Diversity and Fitness Uncertainty Allow for Faster Evolutionary Rates

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I derive uncertainty relations that bound the speed of evolutionary processes in mutation-less and mutation-driven dynamics, modeled by the replicator and replicator-mutator equations. The speed limits derived imply that diversity in the population of a system allows for faster evolutionary rates. In particular, the uncertainty of the fitness function is singled out as necessary for fast evolution. These results generalize Fisher’s fundamental theorem of natural selection to dynamics that allow for mutations in terms of uncertainty relations that constrain evolutionary rates.

How fast can biological evolution occur in nature? What traits of a system enable fast evolutionary processes \cite{1}? How are evolutionary rates affected by different driving forces such as natural selection and mutation? I take a step at mathematically answering these questions by deriving saturable upper bounds on the rate of change of any quantity in an evolutionary process.

In 1945, Mandelstamm and Tamm derived an uncertainty relation, $\frac{d(\hat{A})}{dt} \leq 2 \Delta \hat{A} \Delta \hat{H}$, that constrains the evolution of isolated quantum systems, where $\langle \hat{A} \rangle$ is the quantum-mechanical expectation value of an observable $A$—an operator that describes a physical quantity—, $\Delta \hat{A} := \sqrt{\langle \hat{A}^2 \rangle - \langle \hat{A} \rangle^2}$ is its standard deviation, or uncertainty, and $\Delta \hat{H}$ is the uncertainty of the Hamiltonian $\hat{H}$ that drives the dynamics of the system \cite{2}. The Mandelstamm-Tamm bound on speed implies a trade-off between the rate of change of a physical quantity and the uncertainties of the physical quantity and of the energy of the system. This has given rise to the field of quantum speed limits \cite{3}.

Recently, it was shown that analogous uncertainty relations constrain the dynamics of classical stochastic systems \cite{4}, too. Here, I explore the consequences of such classical speed limits to the field of evolutionary biology.

**Methods: overview of classical speed limits.**—Given a probability distribution $\{p_j\}$, the expectation value $\langle A \rangle = \sum_j p_j a_j$ of a quantity $A$ satisfies the equation of motion \cite{4}

$$\frac{d\langle A \rangle}{dt} = \sum_j p_j \dot{a}_j + \sum_j \dot{p}_j a_j = \langle A \rangle - \text{cov}(A, \dot{I}) = \langle \dot{A} \rangle + \dot{\alpha}, \quad (1)$$

where $\alpha$ is the surprisal, or information content associated to the probability distribution \cite{5}, with components $\{I_j := -\ln p_j\}$, and $\text{cov}(A, B) := \langle (A - \langle A \rangle)(B - \langle B \rangle) \rangle$ denotes the covariance between two quantities. In the context of evolutionary biology, $p_j$ denotes the frequency with which a type $j$ occurs, and Eq. (1) is known as the Price equation \cite{6, 7}. An analogous equation holds for quantum systems with arbitrary dynamics \cite{8}, too.

The second term in the Price equation, $\dot{\alpha} := \sum_j \dot{p}_j a_j = -\text{cov}(A, \dot{I})$, corresponds to the change in the mean $\langle A \rangle$ due to the changes in the underlying probability distribution of the system. This term is constrained by the uncertainty relation \cite{4}

$$|\dot{\alpha}| \leq \Delta A \Delta \dot{I}. \quad (2)$$

Similarly to the result by Mandelstamm and Tamm, the uncertainties $\Delta A := \sqrt{\langle \hat{A}^2 \rangle - \langle \hat{A} \rangle^2}$ and $\Delta \dot{I} := \sqrt{\langle \dot{I}^2 \rangle - \langle \dot{I} \rangle^2}$ of the observable and of the surprisal rate limit the rate at which changes due to the probability distribution influence the observable. The variance in surprisal rate is related to the Fisher information of the probability distribution $p$ parametrized by time,

$$\mathcal{I}_F := \sum_j \frac{p_j^2}{p_j} = \langle \dot{\alpha} \rangle = (\Delta \dot{I})^2. \quad (3)$$

The Fisher information takes a central role in parameter estimation theory, limiting the ultimate precision with which a parameter can be estimated: the larger $\mathcal{I}_F$ the better the parameter of interest can be estimated \cite{9, 10}.

**Limits to replicator evolutionary processes.**—While biological systems are extremely complex, they are nonetheless amenable to mathematical modeling in certain regimes \cite{11}. Under the assumption that mutation rates between types are negligible \cite{12}, the replicator equation,

$$\dot{p}_j = p_j (f_j - \langle f \rangle) \quad (4)$$

can be used to model population dynamics \cite{13, 14, 15, 16, 17} (note applications of the replicator equation to various other fields \cite{18, 19, 20, 21}). The fitness, in general a function $f_j = f_j(p, t)$ of the probability distribution and time, determines whether the population of a type that occurs with probability $p_j$ increases or decreases: types with positive excess fitness, $f_j \geq \langle f \rangle$, tend to grow in frequency.

Using Eq. (3), the Fisher information for a replicator dynamics becomes $\mathcal{I}_F = \sum_j p_j(f_j - \langle f \rangle)^2 \equiv (\Delta f)^2$ (see Refs. \cite{22, 23} for other connections between the Fisher and natural selection frameworks).
Eq. (5) implies that

\[
\frac{d\langle A \rangle}{dt} - \langle \dot{A} \rangle \leq \Delta A \Delta f.
\]  

(5)

The uncertainty relation (5) for the replicator equation implies constraints on the diversity of arbitrary quantities. If the quantity of interest has no explicit time dependence, i.e., if \( \{a_j\} \) are constant, then Eq. (5) becomes a bound on evolutionary rates \( \frac{d\langle A \rangle}{dt} \). In plain terms, the bound says that evolution is slow for systems with well determined fitness functions, where \( \Delta f \approx 0 \). In contrast, evolution can be faster on systems with a diverse population such that \( \Delta f \) is large. Diversity, as quantified by the uncertainty in fitness, serves as a resource [24], in this case by enabling fast evolution. This is pictorially illustrated in Figure 1.

The Shannon entropy \( S := -\sum_j p_j \ln p_j \) can serve as an information-theoretic measure of the diversity, or variability, in the population of the system. While \( S \approx 0 \) if only one type \( k \) occurs with \( p_k \approx 1 \), one has \( S = \ln N \) if the frequencies \( \{p_j\} \) are equal probability \( p_j = 1/N \). Taking \( \{a_j \equiv I_j := -\ln p_j\} \) as the surprisal and using that \( \dot{S} = -\sum_j \dot{p}_j \ln p_j \) from conservation of probability, Eq. (5) implies that [4]

\[
\bar{S} \leq \Delta I \Delta f \leq \sqrt{\frac{1}{2} \ln^2(N - 1) + 1} \Delta f,
\]  

(6)

where Theorem 8 of Ref. [25] was used to obtain the second inequality. A high uncertainty in fitness thus allows for higher entropy rates, with a maximum rate scaling as \( \max \bar{S} \approx \ln N \Delta f/2 \) for large \( N \).

It is natural to wonder whether bound (5) can be saturated. It turns out that quantities \( A \) that have a linear relationship with the surprisal rate \( \dot{f} = -\dot{p}/p \) saturate the speed limit [4]. This is the case for the fitness function under replicator dynamics. Equation (1) and the fact that \( \dot{I}_j = -(f_j - \langle f \rangle) \) imply that

\[
\frac{d(f)}{dt} - \langle \dot{f} \rangle = \sum_j \dot{p}_j f_j = -\text{cov}(f, -f) = (\Delta f)^2.
\]  

(7)

This provides a proof of Fisher’s (controversial [26]) fundamental theorem of natural selection [27–31]. This shows that Fisher’s theorem is exact for (i) evolutionary processes modeled by a replicator equation with (ii) fitness functions that are independent of time and of the populations that determine fitness, where \( \Delta f \approx 0 \). In contrast, evolution can be faster on systems with a diverse population such that \( \Delta f \) is large. Diversity, as quantified by the uncertainty in fitness, serves as a resource [24], in this case by enabling fast evolution. This is pictorially illustrated in Figure 1.

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In cases with more general fitness functions \( f_j \equiv f_j(p, t) \), Eq. (7) provides a generalized version of Fisher’s theorem whereby the velocity with which fitness changes due to changes in populations equals the fitness variance.

Limits to evolutionary processes with mutations.— Mutations are a crucial driving force in realistic evolutionary processes [32–35]. Mutations between types can be modeled by the replicator-mutator equation,

\[
\dot{p}_j = \sum_k Q_{jk} f_k p_k - p_j \langle f \rangle,
\]  

(8)

where \( Q_{jk} \geq 0 \) is a dimensionless transition matrix, with \( \sum_k Q_{jk} = 1 \) [36, 37] (see also [38–41]). The replicator equation (4) is recovered when the mutation matrix is the identity, \( Q_{jk} = \delta_{jk} \).

The general bound (2) implies that

\[
\frac{d\langle A \rangle}{dt} - \langle \dot{A} \rangle \leq \Delta A \sqrt{\mathcal{F}}.
\]  

(9)
Note, though, that while for the replicator dynamics the Fisher information is immediately related to uncertainty in fitness via $\mathcal{I}_F = (\Delta f)^2$, this is no longer the case for dynamics with mutations. Connecting the Fisher information to biologically relevant quantities remains an interesting problem to be explored.

Alternatively, I define the mutation-driven probability distribution

$$\Pi_j := \sum_k p_k Q_{kj}. \quad (10)$$

I interpret $\Pi$ as the probability with which a given type would hypothetically occur in the future if evolution were only driven by mutations, or, possibly more biologically relevant, in regimes where strong mutation dominate over natural selection processes [32].

Let $\delta \Pi a_j := a_j - \langle A \rangle_\Pi$ and $\hat{\delta} f_j := f_j - \langle f \rangle$, where $\langle A \rangle_\Pi := \sum_j \Pi_j a_j$ and $\langle f \rangle := \sum_j p_j f_j$ are averages with respect to the distributions $\Pi$ and $p$. Then, using conservation of probability, it holds that

$$\dot{a} := \sum_j p_j \delta \Pi a_j = \sum_j p_j \delta \Pi a_j - \sum_j p_j \delta \Pi a_j \langle f \rangle$$

$$= \sum_{jk} Q_{kj} f_k p_k \delta \Pi a_j - \sum_j p_j \delta \Pi a_j \langle f \rangle$$

$$= \sum_{jk} Q_{kj} \hat{f}_k p_k \delta \Pi a_j - \langle f \rangle \langle A \rangle - \langle A \rangle_\Pi. \quad (11)$$

Applying the Cauchy-Schwarz inequality to the first term gives

$$\left( \sum_{jk} Q_{kj} \hat{f}_k p_k \delta \Pi a_j \right)^2 \leq$$

$$\left( \sum_{jk} Q_{kj} \hat{f}_k^2 p_k \right) \left( \sum_{jk} Q_{kj} \hat{f}_k \delta \Pi a_j \right)^2$$

$$= \left( \sum_{jk} \hat{f}_k^2 p_k \right) \left( \sum_{jk} \Pi_k \delta \Pi a_j \right)^2, \quad (12)$$

where I used $Q_{kj} \geq 0$ and $\sum_j Q_{kj} = 1$. This bound is tight if and only if $\hat{f}_k \propto \delta \Pi a_k$.

Thus, we have proven that

$$\left| \dot{a} - \langle f \rangle (\langle A \rangle_\Pi - \langle A \rangle) \right| \leq \Delta \Pi A \Delta f, \quad (13)$$

where $\langle A \rangle_\Pi := \sum_j \Pi_j a_j$ and $\Delta \Pi A := \sqrt{\langle A^2 \rangle_\Pi - \langle A \rangle^2_\Pi}$ are the mean and standard deviation with respect to the mutation-driven distribution $\Pi$. The speed with which any quantity $A$ changes is upper bounded by the quantity's uncertainty with respect to the mutation-driven distribution $\Pi$, and the uncertainty in the fitness of the system. As in the mutation-less setting, diversity in the population is seen to give rise to less constrained evolution rates.

To simplify the interpretation of the result, let us momentarily consider the case when $A$ does not explicitly depend on time, i.e., $\{a_j\}$ constant. Then, Eq. (13) and the reverse triangle inequality imply that

$$\left| \frac{d\langle A \rangle}{dt} \right| \geq \langle f \rangle \left| \langle A \rangle_\Pi - \langle A \rangle \right| - \Delta \Pi A \Delta f \quad (14a)$$

$$\left| \frac{d\langle A \rangle}{dt} \right| \leq \Delta \Pi A \Delta f + \langle f \rangle \left| \langle A \rangle_\Pi - \langle A \rangle \right|. \quad (14b)$$

We thus identify two distinct sources to the ultimate speeds achievable by the system. One of the sources, $\Delta \Pi A \Delta f$, involves uncertainties in the fitness function and uncertainties in the quantity of interest evaluated in the mutation-driven distribution. The remaining one depends on the average of the fitness and of the quantity of interest. This is somewhat reminiscent of the speed limits for open quantum systems, where two distinct sources to the dynamics of a system lead to additive contributions to the ultimate speed with which a quantity can evolve, which in turns allows to derive lower bounds on speed [8]. I show how the constraints (14) on the fitness rate $d\langle f \rangle/dt$ compare to the dynamics of a simple system in Fig. 2.

Applying Eq. (13) to the surprisal implies that the entropy rate is bounded by

$$\left| \frac{dS}{dt} - \langle f \rangle S(p||\Pi) \right| \leq \Delta \Pi I \Delta f, \quad (15)$$

where the relative entropy, or Kullback–Leibler divergence, $S(p||\Pi) := -\sum_j p_j \ln \left( \frac{\Pi_j}{p_j} \right)$ serves as a proxy of distance between the probability distribution $p$ and the mutation-driven distribution $\Pi$ [17, 42–44]. Note that $\Delta \Pi I \geq 0$ but is unbounded from above. In cases with a non-diverse population, $\Delta f = 0$, and finite $\Delta \Pi I$, entropy only evolves due to the mismatch between the two distributions, with a rate governed by the average fitness,

$$\frac{dS}{dt} = \langle f \rangle S(p||\Pi).$$

I conclude by considering the most relevant biological example: the rate of change of the fitness function for dynamics that incorporate mutations, $A = f$. Equation (13) becomes

$$\left| \frac{df}{dt} - \langle f \rangle \right| \leq \Delta \Pi A \Delta f. \quad (16)$$

This uncertainty relation imposes the most stringent constraints on evolution when the fitness is completely certain with respect to the distribution $p$ or to the mutation-driven distribution $\Pi$, i.e., when $\Delta \Pi f = 0$ or $\Delta f = 0$. In these cases, dynamics is solely driven by the difference in fitness between the two distributions, with $d\langle f \rangle/dt = \langle f \rangle (f_\Pi - f)$. Faster evolutionary rates are possible for systems with uncertain fitness.
ary biology—have been found to saturate the speed limit for Gibbs states with (arbitrarily) time-dependent temperature [4].

System and the rate at which a system’s entropy changes constrains dynamics. I find it remarkable that these speed limits, while being extremely general, are saturated in certain cases of interest. In stochastic thermodynamics, for example, the rate at which heat is exchanged with a system and the rate at which a system’s entropy changes saturates their speed limits for Gibbs states with (arbitrarily) time-dependent temperature [4].

Recent works, mostly within the fields of quantum physics [3, 8, 46] and classical statistical mechanics [47–51], have shown that uncertainty relations constrain dynamics. I find it remarkable that these speed limits, while being extremely general, are saturated in certain cases of interest. In stochastic thermodynamics, for example, the rate at which heat is exchanged with a system and the rate at which a system’s entropy changes saturates their speed limits for Gibbs states with (arbitrarily) time-dependent temperature [4].

From the derivation of Eq. (12), we have that a necessary and sufficient condition for bound (16) to be saturated is $\delta f_k \propto \delta f_k$, which happens if and only if $\langle f \rangle = \langle f \rangle_\Pi$ and $\Delta f = \Delta f$. If this is the case and the fitness is time-independent, Fisher’s fundamental relation, $d\langle f \rangle/\langle f \rangle = (\Delta f)^2$, holds true [45]. In all other cases, Eqs. (13) and (16) provide generalizations of Fisher’s fundamental theorem of natural selection to replicator-mutator dynamics in terms of universal constraints on evolutionary rates.

**Discussion.**— Recent works, mostly within the fields of quantum physics [3, 8, 46] and classical statistical mechanics [47–51], have shown that uncertainty relations constrain dynamics. I find it remarkable that these speed limits, while being extremely general, are saturated in certain cases of interest. In stochastic thermodynamics, for example, the rate at which heat is exchanged with a system and the rate at which a system’s entropy changes saturates their speed limits for Gibbs states with (arbitrarily) time-dependent temperature [4].

Here, replicator dynamics—a toy model often used to describe mutation-less population dynamics in evolutionary biology—have been found to saturate the speed limit for the fitness of a population. Higher uncertainty in fitness leads to higher evolutionary rates. This last result was, in fact, known by Fisher, who connected the rate of change of the average fitness to the uncertainty in the fitness of a population.

More generally, I have shown that the connection between the uncertainty in fitness and evolutionary rates holds for dynamics that incorporate mutations. This allows identifying regimes in which Fisher’s relation holds even for dynamics with mutations. In all other regimes, our results generalize Fisher’s by imposing constraints on evolutionary rates.

The overarching aim of this work was to investigate how diversity—in this case, as quantified by the variance in fitness—relates to evolution. The results in this letter show that diversity provably serves as a resource by allowing for faster evolution. It is tempting to ponder what implications may exist for other fields.

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Note added.— During the preparation of this work, I became aware of a recent pre-print, Ref. [52], that derives constrains on evolutionary processes. I encourage interested readers to refer it as well.

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