $\lambda_{1,r} > 0$  and a strictly positive eigenvector. Normalize that vector to obtain

$$\mathbf{x}_r^* \in \Delta_S^\circ, \quad W_r \mathbf{x}_r^* = \lambda_{1,r} \mathbf{x}_r^*. \quad (4.7)$$

Now notice that since normalization gives  $\mathbf{1}^\top \mathbf{x}_r^* = 1$ , and column-stochasticity gives  $\mathbf{1}^\top Q = \mathbf{1}^\top$ ,

$$\begin{aligned} \lambda_{1,r} &= \lambda_{1,r} \mathbf{1}^\top \mathbf{x}_r^* \\ &= \mathbf{1}^\top W_r \mathbf{x}_r^* \\ &= \mathbf{1}^\top Q \operatorname{diag}(\mathbf{f}_r) \mathbf{x}_r^* \\ &= \mathbf{1}^\top \operatorname{diag}(\mathbf{f}_r) \mathbf{x}_r^* \\ &= \mathbf{f}_r^\top \mathbf{x}_r^* \\ &= \bar{f}_r(\mathbf{x}_r^*). \end{aligned}$$

Thus, this  $\mathbf{x}_r^*$  is the unique interior equilibrium of (2.6). Applying Lemma 4.1 with one trajectory fixed at equilibrium gives

$$d_H(\Phi_r^t(\mathbf{x}), \mathbf{x}_r^*) \leq \exp(-\kappa_r t) d_H(\mathbf{x}, \mathbf{x}_r^*). \quad (4.8)$$

The next lemma provides one compact set that controls every possible switching history, rather than only a single fixed-environment trajectory.

**Lemma 4.2** (Uniform interior bound). *Define*

$$a := \min_{r,i,j} (W_r)_{ij} > 0, \quad b := \max_{r,i} f_{ir} > 0, \quad \epsilon := \min \left\{ \min_i x_{0,i}, \frac{a}{b} \right\} > 0. \quad (4.9)$$

*The set*

$$\mathcal{K} := \{\mathbf{x} \in \Delta_S^\circ : x_i \geq \epsilon \text{ for every } i\} \quad (4.10)$$

*is compact, contains  $\mathbf{x}_0$  and every equilibrium  $\mathbf{x}_r^*$ , and  $\mathbf{X}(t) \in \mathcal{K}$  for every time and every environmental history.*

*Proof.* Fix an arbitrary environmental history and consider the corresponding population trajectory  $\mathbf{X}(t)$ , with  $\mathbf{X}(0) = \mathbf{x}_0$ . Whenever the current environment is  $\varepsilon_r$ , the definitions of  $a$  and  $b$  give

$$(W_r \mathbf{X}(t))_i = \sum_{j=1}^S (W_r)_{ij} X_j(t) \geq a \sum_{j=1}^S X_j(t) = a$$

and

$$\bar{f}_r(\mathbf{X}(t)) = \sum_{j=1}^S f_{jr} X_j(t) \leq b \sum_{j=1}^S X_j(t) = b.$$

where  $\bar{f}_r$  is the mean fitness defined at (2.5). Consequently,

$$\dot{X}_i(t) = (W_r \mathbf{X}(t))_i - \bar{f}_r(\mathbf{X}(t)) X_i(t) \geq a - b X_i(t).$$

These bounds are uniform over environments, so the differential inequality holds almost everywhere, including along trajectories with environmental switches. The trajectory is absolutely continuous on every finite time interval.

Now we use some trick to give a lower bound on  $X_i(t)$ . Notice that the product rule gives

$$\frac{d}{dt}(e^{bt} X_i(t)) = e^{bt} (\dot{X}_i(t) + b X_i(t)) \geq a e^{bt}.$$

Integrating both sides from 0 to  $t$  yields

$$e^{bt} X_i(t) - X_i(0) \geq a \int_0^t e^{bs} ds = \frac{a}{b} (e^{bt} - 1).$$

Since  $X_i(0) = x_{0,i}$ , this becomes

$$e^{bt} X_i(t) \geq x_{0,i} + \frac{a}{b} (e^{bt} - 1).$$

Dividing by  $e^{bt} > 0$  gives

$$X_i(t) \geq e^{-bt} x_{0,i} + (1 - e^{-bt}) \frac{a}{b} \geq \min\{x_{0,i}, a/b\} \geq \epsilon.$$

Thus  $\mathbf{X}(t) \in \mathcal{K}$  for every time and every environmental history.

The set  $\mathcal{K}$  is closed and bounded, hence compact. Since  $\epsilon > 0$ , it lies entirely within the interior simplex.

Finally, at the equilibrium associated with environment  $\varepsilon_r$ ,

$$\lambda_{1,r} = \bar{f}_r(\mathbf{x}_r^*) \leq b.$$

The eigenvector equation therefore gives

$$x_{i,r}^* = \frac{(W_r \mathbf{x}_r^*)_i}{\lambda_{1,r}} \geq \frac{a}{\lambda_{1,r}} \geq \frac{a}{b} \geq \epsilon.$$

Thus  $\mathcal{K}$  also contains every environmental equilibrium. □

*Remark 4.3.* The same estimate applies when starting from any point of  $\mathcal{K}$ . Both the initial coordinates and  $a/b$  are then at least  $\epsilon$ , so every coordinate remains at least  $\epsilon$ . Hence if the population starts anywhere in  $\mathcal{K}$ , it stays in  $\mathcal{K}$  while evolving under any fixed environment

#### 4.4 When are different environments distinguishable at equilibrium?

Distinct environmental labels or distinct fitness vectors do not by themselves guarantee distinct equilibria. For example, proportional fitness vectors always have the same equilibrium, because they give proportional matrices  $W_r$ . The next proposition shows that it is also the only case where equilibria can coincide, provided that  $Q$  is invertible. Notice that this assumption is natural. For example, by Levy–Desplanques theorem,  $Q$  is invertible as long as it is strictly diagonally dominant, i.e. the chance of mutating to other species is less than half.

**Proposition 4.4** (Equilibrium identifiability). *If the fixed, entry-wise strictly positive column-stochastic mutation matrix  $Q$  is also invertible, then*

$$\mathbf{x}_r^* = \mathbf{x}_q^* \iff \mathbf{f}_r = \alpha \mathbf{f}_q \text{ for some } \alpha > 0. \quad (4.11)$$

*Thus pairwise nonproportional fitness vectors are equivalent to pairwise distinct equilibrium compositions under these assumptions.*

*Proof.* If  $\mathbf{x}^*$  is a common equilibrium under two different environments  $r$  and  $q$ , the two equilibrium equations are

$$Q \operatorname{diag}(\mathbf{f}_r) \mathbf{x}^* = \lambda_{1,r} \mathbf{x}^*, \quad Q \operatorname{diag}(\mathbf{f}_q) \mathbf{x}^* = \lambda_{1,q} \mathbf{x}^*.$$

Since  $\lambda_{1,q} > 0$ , multiplying the second equation by  $\lambda_{1,r}/\lambda_{1,q}$  gives

$$Q \operatorname{diag}(\mathbf{f}_r) \mathbf{x}^* = \lambda_{1,r} \mathbf{x}^* = \frac{\lambda_{1,r}}{\lambda_{1,q}} Q \operatorname{diag}(\mathbf{f}_q) \mathbf{x}^*.$$

Multiplying both sides by  $Q^{-1}$  on the left yields

$$\operatorname{diag}(\mathbf{f}_r) \mathbf{x}^* = \frac{\lambda_{1,r}}{\lambda_{1,q}} \operatorname{diag}(\mathbf{f}_q) \mathbf{x}^*.$$

Every coordinate of  $\mathbf{x}^*$  is positive, so cancellation gives  $\mathbf{f}_r = (\lambda_{1,r}/\lambda_{1,q}) \mathbf{f}_q$ .

To prove the other direction,  $\mathbf{f}_r = \alpha \mathbf{f}_q$  implies  $W_r = \alpha W_q$ , preserving the normalized positive dominant eigenvector.  $\square$

For the symmetric family, the eigenvalue of  $Q(u)$  along  $\mathbf{1}$  is 1; its eigenvalue on  $\mathbf{1}^\perp$  is  $1 - Su/(S-1)$ , with multiplicity  $S-1$ . Thus, within  $0 < u < 1$ , it is invertible precisely when  $u \neq (S-1)/S$ . The usual type-preserving range

$$0 < u < \frac{S-1}{S} \quad (4.12)$$

is a convenient sufficient range for both positivity and invertibility. At  $u = (S-1)/S$ , all entries equal  $1/S$ , and the uniform composition is the equilibrium for every positive fitness vector. Invertibility is used to translate equilibrium distinguishability into a fitness condition; for the rest of this section, we will assume distinct equilibria (i.e. the fitness matrix is nondegenerate).

#### 4.5 A sufficient duration for full environmental information

Define the equilibrium distances and invariant-set radii by

$$\delta_{rq} := d_H(\mathbf{x}_r^*, \mathbf{x}_q^*) > 0, \quad R_r := \max_{\mathbf{x} \in \mathcal{K}} d_H(\mathbf{x}, \mathbf{x}_r^*). \quad (4.13)$$

The maximum is finite because  $\mathcal{K}$  is compact and bounded away from the simplex boundary. It is determined by the initial composition and the model parameters, with no dependence on the environmental history. Now, we proved in Lemma 4.1 that every fixed-environment ODE is a contraction under the Hilbert projective distance, so the endpoint image of  $\mathcal{K}$  in environment  $r$  is contained in

$$\mathcal{B}_r(t) := \{\mathbf{x} \in \Delta_S^\circ : d_H(\mathbf{x}, \mathbf{x}_r^*) \leq R_r \exp(-\kappa_r t)\}. \quad (4.14)$$

which is a ball that is shrinking with time. Our next goal is to establish a sufficiently large time duration  $T_{\text{suff}}$  that ensures these balls arising from different possible environments are small enough such that they become pairwise disjoint.

**Definition 4.5** (Explicit sufficient separation duration). Set

$$T_{\text{suff}} := \max_{1 \leq r < q \leq M} \frac{1}{\min(\kappa_r, \kappa_q)} \ln \left( \frac{R_r + R_q}{\delta_{rq}} \right). \quad (4.15)$$

This is a finite positive number. Indeed,  $\mathcal{K}$  contains both equilibria, so  $R_r \geq \delta_{rq}$  and  $R_q \geq \delta_{rq}$ . By construction, for any  $t > T_{\text{suff}}$ ,

$$R_r \exp(-\kappa_r t) + R_q \exp(-\kappa_q t) \leq (R_r + R_q) \exp(-\min(\kappa_r, \kappa_q)t) < \delta_{rq}. \quad (4.16)$$

This guarantees that all these balls are pairwise disjoint. Indeed, if a point  $\mathbf{x}$  belonged to both  $\mathcal{B}_r(t)$  and  $\mathcal{B}_q(t)$ , the triangle inequality would give

$$\begin{aligned} \delta_{rq} &\leq d_H(\mathbf{x}_r^*, \mathbf{x}) + d_H(\mathbf{x}, \mathbf{x}_q^*) \\ &\leq R_r e^{-\kappa_r t} + R_q e^{-\kappa_q t} < \delta_{rq}, \end{aligned}$$

a contradiction.

**Theorem 4.6** (History-uniform full recovery). *Assume positive reproduction rates, a fixed strictly positive column-stochastic mutation matrix, a deterministic interior initial composition, and non-degenerate fitness matrix. Let  $(E_n)_{n \geq 0}$  be any stochastic process taking values in  $\mathcal{E}$ . If  $T > T_{\text{suff}}$ , then*

$$I(E_n; \mathbf{X}_{n+1}) = H(E_n) \quad \text{for every } n \geq 0. \quad (4.17)$$

*Because a single measurable decoder recovers  $E_n$  from  $\mathbf{X}_{n+1}$  for every earlier environmental history and every epoch.*

*Proof.* Lemma 4.2 gives  $\mathbf{X}_n \in \mathcal{K}$  for every history. Whenever  $E_n = \varepsilon_r$ , contraction toward equilibrium yields

$$d_H(\mathbf{X}_{n+1}, \mathbf{x}_r^*) = d_H(\Phi_r^T(\mathbf{X}_n), \mathbf{x}_r^*) \leq R_r \exp(-\kappa_r T).$$

Thus  $\mathbf{X}_{n+1} \in \mathcal{B}_r(T)$ . Since these balls are pairwise disjoint for  $T > T_{\text{suff}}$ , define  $d : \Delta_S^\circ \rightarrow \mathcal{E}$  by assigning label  $\varepsilon_r$  on  $\mathcal{B}_r(T)$  and an arbitrary label outside their union. Then this decoder  $d$  recovers  $E_n$  from  $\mathbf{X}_{n+1}$ . In other words,  $E_n = d(\mathbf{X}_{n+1})$  for every history and every  $n$ . Therefore  $H(E_n | \mathbf{X}_{n+1}) = 0$ , proving (4.17).  $\square$

*Remark 4.7* (Explicit information with known environment distribution and information within epoch). Further, if we know the oracle environment distribution, this recovered mutual information can be written exactly. For marginal probabilities  $p_{n,r} = \mathbb{P}(E_n = \varepsilon_r)$ , the recovered information is

$$H(E_n) = - \sum_{r=1}^M p_{n,r} \log_2 p_{n,r}, \quad 0 \log_2 0 := 0.$$

Uniform marginals give  $\log_2 M$  bits. Independence is unnecessary because the proof separates all admissible histories deterministically.

The same argument applies inside an epoch. If an elapsed time  $\tau \in (T_{\text{suff}}, T]$  is observed, then  $I(E_n; \mathbf{X}(nT + \tau)) = H(E_n)$ . At  $\tau = T$ , the frequency is still the continuous endpoint produced by  $E_n$ , even though the next environment is about to act.

*Remark 4.8* (Possible simpler bounds and possible sharper bounds). We can try to make the lower bound on  $T$  either simpler or sharper than  $T_{\text{suff}}$ . A simpler, potentially looser condition is

$$T > \frac{1}{\kappa_{\min}} \ln \frac{2R}{\delta_{\min}}, \quad \kappa_{\min} := \min_r \kappa_r, \quad R := \max_r R_r, \quad \delta_{\min} := \min_{r < q} \delta_{rq}. \quad (4.18)$$

In addition, to avoid the maximization defining  $R_r$ , one may use a certified upper bound. For example, on  $\mathcal{K}$  all coordinates lie between  $\epsilon$  and  $1 - (S - 1)\epsilon$ , so

$$R_r \leq \ln \frac{1 - (S - 1)\epsilon}{\epsilon} + \ln \frac{\max_i x_{i,r}^*}{\min_i x_{i,r}^*}. \quad (4.19)$$

This follows by separately bounding the maximum and minimum of  $\ln(x_i/x_{i,r}^*)$ . Replacing  $R_r$  by this bound in (4.15) remains sufficient.

On the other hand, a sharper pairwise time is the unique positive solution of

$$R_r \exp(-\kappa_r t) + R_q \exp(-\kappa_q t) = \delta_{rq}.$$

Uniqueness follows because the left side decreases strictly from  $R_r + R_q > \delta_{rq}$  to zero. Taking the maximum of these pairwise solutions improves the bound without changing the argument.

*Remark 4.9* (Sufficiency is not necessity). The condition  $T > T_{\text{suff}}$  guarantees that the enclosing balls  $\mathcal{B}_r(T)$  are pairwise disjoint, ensuring full environmental information at every epoch. This condition need not be necessary.

At a fixed finite epoch  $n$ , the conditional endpoint distributions have finite support. These supports may be pairwise disjoint even when the enclosing balls overlap. If they are disjoint for all environments, exact observation of the trajectory endpoint still determines  $E_n$ . Thus we would still have

$$I(E_n; \mathbf{X}_{n+1}) = H(E_n).$$

Therefore  $T \leq T_{\text{suff}}$  alone does not imply information loss.

## 4.6 Full memory of the entire history, including event order

**Corollary 4.10** (Exact recovery of the full environmental history). *Under the assumptions of Theorem 4.6, suppose that  $T > T_{\text{suff}}$ . For every known finite horizon  $L \geq 1$ , the exact endpoint  $X_L$  uniquely determines the ordered environmental history*

$$\mathcal{H}_L = (E_0, \dots, E_{L-1}).$$

Consequently,

$$H(\mathcal{H}_L | X_L) = 0, \quad I(\mathcal{H}_L; X_L) = H(\mathcal{H}_L).$$

If the environments are iid with distribution  $p$ , then

$$I(\mathcal{H}_L; X_L) = L H(p).$$

*Proof.* Theorem 4.6 provides a single measurable decoder  $d$  satisfying

$$d(X_{n+1}) = E_n$$

for every epoch and every environmental history. Thus, observing  $X_L$  exactly determines the last environment  $E_{L-1}$ .

Suppose that  $E_{L-1} = \varepsilon_r$ . The fixed-environment flow is

$$X_L = \frac{\exp(TW_r)X_{L-1}}{\mathbf{1}^\top \exp(TW_r)X_{L-1}}.$$

Since the matrix exponential is invertible, the preceding composition is recovered by

$$X_{L-1} = \frac{\exp(-TW_r)X_L}{\mathbf{1}^\top \exp(-TW_r)X_L}.$$

For this exact, reachable endpoint, the numerator is a positive scalar multiple of  $X_{L-1}$ , so the normalization is well-defined and yields a positive composition. Applying the same decoder to  $X_{L-1}$  recovers  $E_{L-2}$ . Inverting the corresponding flow then recovers  $X_{L-2}$ . Repeating this argument determines all environments  $E_{L-1}, E_{L-2}, \dots, E_0$ . Therefore  $\mathcal{H}_L$  is a deterministic function of  $X_L$ , which gives

$$H(\mathcal{H}_L | X_L) = 0$$

and hence

$$I(\mathcal{H}_L; X_L) = H(\mathcal{H}_L).$$

For iid environments, independence gives  $H(\mathcal{H}_L) = L H(p)$ .  $\square$

This means that under the separation condition of Theorem 4.6, the endpoint contains enough information to reconstruct the entire ordered environmental history at every finite horizon. In particular, it determines the number of visits to each environment and their order.

This differs from the mutation-free case, where the endpoint depends only on environmental counts and cannot distinguish different orderings of the same counts. With mutation and sufficient separation, each epoch's environment can be decoded and its action reversed, allowing the history to be reconstructed one epoch at a time.

This conclusion does not contradict contraction (Lemma 4.1). Contraction makes differences between trajectories smaller, but the fixed-environment flow remains injective at every finite time. Consequently, distinct histories can produce extremely close endpoints without producing identical endpoints. Exact recoverability must therefore be distinguished from recovery at finite measurement or numerical precision.

Finally we note that this reconstruction is a finite-history application of symbolic coding for injective iterated maps with disjoint images Hutchinson [1981]. The separation identifies the last map applied, and invertibility allows the preceding state to be recovered recursively.

**An algorithm: Recovery of the ordered environmental history from an exact endpoint.** The inputs are: the exact endpoint  $x_L$ , the known horizon  $L$ , the epoch duration  $T > T_{\text{suff}}$ , the model matrices  $W_1, \dots, W_M$ , and the decoder  $d$  constructed in Theorem 4.6.

The decoder can be implemented using the disjoint sets

$$B_r(T) = \{x \in \Delta_S^\circ : d_H(x, x_r^*) \leq R_r \exp(-\kappa_r T)\}.$$

For every reachable endpoint, exactly one of these sets contains the endpoint.

1. Set  $x^{(L)} = x_L$ .
2. For  $m = L, L-1, \dots, 1$ , perform the following steps:

- (a) Find the unique label  $r_m$  such that

$$x^{(m)} \in B_{r_m}(T).$$

Record

$$E_{m-1} = \varepsilon_{r_m}.$$

- (b) Compute

$$v^{(m-1)} = \exp(-TW_{r_m})x^{(m)}.$$

- (c) Normalize to recover the preceding composition:

$$x^{(m-1)} = \frac{v^{(m-1)}}{\mathbf{1}^\top v^{(m-1)}}.$$

3. Return the sequence in chronological order:

The output of this algorithm is the complete ordered environmental history.

Under the assumptions of Corollary 4.10 and exact arithmetic, every step returns the true preceding composition and the true environmental label.

**Practical limitation: increasingly close endpoints.** The reconstruction algorithm is exact, but its sensitivity to error can grow rapidly with the history length. To see why, consider two histories whose last  $m$  environments agree. Let  $x$  and  $z$  be their compositions immediately before this common suffix. Repeated application of Lemma 4.1 gives

$$d_H(X_L, X'_L) \leq \exp\left(-T \sum_{j=L-m}^{L-1} \kappa_{r_j}\right) d_H(x, z) \leq \exp(-\kappa_{\min} T m) d_H(x, z),$$

where

$$\kappa_{\min} = \min_r \kappa_r > 0.$$

Thus, differences caused by earlier environments are exponentially compressed during a common recent sequence.

Numerical errors during backward reconstruction can produce nonpositive coordinates or incorrect environmental labels, compromising subsequent steps. Higher arithmetic precision reduces roundoff but cannot restore information lost through measurement noise or rounding. Thus, exact history recovery is guaranteed at every finite horizon, while reliable recovery at fixed precision becomes more demanding for longer histories.

## 4.7 Recovery with bounded observation error

For  $T > T_{\text{suff}}$ , define

$$\gamma(T) := \min_{r < q} \{\delta_{rq} - R_r \exp(-\kappa_r T) - R_q \exp(-\kappa_q T)\} > 0. \quad (4.20)$$

**Corollary 4.11** (Robust environmental identification). *If the observed positive composition  $\widetilde{\mathbf{X}}_{n+1}$  satisfies*

$$d_H(\widetilde{\mathbf{X}}_{n+1}, \mathbf{X}_{n+1}) \leq \eta \quad \text{almost surely,} \quad 2\eta < \gamma(T),$$

*then one measurable decoder recovers  $E_n$  from the noisy observation for every epoch, and*

$$I(E_n; \widetilde{\mathbf{X}}_{n+1}) = H(E_n).$$

*Proof.* An observation produced in environment  $r$  belongs to the projective ball around  $\mathbf{x}_r^*$  of radius  $R_r \exp(-\kappa_r T) + \eta$ . The sum of the radii of any two such balls is smaller than  $\delta_{rq}$ . The enlarged balls are therefore disjoint, and the decoding proof of Theorem 4.6 applies.  $\square$

Note that this corollary guarantees robust identification of the latest environment, but not robust reconstruction of an arbitrarily long history.

## 4.8 With mutation: numerical illustrations

We next consider the same two-species, two environment system with a symmetric mutation rate of  $\mu = 10^{-3}$ , as in Section 3.5. The fitness vectors are  $f_1 = (1.00, 0.98)$  and  $f_2 = (0.97, 0.99)$ , the environments are sampled independently with equal probabilities, and  $x_0 = (0.5, 0.5)$ . We again use  $T \in 1, 5, 10, 20, 50, 100, 200, 500, 100$  epochs, and 10,000 independent trajectories for each  $T$ . The first species frequency is rounded to 0.001 before computing empirical  $I(E_n; \mathbf{X}_{n+1})$  in bits, consistently with Section 3.5.

In contract to the mutation-free system, the estimated mutual information exhibits a strong dependence on the epoch duration, see figure 3. For short durations, the information about the current environment decreases after the initial transient and remains relatively small. As  $T$  increases, the estimated mutual information increases substantially. At  $T = 50$ , the estimate stabilizes near 0.43 bits, while at  $T = 100$  it approaches approximately 0.89 bits. For  $T = 200$  and  $T = 500$ , the estimates remain close to the environmental entropy of 1 bit.

This behavior is consistent with the mechanism underlying Theorem 4.6. With strictly positive mutation, the fixed-environment dynamics possess interior attracting equilibria. For sufficiently long epochs, the population composition approaches the equilibrium associated with the current environment, making that environment identifiable from the observed endpoint. The near-saturation of the numerical curves supports the theorem's equilibrium-separation mechanism; it is not, by itself, a numerical verification of the explicit sufficient threshold  $T_{\text{suff}}$ .

We further investigate the ordered environmental history recovery algorithm developed in Section 4.6. For this recovery experiment, we use the same fitness vectors  $f_1 = (1.00, 0.98)$  and  $f_2 = (0.97, 0.99)$ , symmetric mutation  $\mu = 10^{-3}$ , epoch duration  $T = 500$ , and a horizon of  $N = 100$  epochs. We generate 100 independent environmental histories, each starting at  $x_0 = (0.5, 0.5)$  and inheriting its endpoint composition across epochs. Starting from the final floating endpoint, we identify the latest environment and apply the corresponding inverse flow to reconstruct earlier states and labels recursively. A depth- $k$  recovery is counted as successful only if the corresponding environmental label is correctly recovered along the backward procedure.

As shown in figure 4, the most recent three environments are covered in all 100 trajectories, but the success rate falls to approximately 85% at backward depth  $k = 3$  and 28% at  $k = 4$ ; no trajectories are recovered successfully at larger depths. This is consistent with the contraction mechanism in Lemma 4.1: forward dynamics compress distinctions between different initial compositions, whereas inversion must expand those small differences. Consequently, finite endpoint precision and forward

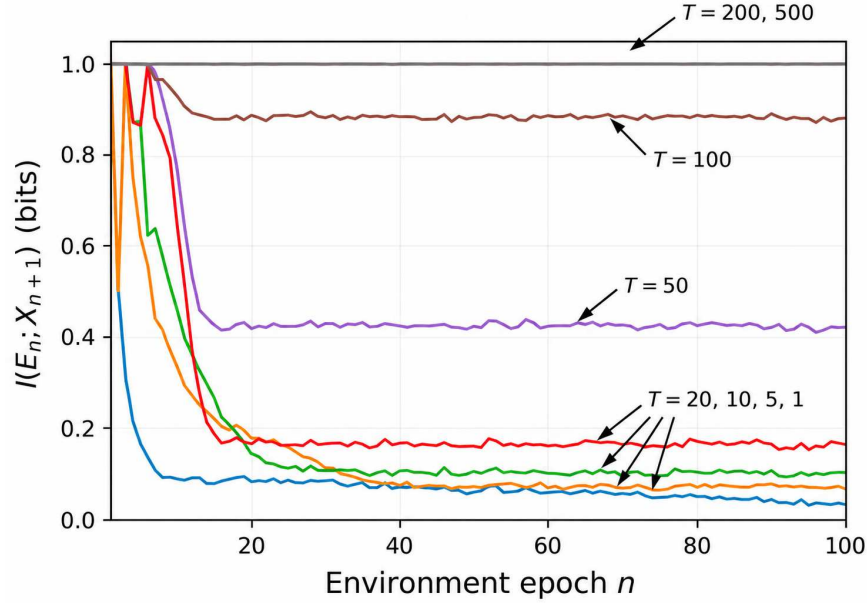


Figure 3: **Environment-frequency mutual information with mutation.** Estimated  $I(E_n; X_{n+1})$  across environmental epochs for  $\mu = 10^{-3}$  and eight epoch durations  $T$ . Longer epochs yield substantially more information about the latest environment, approaching the one-bit entropy ceiling when the environment-specific endpoint distributions are well separated. Arrows identify the plotted durations.

simulation errors are amplified by repeated inverse steps, eventually corrupting the inferred preceding states and labels. Importantly, contraction does not destroy mathematical invertibility at a fixed finite time; the experiment demonstrates numerical ill-conditioning, not a counterexample to exact ordered-history recovery in Corollary 4.10.

## 5 Discussion

Population composition can encode several different aspects of environmental experience, and these need not be retained equally well. Our results distinguish information about the latest environment, information about accumulated environmental counts, and information about the complete ordered history. This distinction is essential for interpreting an evolving population as an environmental record: little information about the most recent conditions does not necessarily imply little information about the past.

Without mutation, the endpoint composition depends on the environmental history through cumulative selection. In log-ratio coordinates, the contributions of successive epochs add, so their order is irretrievably lost. Nevertheless, under the rational-independence condition of Theorem 3.3, the endpoint uniquely determines the number of visits to each environment. The coexistence of exact count memory with vanishing information about the latest environment is initially surprising. It follows because the counts identify how often each environment occurred without identifying which occurrence came last. Under iid sampling, the conditional probability of the latest environment given the counts is its empirical frequency, which approaches the underlying sampling probability as the history grows. The population can therefore retain a precise aggregate record while providing progressively less information about the environmental label of a particular epoch.

A second notable feature of the mutation-free system is that its matched mutual information

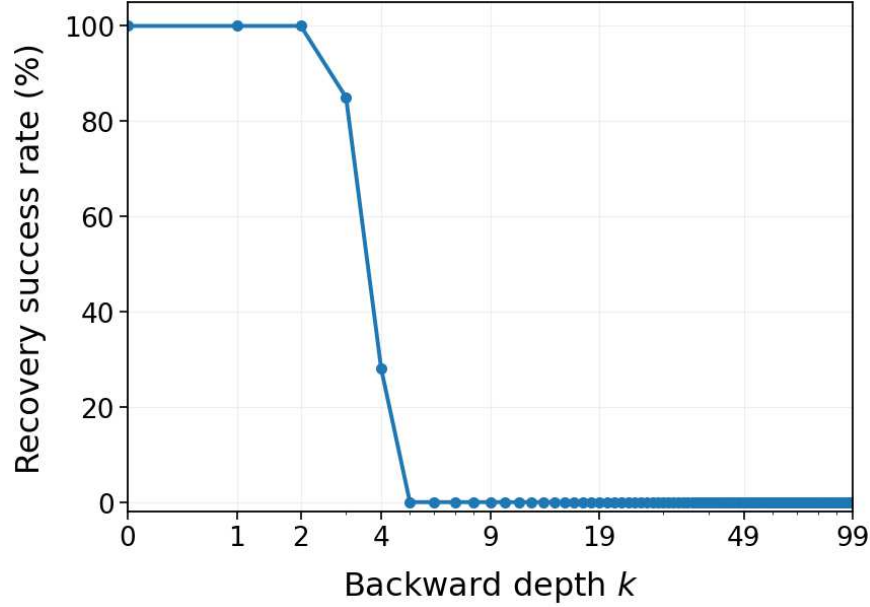


Figure 4: **Finite-precision ordered-history recovery with mutation.** Percentage of 100 independent trajectories for which the environmental label is correctly recovered at backward depth  $k$ , with  $k = 0$  denoting the latest environment. Parameters:  $f_1 = (1.00, 0.98)$ ,  $f_2 = (0.97, 0.99)$ ,  $\mu = 10^{-3}$ ,  $T = 500$ , and  $N = 100$ . Rapid deterioration beyond the most recent epochs illustrates the numerical sensitivity of successive inverse flows.

is independent of epoch duration. Longer exposure changes the composition, potentially bringing it extremely close to the simplex boundary, but simply rescales cumulative selection in log-ratio coordinates. Under exact observation, this rescaling is invertible and therefore preserves information. This conclusion concerns distinguishability rather than the magnitude of compositional differences. With measurement noise, rounding, or binning, the observation map need not preserve that distinction, and epoch duration may affect the information accessible to an observer.

Strictly positive mutation produces a different organization of environmental memory. For sufficiently long epochs and distinct environmental equilibria, contraction brings all possible endpoint compositions for a given environment into a region separated from those associated with other environments. The latest environment can then be identified independently of the preceding history, and this identification remains valid under sufficiently small bounded observation error. Mutation alone does not guarantee this conclusion: distinguishability depends on the environmental equilibria and on separation of the corresponding endpoint regions. Moreover, the duration derived here is sufficient rather than necessary; failure to satisfy it does not by itself imply information loss.

Perhaps the most striking result is that contraction is compatible with exact recovery of the complete ordered history. Once the latest environment is identified, its finite-time flow can be inverted, revealing the preceding composition and allowing reconstruction to continue backward. Thus, under the separation assumptions, mutation permits a form of ordered historical encoding that is absent from the additive mutation-free dynamics. This does not imply unlimited practical memory. Histories with a common recent sequence have endpoints whose differences are exponentially compressed, making their earlier differences increasingly difficult to resolve. Exact finite-horizon recoverability and robust reconstruction are therefore distinct properties. The backward algorithm makes this distinction concrete: every step is well-defined for an exact reachable endpoint, whereas

errors can be amplified and can eventually cause incorrect environmental assignments.

These results complement previous studies of evolutionary information and memory. [Guttenberg \[2019\]](#) investigated information acquisition and decay in finite-population simulations with binary genomes, using estimated information measures based on discretized frequencies. Our deterministic, exact-observation analysis identifies mechanisms that can preserve distinguishability even when compositional differences become very small; its conclusions therefore need not coincide with information decay observed at finite resolution. [Chatterjee et al. \[2025\]](#) studied the relationship between fitness and environment–phenotype mutual information in two-state systems. Their observable is a sampled phenotype, with joint probabilities obtained from time-averaged population fractions, whereas ours is the complete composition at a specified endpoint. These observables provide different amounts and kinds of environmental information. Likewise, the connections between evolution and Bayesian computation developed by [Czégel et al. \[2022\]](#) motivate an inference-based interpretation of population dynamics, but do not by themselves establish which realized environmental histories are identifiable from an endpoint.

Historical recoverability also differs from the adaptive usefulness of memory. [Marzen and Crutchfield \[2018\]](#) study memories that improve prediction of future environmental conditions, while [Donaldson-Matasci et al. \[2010\]](#); [Rivoire and Leibler \[2011\]](#); [Mafessoni et al. \[2021\]](#); [Piñero et al. \[2026\]](#) relate environmental information to growth or productivity. Our results concern the information present in composition, without assuming that organisms use it or that retaining it improves fitness. In particular, under iid environmental sampling, even complete knowledge of the past cannot predict the next independently drawn environment. The contribution here is therefore a characterization of environmental identifiability and its dependence on mutation and observation precision, rather than an equivalence between memory and adaptive performance.

An important next step is to quantify memory under explicit observation models and finite-population dynamics. Sampling a finite number of individuals, rounding frequencies, and adding measurement noise impose different limits on historical reconstruction. Bounds on decoding error and recoverable history length would connect the exact results to experimental inference, while demographic stochasticity would test which conclusions remain when population trajectories are themselves random. The algorithms also raise computational questions: count recovery currently requires enumeration, and backward reconstruction can be poorly conditioned. More efficient decoders, uncertainty estimates, and methods that recover only recent environments or aggregate features of history may be more useful in practice.

Further extensions concern both environmental structure and evolutionary dynamics. Temporally correlated environments may change the mutation-free information decay and give retained history predictive value, although the mutation-based separation theorem already applies to arbitrary environmental processes. Sparse mutation networks, variable or unknown epoch durations, and uncertainty in fitness parameters would bring the model closer to biological applications. Finally, sharper conditions for separation could clarify when full recovery occurs below the sufficient duration established here. These extensions would help determine how much of the exact environmental record remains accessible when observations are limited.

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