nature portfolio

Peer Review File

Universal constraint on nonlinear population dynamics

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

see attached document

Reviewer #2 (Remarks to the Author):

In their manuscript "Universal constraint on nonlinear population dynamics", the authors derive and discuss an upper bound on the evolution speed of general population dynamics. Their main result is the inequality (3), which relates the rate of change and standard deviation of a type-dependent quantity to the Fisher information associated with the population vector. This relation is then applied to three specific types of population dynamics and used to derive bounds on the scaling exponents near bifurcations.

The paper is very well written; the main results, their derivation and their consequences are explained clearly. The authors also provide concise summaries of the investigated models and their main features, as well as the consequences of their bound in each case.
The presented results are scientifically sound and novel, and well supported by the presented examples. As mentioned by the authors, population dynamics encompasses a very wide range of systems with wildly different phenomenology, so obtaining general bounds that are universally valid is certainly a valuable contribution to the field. The authors' conjecture that the bound should lead to universal constraints on the scaling exponents near bifurcations is very interesting and has the potential to inspire follow-up research.
In summary, I find this paper to be well-suited to Communications Physics and recommend publication as-is.

Reviewer #3 (Remarks to the Author):

This is an excellent paper, providing a very general theorem for the rate of change in a quantity in population dynamics. This can be thought of as a generalization of Fisher's Fundamental Theorem of Natural Selection; the more aligned a quantity is with the reproduction rates of the subpopulations, the closer the rate of change of the quantity can be to the limiting quantity.

The paper illustrates how generally this can be applied with an excellent variety of population models, and shows how this limiting rate is relevant to each situation, showing for example how extinction of a subpopulation relates to this limiting rate and a transcritical bifurcation.

My only recommendation is that there is some research using the quasispecies-type models for Fishers FTNS that should be discussed, particularly because these address Fisher's FTNS in the presence of mutations in a model similar to that used in this paper. This work should be discussed (there are a few statements that are out of date in the paper - see comments in the attached pdf - which need to be updated). It would be very interesting to see if the limiting rate of this paper relates to the more general Fisher's Fund. Thm with Mutations, but I do not consider that a requirement for publication. I also had some comments where terminology or definitions could be modified to make this paper more generally accessible to readers in related fields - there should be

at least a comment added to mention that the definitions in the paper differ than what is common in some fields.

Overall I recommend this paper highly for publication with the minor changes addressing some of the recent work in incorporating mutations in Fisher's Thm in the context of quasispecies-type models used in this paper.

The authors derive a time-information uncertainty relation for evolutionary processes which they show places an upper bound on the speed in which observables for various ecological models can evolve. They purport that their bound is universal.

My only main concern has to do with wording. Eq. (3) is not new, in the sense that it is an application of the time information uncertainty relation, (Nicholson et.al. [17] in their work) where the distribution for type populations is playing the role of information rate. As they note, the fact the time information uncertainty relation is related to the price equation is also not new, as is noted in their citation Frank and Bruggeman Entropy 2020. It is my opinion that the wording around Eq. (3) could be modified in order to avoid confusion by readers coming from other fields.

That said, in general I found this paper very exciting and interesting. The authors find scaling limits at the critical points for a set of ecological models. These rates come directly from the Fisher information and thus place speed limits on the rate that an observable can change around the critical point. Due to the Price equation being seen as placing limits on evolutionary Biology, these seems very novel and potentially impactful. Though scaling of the Fisher information has also been found before, see *R. Hollerbach, D. Dimarche and E. Kim, Entropy, 20, (8) 2018* as one example, to my knowledge this has never been shown for evolutionary models and never in the context of non-equilibrium speed limits of the form shown here. I have several comments below, but otherwise I recommend for publication.

1. While I found the results novel, perhaps the authors could expand on the consequences of limiting the speed for say, the growth of types? Or other physically relevant variables. These results are after all placing a constraint on the Price equation itself.

2. The authors note that the velocity of the type dependent growth rate s_i saturates the speed limit. While they show this is true for their specific example of type growth rate. Could their be a more general explanation? With the rate $F_i = s_i N_i$, this makes s_i be explicitly independent of time, i.e. the time dependence for the moments of s_i are in P_i. Since s_i is time independent, this is the special case of the Cramer-Rao bound, which is known to saturate when the distribution for the random variable in this case type number is Gaussian, see *A. Cianchi, E. Lutwak, D Yang and G. Zhang et.al IEEE Transactions on Information Theory, 60, (1) 2014.*

3. Line 328/329 switch the order of we and here.

4. Line 299 is there a missing $\|$?

Universal constraint on nonlinear population dynamics

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(Dated: January 24, 2022)

Ecological and evolutionary processes show various population dynamics depending on internal interactions and environmental changes. While crucial in predicting biological processes, discovering general relations for such nonlinear dynamics has remained a challenge. Here, we derive a universal information-theoretical constraint on a broad class of nonlinear dynamical systems represented as population dynamics. The constraint is interpreted as a generalization of Fisher's fundamental theorem of natural selection. Furthermore, the constraint indicates nontrivial bounds for the speed of critical relaxation around bifurcation points, which we argue are universally determined only by the type of bifurcation. Our theory is verified for an evolutionary model and an epidemiological model, which exhibit the transcritical bifurcation, as well as for an ecological model, which undergoes limit-cycle oscillation. This work paves a way to predict biological dynamics in light of information theory, by providing fundamental relations in nonequilibrium statistical mechanics of nonlinear systems.

Introduction

Nonlinear dynamics appears in a variety of fields, including classical mechanics, chemical reaction systems, and population biology, to name a few [1]. Nonlinearity can trigger complex temporal and spatial patterns and even chaotic behaviors, making it challenging to find universal relations within the properties of dynamics. In particular, slight perturbations in external parameters can result in qualitative changes in the dynamical property through a bifurcation such as the Hopf bifurcation, where self-sustained oscillation emerges. It is of pivotal importance to explore universal relations shared by a broad class of dynamical phenomena with nonlinearity.

Ecological and evolutionary processes often exhibit nonlinear population dynamics [2, 3] such as temporal oscillation in population sizes and irreversible extinction of certain species [4]. Typical biological systems consist of identifiable units such as genotypes and species (called "types" in this paper), and intra-type and inter-type interactions cause nonlinear dynamics [2, 4]. Besides interactions, type-dependent growth rates determined by natural selection lead to nonlinear dynamics of the proportions of each type. In evolutionary theory, Fisher's fundamental theorem of natural selection [5, 6] establishes a simple relation between the variance of the growth rate and the temporal increase in the average growth rate. Though the theorem has been extended to ecological models [7], mutation processes have been outside the scope of the theorem.

Bifurcations and associated critical dynamics play significant roles in biological processes [8]. In ecological [9, 10] and epidemiological [11] systems, critical slowing down around bifurcation points has been discussed as an early warning signal for catastrophic shifts. In evolutionary systems, bifurcation points can appear as critical mutation rates beyond which heredity does not persist [12, 13], and the self-organized criticality has also been discussed as a possible mechanism of mass extinction of species [14]. Since such critical dynamics reflects instabilities behind nonlinear systems [15], fundamental relations near bifurcation points are crucial in predicting dramatic changes in ecological and evolutionary processes.

We here derive a general constraint on nonlinear population dynamics by extending the formulation developed for stochastic processes [16, 17] to nonlinear dynamical systems. In particular, Fisher's fundamental theorem of natural selection is a special case of the constraint. As a unique consequence of the constraint, we show that the critical scaling exponents of speeds near the bifurcation point should have nontrivial bounds that are universally determined by the type of bifurcation. We verify our theory for an evolutionary model with mutation and the SIR model with birth and death, which show the transcritical bifurcation, as well as for the competitive Lotka-Volterra model, which undergoes limit-cycle oscillation.

Results

Constraint on general population dynamics. We consider a general population dynamics described by

$$\partial_t N_i = F_i(N_1, ..., N_L), \tag{1}$$

where i is the label for each type, L is the total number of types, and $N_i(t)$ is the density of type i at time t. If there are interactions between types, $F_i(N_1, ..., N_L)$ is generally a nonlinear function. Defining the proportion $P := \{P_i\}_{i=1}^L := \{N_i/N_{\rm tot}\}_{i=1}^L$ with the total population density $N_{\rm tot} := \sum_{i=1}^L N_i$, we obtain equations for P_i and $N_{\rm tot}$ as

$$\partial_t P_i = \frac{F_i(N_{\rm tot}P_1, ..., N_{\rm tot}P_L)}{N_{\rm tot}} - P_i \sum_{j=1}^{L} \frac{F_j(N_{\rm tot}P_1, ..., N_{\rm tot}P_L)}{N_{\rm tot}} \tag{2}$$

and $\partial_t N_{\rm tot} = \sum_{i=1}^L F_i(N_{\rm tot}P_1, ..., N_{\rm tot}P_L)$, respectively. Even if $F_i(N_1, ..., N_L)$ is a linear function for all i, Eq. (2) can be a

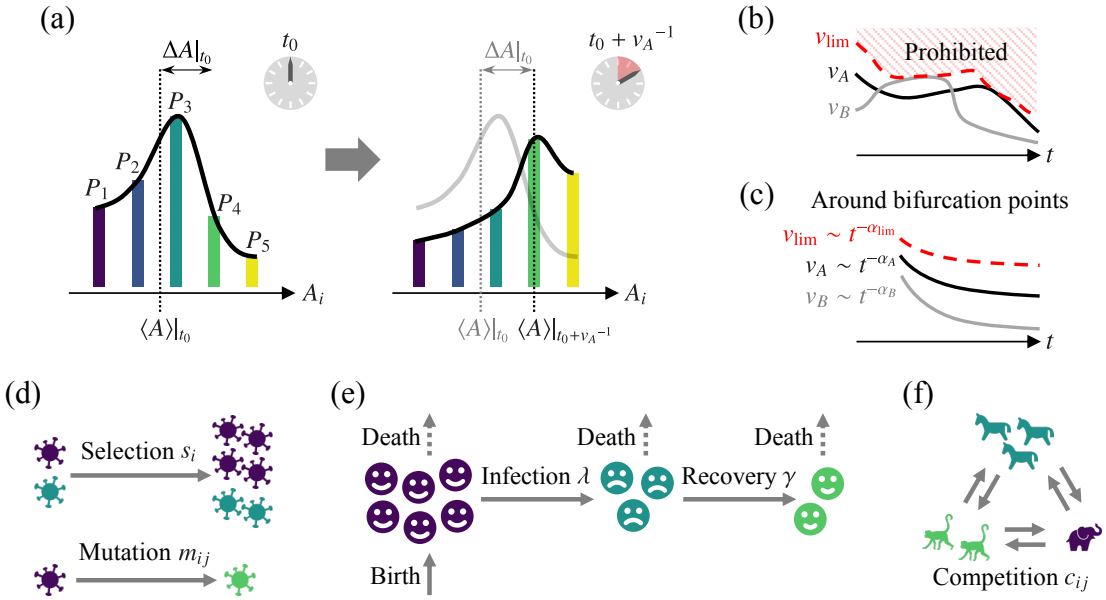

Fig. 1. **Speed-limit inequality in ecological and evolutionary dynamics.** (a) Inverse of the speed, $v_A{}^{-1}$, represents the time required for the instantaneous average $\langle A\rangle$ to change by the instantaneous standard deviation ΔA. In (a), we assume $A_1 < A_2 < A_3 < A_4 < A_5$ without loss of generality. (b) For any quantity A and at any time, speeds faster than $v_{\rm lim}$ are prohibited. (c) Around bifurcation points, the speed and speed limit show power-law decays as $v_A \sim t^{-\alpha_A}$ and $v_{\rm lim} \sim t^{-\alpha_{\rm lim}}$ with a constraint $\alpha_A \geq \alpha_{\rm lim}$ for any A, where $\alpha_{\rm lim}$ is universally determined by the bifurcation type. In this study, we mainly consider three models: (d) the evolutionary model with natural selection and mutation, (e) the SIR model, and (f) the competitive Lotka-Volterra model.

nonlinear equation, and bifurcations can occur as we discuss later.

Applying the Cauchy-Schwarz inequality to the Price equation [18, 19], which is derived from the conservation of the total proportion ($\sum_{i=1}^{L} P_i = 1$), we obtain the speed-limit inequality (Methods):

$$v_A \leq v_{\rm lim} := \sqrt{I_{\rm F}} := \sqrt{\langle (\partial_t P/P)^2\rangle}, \tag{3}$$

where we define the Fisher information $I_{\rm F}$ [20, 21] and the speed $v_A := |\partial_t \langle A\rangle - \langle \partial_t A\rangle|/\Delta A$, which characterizes the temporal change rate of a type-dependent quantity $A := \{A_i\}_{i=1}^{L}$ that can depend on time in general [Methods, Fig. 1(a)]. Here, the average and standard deviation are defined as $\langle A\rangle := \sum_{i=1}^{L} P_i A_i$ and $\Delta A := (\langle A^2\rangle - \langle A\rangle^2)^{1/2}$, respectively. Inequality (3) provides a universal upper bound on the speed of population dynamics, independent of the choice of quantity A [Fig. 1(b)]. We stress that (3) applies to nonlinear dynamics though the expression is equivalent to that for Markov processes [16, 17], where the probability distribution follows linear dynamics. For example, $v_{\rm lim}$ in (3) can be a non-monotonic function of time, in contrast to Markovian relaxation processes, where $v_{\rm lim}$ decays monotonically [16]. Note that (3) is different from the previously obtained speed-limit inequalities in nonlinear systems [22, 23], which have been discussed mainly for chemical reaction networks. Following Ref. [17], we can interpret (3) as the uncertainty relation between the timescale of dynamical quantities ($v_A{}^{-1}$) and the information of dynamics ($\sqrt{I_{\rm F}}$).

Relation to Fisher's fundamental theorem. Notably, our general constraint includes Fisher's fundamental theorem as a special case when applied to an evolutionary model with natural selection. We take $F_i = s_i N_i$ in Eq. (1), where $s_i > 0$ is the type-dependent growth rate. In such systems, Fisher's fundamental theorem of natural selection asserts that the increase in the average growth rate is equal to the variance of the growth rate [5], i.e., $\partial_t \langle s\rangle = (\Delta s)^2$. As shown in Methods, we find that Fisher's fundamental theorem is a special case of (3), $v_s = v_{\rm lim}$. Note that $v_{\rm lim}$ in (3) is equivalent to Crow's index of opportunity for selection, which provides an empirical estimate of the maximum strength of natural selection acting on a given population [24, 25]. Furthermore, even when the growth rate depends on time and densities, we show that an extended version of the fundamental theorem [6, 7] is a special case of (3) (Methods). Our result therefore covers a variety of previous results established in population biology in light of information theory and statistical physics. For more general dynamics with mutation, Fisher's fundamental theorem does not hold. Nevertheless, the speed-limit inequality (3) is satisfied and thus regarded as a generalization of the fundamental theorem.

Speed limit for evolutionary dynamics. We next consider another evolutionary model with natural selection and mutation [Fig. 1(d)] by taking $F_i = s_i N_i + \sum_{j=1}^{L} m_{ij} N_j$ in Eq. (1) [12, 26]. Here, $s_i > 0$ is the growth rate and $m_{ij} \geq 0$ $(i \neq j)$ is the mutation rate from type j to i. To demonstrate inequality (3), we take $L = 3$ with $s_2 = s_3 = \bar{s}$ and examine a situation where type

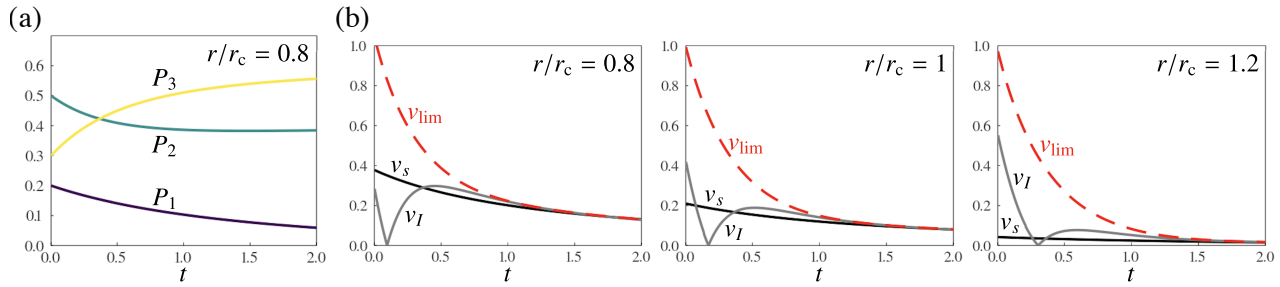

Fig. 2. **Speed limit for the evolutionary dynamics with natural selection and mutation.** (a) Typical time dependence of the proportion P_i for $r/r_c = 0.8$. (b) Inequality (3) holds, regardless of the parameters (r/r_c) and quantities (growth rate s or diversity I). The speed of the growth rate v_s and that of change in diversity v_I are compared with the speed limit v_{lim} for $r/r_c = 0.8$ (left), $r/r_c = 1$ (center), and $r/r_c = 1.2$ (right). See Methods for the other parameters used.

1 will survive (become extinct) after a long time if the growth rate $s_1 = \bar{s} + r$ is larger (smaller) than a critical value $\bar{s} + r_c$ (Methods). The extinction transition at $r = r_c$ corresponds to the transcritical bifurcation [1].

Figure 2(a) shows typical time dependence of the proportion P_i. As shown in Fig. 2(b), regardless of the value of r/r_c, the speed of the growth rate v_s (black solid lines) is bounded by the speed limit v_{lim} (red dashed lines), which verifies (3). To confirm the generality of (3), we introduce the Shannon entropy $I_S := \langle I \rangle$ with $I := \{I_i\}_{i=1}^L := \{-\ln P_i\}_{i=1}^L$ [21] as the (logarithm of) diversity of population (see Supplementary Fig. 1 for typical time dependence of I_S). We show that the speed of change in diversity, v_I (gray solid lines), is also bounded by v_{lim}.

Universal constraint around transcritical bifurcation point. A notable consequence of the speed limit follows at the transcritical bifurcation point ($r = r_c$), where an observable A typically exhibits critical slowing down [8, 11] with a power-law decay of the speed, $v_A \sim t^{-\alpha_A}$. While α_A can vary for different A, inequality (3) indicates that α_A is bounded by a universal factor α_{lim} determined by the Fisher information [Fig. 1(c)]. In the evolutionary model with natural selection and mutation, we find $P_1 \sim t^{-1}$ (Methods) and thus

$$v_{lim} \sim \sqrt{(\partial_t P_1)^2/P_1} \sim t^{-\alpha_{lim}^{TC}} \quad (4)$$

with $\alpha_{lim}^{TC} = 3/2$. Then, we have

$$\alpha_A \geq \alpha_{lim}^{TC} = 3/2 \quad (5)$$

for arbitrary A in this process.

Additionally, if the parameter is slightly off the bifurcation point, the system can exhibit dynamical scaling, in a manner similar to critical phenomena [27–29]. Assuming that the relaxation times of the speed and speed limit diverge at the bifurcation point as $\sim |r - r_c|^{-\beta_A}$ and $\sim |r - r_c|^{-\beta_{lim}^{TC}}$, respectively, we obtain the dynamical scaling laws as

$$v_A(r - r_c, t) \simeq t^{-\alpha_A} f_A^{\pm}(t^{1/\beta_A}|r - r_c|), \quad (6)$$

$$v_{lim}(r - r_c, t) \simeq t^{-\alpha_{lim}^{TC}} f_{lim}^{\pm}(t^{1/\beta_{lim}^{TC}}|r - r_c|), \quad (7)$$

where f_A^+ and f_{lim}^+ (f_A^- and f_{lim}^-) are scaling functions for $r - r_c > 0$ (< 0). Combining inequality (3) and the scaling laws (6) and (7), we derive another constraint on the exponents as $\beta_A \leq \beta_{lim}^{TC}$ (Methods). In the numerical simulations, we have only found the case with $\beta_A = \beta_{lim}^{TC}$ (see below), which suggests that the diverging relaxation time of any speed should be proportional to the relaxation time of a single quantity (i.e., P_1 in the present model) in a similar way to critical phenomena [27, 28].

To confirm the above argument, we demonstrate the long-time relaxation of v_{lim}, v_s, v_I, and a speed v_b for the type index $b := \{b_i\}_{i=1}^L := \{i\}_{i=1}^L$ at the bifurcation point ($r = r_c$) [Fig. 3(a)]. We find $v_{lim} \sim t^{-3/2}$ [red dotted line in Fig. 3(a)], which is consistent with (4). We also obtain $v_s \sim t^{-3/2}$, $v_I \sim t^{-2} \ln t$, and $v_b \sim t^{-2}$ (see Methods for the derivation), and the corresponding exponents are $\alpha_s = 3/2$, $\alpha_I = 2$ (neglecting the logarithmic dependence), and $\alpha_b = 2$, which indeed satisfy inequality (5). Moreover, slightly off the bifurcation point, we find the expected scaling laws [(6) and (7)] of v_s, v_b (Supplementary Fig. 2), and v_{lim} [Fig. 3(b)] with $\beta_s = \beta_b = \beta_{lim}^{TC} = 1$.

Beyond specific dynamics, we conjecture that the exponents for the power-law decay of the speeds at the bifurcation point in population dynamics are bounded by a universal constant α_{lim} that only depends on the type of bifurcation. Similarly, the exponent β_{lim} is also conjectured to be determined by the bifurcation type. These conjectures are plausible because critical properties associated with the bifurcation can be essentially described by the normal form for each bifurcation type [1, 29]. This universal constraint on the exponents is a unique property of nonlinear dynamics, in contrast to the previous works on speed limits for linear dynamics [16, 17].

As a primary example, inequality (5) can be generally applied to nonlinear dynamics that undergoes an extinction transition through the transcritical bifurcation. We consider the SIR model with birth and death [Fig. 1(e)], where N_1, N_2, and N_3 are the densities of susceptible, infected, and recovered individuals, respectively [30] (Methods). This model is genuinely nonlinear in that $F_i(N_1, N_2, N_3)$ in Eq. (1) is a nonlinear function. In this model, the transcritical

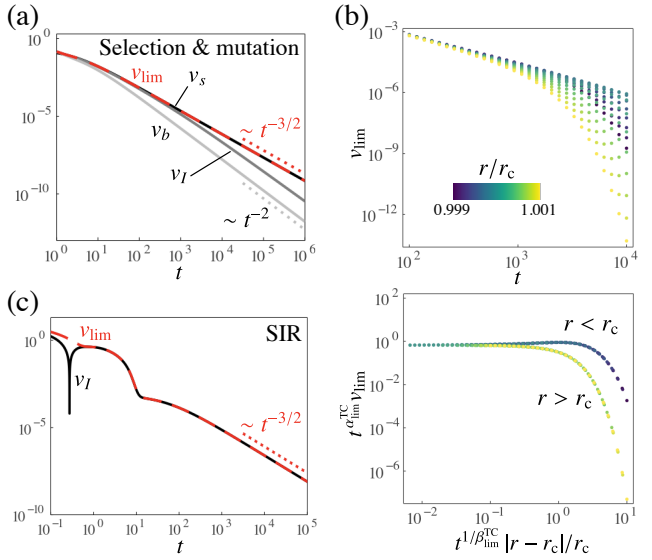

Fig. 3. **Universal bounds for the critical scaling exponents at the transcritical bifurcation.** (a) Power-law decay of the speeds v_s, v_I, v_b, and $v_{\rm lim}$ at the transcritical bifurcation point ($r = r_{\rm c}$) of the evolutionary model with selection and mutation. The asymptotic forms ($v_{\rm lim} \sim t^{-3/2}$ and $v_b \sim t^{-2}$) are shown with dotted lines. (b) Time and parameter dependence of $v_{\rm lim}$ (upper panel) and the corresponding scaling plot (lower panel) near the bifurcation point ($0.999 \le r/r_{\rm c} \le 1.001$). The exponents are given as $\alpha^{\rm TC}_{\rm lim} = 3/2$ and $\beta^{\rm TC}_{\rm lim} = 1$. (c) Power-law decay of v_I and $v_{\rm lim}$ at the transcritical bifurcation point of the SIR model. The asymptotic form ($v_{\rm lim} \sim t^{-3/2}$) is shown with a dotted line. For (a) and (b), we use the same parameters as those for Fig. 2. See Methods for the parameters used for (c).

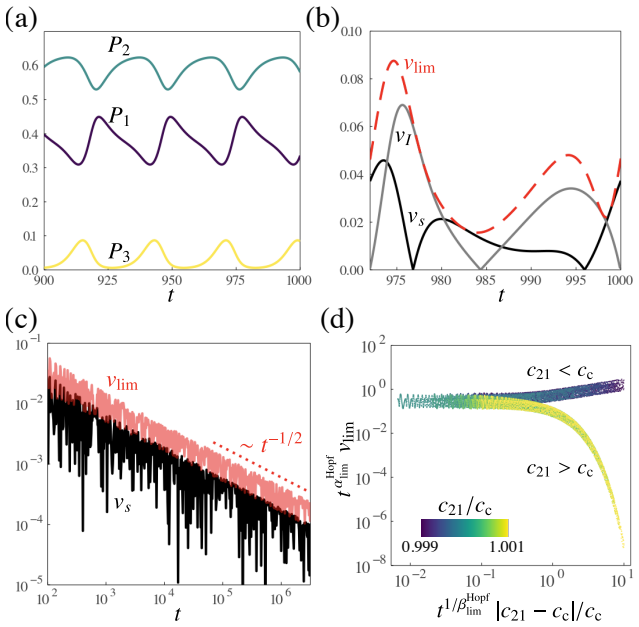

Fig. 4. **Universal bounds for the critical scaling exponents at the supercritical Hopf bifurcation.** Limit-cycle oscillation of (a) the proportion P_i and (b) the speeds v_s, v_I, and $v_{\rm lim}$ in the competitive Lotka-Volterra model. (c) Power-law decay of $v_{\rm lim}$, compared with v_s at the Hopf bifurcation point. The asymptotic form of the amplitude relaxation ($v_{\rm lim} \sim t^{-1/2}$) is shown with a dotted line. The curves are rattling since the number of plotted points is finite; similarly to (b), v_s oscillates between zero and nonzero values, while $v_{\rm lim}$ stays nonzero. (d) Scaling plot of the time and interaction dependence of $v_{\rm lim}$ near the bifurcation point ($0.999 \le c_{21}/c_{\rm c} \le 1.001$). The limit cycle appears for $c_{21} < c_{\rm c}$, while the steady-state coexistence of three types appears for $c_{21} \ge c_{\rm c}$, where $c_{\rm c}$ is the Hopf bifurcation point (Methods). The exponents are given as $\alpha^{\rm Hopf}_{\rm lim} = 1/2$ and $\beta^{\rm Hopf}_{\rm lim} = 1$. See Methods for the parameters used.

bifurcation occurs as an extinction transition of the infected and recovered individuals, i.e., a transition between the disease-free and endemic states, and the critical slowing down occurs ($P_2 \sim P_3 \sim t^{-1}$) at the bifurcation point (Methods). In Supplementary Fig. 3, we show typical time dependence of the proportion at the bifurcation point. We find that the speed of change in diversity v_I and the speed limit $v_{\rm lim}$ follow the same power-law decay as $v_I \sim v_{\rm lim} \sim t^{-3/2}$ [Fig. 3(c)], satisfying the formulae (4) and (5).

Universal constraint around Hopf bifurcation point. To verify our conjecture for other types of bifurcations, we focus on the Hopf bifurcation, at which a limit cycle starts to appear [1]. According to the normal form of the supercritical Hopf bifurcation, the deviation from the steady state decays with oscillation as $\sim t^{-1/2}\cos\omega t$ at the bifurcation point (Methods). Thus, for population dynamics undergoing the supercritical Hopf bifurcation, the proportion follows $P_i \sim$ const. $+ t^{-1/2}\cos\omega t$, and the speed limit decays as

$$v_{\rm lim} = \sqrt{\sum_{i=1}^{L} (\partial_t P_i)^2 / P_i} \sim t^{-\alpha^{\rm Hopf}_{\rm lim}}, \tag{8}$$

with $\alpha^{\rm Hopf}_{\rm lim} = 1/2$, where we only consider the amplitude relaxation by neglecting the oscillatory component. Correspondingly, if we assume a power-law decay of the speed amplitude as $v_A \sim t^{-\alpha_A}$, α_A should satisfy

$$\alpha_A \ge \alpha^{\rm Hopf}_{\rm lim} = 1/2. \tag{9}$$

As an ecological model that undergoes the supercritical Hopf bifurcation, we consider the competitive Lotka-Volterra model [Fig. 1(f)] by taking $F_i = s_i N_i - \sum_{j=1}^{L} c_{ij} N_i N_j$ in Eq. (1) [4, 31]. Here, s_i is the growth rate, $c_{ij} > 0$ represents the competitive interaction between type i and j, and these parameters are set around the Hopf bifurcation (Methods).

We first show typical limit-cycle oscillation of the proportion [Fig. 4(a)]. Comparing v_s, v_I, and $v_{\rm lim}$ within a single period [Fig. 4(b)], we confirm that inequality (3) holds even when the limit cycle appears. By tuning the parameters to the Hopf bifurcation point, we numerically find the power-law decay of the speed amplitudes [32] as $v_s \sim v_I \sim v_{\rm lim} \sim t^{-1/2}$ [Fig. 4(c) and Supplementary Fig. 4], verifying (8) and (9). Then, changing the parameters slightly off the bifurcation point, we find that the counterparts of the scaling laws (6) and (7) hold for the speed amplitudes [Fig. 4(d) and

Supplementary Fig. 5] with $\beta_s = \beta_I = \beta_{\rm lim}^{\rm Hopf} = 1$.

Discussion

We have illustrated the applications of the dynamical constraint (3) to ecological and evolutionary models. Focusing on the bifurcation unique to nonlinear dynamics, we have argued that the exponents of speeds at critical slowing down have the universal bounds that depend only on the bifurcation type. In particular, for the transcritical and supercritical Hopf bifurcations, we have confirmed the theoretically obtained formulae (4)-(9) using numerical simulations. Similar formulae are obtained for other bifurcations, e.g., $\alpha_A \geq \alpha_{\rm lim}^{\rm SN} = 2$ for the saddle-node bifurcation (Methods), which appears in population dynamics [9, 10, 15].

Considering the probability [16, 17] instead of the proportion, we may extend our argument to critical phenomena in many-body stochastic systems, which can express nonequilibrium phenomena different from ecological and evolutionary dynamics. For instance, lattice gas models [27], the contact process [28], and biological systems such as swarms [33] are potentially subject to constraints corresponding to (5) or (9) with possibly irrational lower bounds.

The methodologies of ecology and evolution have been developed almost independently [34]. However, ecological and evolutionary dynamics may not be separable in some situations. For example, rapid evolution can occur on the same timescale as that of ecological processes when there are drastic environmental changes [34]. General relations such as (3) will be useful in quantitative understanding of even inseparable eco-evolutionary dynamics.

Methods

Price equation and speed-limit inequality. Purely from the conservation of the total proportion, $\sum_{i=1}^{L} P_i = 1$, we can derive the Price equation [18, 19],

$$\partial_t \langle A \rangle = {\rm cov}(A, \partial_t P/P) + \langle \partial_t A \rangle \,. \tag{10}$$

Here, $A := \{A_i\}_{i=1}^{L}$ is a generally time-dependent quantity depending on each type, e.g., the growth rate, $\langle A \rangle := \sum_{i=1}^{L} P_i A_i$, ${\rm cov}(A, B) := \langle (A - \langle A \rangle)(B - \langle B \rangle) \rangle$, and $\partial_t P/P := \{\partial_t P_i / P_i\}_{i=1}^{L}$.

We define the speed of A as $v_A := |\partial_t \langle A \rangle - \langle \partial_t A \rangle| / \Delta A$ [16, 17] with $\Delta A := \sqrt{\langle (A - \langle A \rangle)^2 \rangle}$. The inverse of the speed, ${v_A}^{-1}$, represents the time required for A to change to a statistically distinguishable value [17], and thus v_A characterizes the speed of the temporal change in A [Fig. 1(a)]. From Eq. (10), we obtain the speed-limit inequality (3) as

$$\begin{aligned} v_A &= \frac{|{\rm cov}(A, \partial_t P/P)|}{\Delta A} \\ &\leq \frac{1}{\Delta A} \sqrt{\sum_{i=1}^{L} P_i (A_i - \langle A \rangle)^2} \sqrt{\sum_{i=1}^{L} P_i \left(\frac{\partial_t P_i}{P_i} \right)^2} \\ &= \sqrt{\langle (\partial_t P/P)^2 \rangle}, \end{aligned}$$

where $\langle \partial_t P/P \rangle = \partial_t \sum_{i=1}^{L} P_i = 0$ and the Cauchy-Schwarz inequality are used in the second line.

The equal sign in (3) is achieved when $A - \langle A \rangle$ is parallel or anti-parallel to $\partial_t P/P$ in the L-dimensional vector space, where $\partial_t P_i / P_i$ is regarded as the ith component of $\partial_t P/P$, for instance. When there are only two types ($L = 2$), we can explicitly obtain $(A_1 - \langle A \rangle, A_2 - \langle A \rangle) = (A_1 - A_2)(P_2, -P_1)$ and $(\partial_t P_1/P_1, \partial_t P_2/P_2) = [\partial_t P_1/(P_1 P_2)](P_2, -P_1)$, leading to $A - \langle A \rangle \parallel \partial_t P/P$, and the equal sign in (3) is achieved regardless of the details of dynamics.

Fisher's fundamental theorem of natural selection. We first take $F_i = s_i N_i$ in Eq. (1), where $s_i > 0$ is the type-dependent growth rate. Since $\partial_t P_i = (s_i - \langle s \rangle) P_i$ from Eq. (2), Eq. (10) leads to

$$\partial_t \langle s \rangle = {\rm cov}(s, s - \langle s \rangle) = (\Delta s)^2, \tag{11}$$

which means that the rate of increase in the average growth rate is equal to the variance of the growth rate, known as Fisher's fundamental theorem of natural selection [5, 20, 35–39]. On the other hand, the equation $\partial_t P_i = (s_i - \langle s \rangle) P_i$ also leads to $v_{\rm lim} = [\langle (s - \langle s \rangle)^2 \rangle]^{1/2} = \Delta s$. Since $v_s = |\partial_t \langle s \rangle| / \Delta s$ by definition, Eq. (11) is equivalent to $v_s = v_{\rm lim}$, suggesting that Fisher's fundamental theorem is nothing but a special case of (3).

We next take $F_i = f_i(\{N_i\}_{i=1}^{L}, t) N_i$ in Eq. (1) with an arbitrary function f_i, which is the so-called fitness [7] and represents the growth rate that can depend on the effects of interactions among types. From Eqs. (2) and (10), we obtain $\partial_t \langle f \rangle - \langle \partial_t f \rangle = (\Delta f)^2$, which is known as an extended version of Fisher's fundamental theorem [6, 7]. Since we can obtain $v_{\rm lim} = \Delta f$ and $v_f = |\partial_t \langle f \rangle - \langle \partial_t f \rangle| / \Delta f$ in the same way as explained above, the extended version of the fundamental theorem is equivalent to a special case of (3), $v_f = v_{\rm lim}$.

Evolutionary model with natural selection and mutation. We take $F_i = s_i N_i + \sum_{j=1}^{L} m_{ij} N_j$ in Eq. (1) [12, 26], where $s_i > 0$ is the growth rate, $m_{ij} \geq 0$ ($i \neq j$) is the mutation rate from type j to i, and $\sum_{i=1}^{L} m_{ij} = 0$ for all j. Note that we here consider a large and well-mixed population where noise and spatial effects [40, 41] are negligible. In the following, we further assume $s_i = \bar{s} + r\delta_{i1}$ ($\bar{s}, r > 0$), $m_{1j} = 0$ for $j \neq 1$, and $m_{ij} > 0$ for $i \neq 1$ and $i \neq j$, where δ_{ij} is the Kronecker delta. From Eq. (2), we can obtain the equation for P_1 as $\partial_t P_1 = (r + m_{11} - r P_1) P_1$. Thus, $r_{\rm c}$ ($:= -m_{11} = \sum_{i=2}^{L} m_{i1}$) is a transcritical bifurcation point [1]: $P_1^{\rm s} = 0$ for $r \leq r_{\rm c}$, while $P_1^{\rm s} = (r - r_{\rm c})/r > 0$ for $r > r_{\rm c}$, provided $P_1(t = 0) > 0$, where $P_i^{\rm s} := P_i(t \to \infty)$ is the steady-state proportion of type i. The qualitative change in $P_1^{\rm s}$ at $r = r_{\rm c}$ represents the transition between survival and extinction of type 1.

At the bifurcation point ($r = r_{\rm c}$), P_1 satisfies

$$\partial_t P_1 = -r_{\rm c} {P_1}^2, \tag{12}$$

which leads to $P_1 \sim t^{-1}$ after a long time. If a quantity A is independent of time, e.g., $A = s$ (growth rate) or $A = b$ (type index), we can obtain $\partial_t \langle A \rangle \sim t^{-2}$ according to $P_1 \sim t^{-1}$. Then,

assuming that ΔA shows a power-law decay as $\Delta A \sim t^{-\delta_A}$ with a certain exponent δ_A, we obtain $v_A = |\partial_t \langle A \rangle|/\Delta A \sim t^{-2+\delta_A}$. On the other hand, if A is time-dependent, e.g., $A = I = -\ln P$ (diversity), the asymptotic time dependence of $\partial_t \langle A \rangle - \langle \partial_t A \rangle$, ΔA, and $v_A = |\partial_t \langle A \rangle - \langle \partial_t A \rangle|/\Delta A$ generally depends on the time dependence of A. Thus, the asymptotic forms of the speeds follow $v_s \sim t^{-3/2}$ since $\Delta s = [P_1(1-P_1)]^{1/2} r_c \sim t^{-1/2}$ (i.e., $\delta_s = 1/2$), $v_b \sim t^{-2}$ since $\Delta b(t \to \infty) \neq 0$ (i.e., $\delta_b = 0$), and $v_I \sim t^{-2} \ln t$ since $|\partial_t \langle I \rangle - \langle \partial_t I \rangle| \sim t^{-2} \ln t$ and $\Delta I(t \to \infty) \neq 0$.

Near but off the bifurcation point ($r \simeq r_c$), we can linearize the equation of P_1 after a long time as

$$\partial_t (P_1 - P_1^s) \simeq -|r - r_c|(P_1 - P_1^s), \tag{13}$$

both for $r > r_c$ and $r < r_c$. Thus, P_1 shows an exponential relaxation with the relaxation time proportional to $|r - r_c|^{-1}$, which diverges at the bifurcation point. Such divergence suggests that the relaxation times τ_A (for v_A) and $\tau_{\rm lim}$ (for $v_{\rm lim}$) should also diverge at the bifurcation point as $\tau_A \sim |r - r_c|^{-\beta_A}$ and $\tau_{\rm lim} \sim |r - r_c|^{-\beta_{\rm lim}^{\rm TC}}$ with certain exponents β_A and $\beta_{\rm lim}^{\rm TC}$. This motivates us to consider the dynamical scaling laws (6) and (7) since similar dynamical scaling is applied to order parameters with diverging relaxation time in critical phenomena [27, 28]. Since inequality (3) indicates that v_A should show an exponential decay earlier than $v_{\rm lim}$, we obtain an inequality between the relaxation timescales as $\tau_A \leq \tau_{\rm lim}$ near the bifurcation point, which leads to $\beta_A \leq \beta_{\rm lim}^{\rm TC}$.

For Figs. 2, 3(a), 3(b), Supplementary Figs. 1, and 2, we used the mutation rates

$$(m_{ij}) = \begin{pmatrix} -2.1 & 0 & 0 \\ 1 & -1.2 & 0.8 \\ 1.1 & 1.2 & -0.8 \end{pmatrix}$$

with $r_c = -m_{11} = 2.1$ and the initial state $(P_1, P_2, P_3)|_{t=0} = (0.2, 0.5, 0.3)$.

SIR model with birth and death. We take $L = 3$, $F_1 = 1 - \lambda N_1 N_2/N_{\rm tot} - N_1$, $F_2 = \lambda N_1 N_2/N_{\rm tot} - \gamma N_2 - N_2$, and $F_3 = \gamma N_2 - N_3$ in Eq. (1), where N_1, N_2, and N_3 are the densities of susceptible, infected, and recovered individuals, respectively [30]. Here, λ is the infection rate, γ is the recovery rate, and we take both the birth and death rates as unity by rescaling time t and $N_{\rm tot}$, where the death rate is assumed to be the same for all three types. Assuming a nonzero proportion of the infected individuals at the initial time $[P_2(t=0) > 0]$, we can obtain the steady-state proportions as

$$(P_1^s, P_2^s, P_3^s) = \begin{cases} (1, 0, 0) & (\lambda \leq \lambda_c) \\ \left(\frac{\lambda_c}{\lambda}, \frac{\lambda - \lambda_c}{\lambda_c \lambda}, \frac{(\lambda_c - 1)(\lambda - \lambda_c)}{\lambda_c \lambda}\right) & (\lambda > \lambda_c) \end{cases},$$

where the extinction transition for the infected and recovered individuals occurs through the transcritical bifurcation at $\lambda = \lambda_c$ ($:= \gamma + 1$).

We consider the long-time dynamics of N_i at the bifurcation point ($\lambda = \lambda_c$). First, since $N_{\rm tot}$ shows an exponential relaxation according to $\partial_t N_{\rm tot} = 1 - N_{\rm tot}$, $N_{\rm tot} \simeq 1$ after a long time. Defining the deviation from the steady state as $\Delta N_i := N_i - N_i^s$ with $(N_1^s, N_2^s, N_3^s) := (1, 0, 0)$, we can linearize Eq. (1) as $\partial_t \Delta N_1 = -\Delta N_1 - \lambda_c \Delta N_2$, $\partial_t \Delta N_2 = 0$, and $\partial_t \Delta N_3 = -\Delta N_3 + (\lambda_c - 1)\Delta N_2$. These linearized equations suggest that N_1 and N_3 should adiabatically follow the dynamics of N_2, which is expected to show a power-law decay if nonlinearity is taken into account. Thus, we apply the adiabatic approximation ($\partial_t N_1 \simeq 0$) to the equation for N_1 and obtain $N_1 \simeq (1 + \lambda_c N_2/N_{\rm tot})^{-1} \simeq (1 + \lambda_c N_2)^{-1}$ on the timescale where N_2 changes. Then, $\partial_t N_2 = \lambda_c (N_1/N_{\rm tot} - 1) N_2 \simeq -{\lambda_c}^2 {N_2}^2 + O({N_3}^3)$, leading to a power-law decay of N_2 as expected: $N_2 \simeq ({\lambda_c}^2 t)^{-1}$. Lastly, applying the adiabatic approximation ($\partial_t N_3 \simeq 0$) to the equation for N_3, we obtain $N_3 \simeq (\lambda_c - 1) N_2 \simeq (\lambda_c - 1)({\lambda_c}^2 t)^{-1}$. In terms of the proportion, $P_2 \sim P_3 \sim t^{-1}$ is followed. Regarding the power-law decay of the speed of change in diversity, we obtain $v_I \sim t^{-3/2}$ since $|\partial_t \langle I \rangle - \langle \partial_t I \rangle| = |\sum_i (\partial_t P_i) \ln P_i| \sim t^{-2} \ln t$ and $\Delta I = [\sum_i P_i (\ln P_i)^2 - (\sum_i P_i \ln P_i)^2]^{1/2} \sim t^{-1/2} \ln t$.

For Fig. 3(c) and Supplementary Fig. 3, we used the recovery rate $\gamma = 15$, the infection rate $\lambda = \lambda_c = 16$, and the initial state $(N_1, N_2, N_3)|_{t=0} = (1.1, 0.1, 0)$.

Power-law decay at the supercritical Hopf bifurcation. The normal form of the supercritical Hopf bifurcation is given as $\partial_t z = (\mu + i\omega) z - |z|^2 z$, where z is a complex variable and $\omega > 0$ [1]. The only fixed point is $z = 0$ for $\mu \leq 0$, while the limit cycle appears with the amplitude $|z| = \sqrt{\mu}$ and the period $2\pi/\omega$ for $\mu > 0$. At the bifurcation point ($\mu = 0$), the amplitude follows $\partial_t |z| = -|z|^3$, which leads to a power-law decay of the amplitude as $|z| \sim t^{-1/2}$ and correspondingly an oscillatory decay of $\mathrm{Re}\, z$ or $\mathrm{Im}\, z$ as $\sim t^{-1/2} \cos \omega t$.

Competitive Lotka-Volterra model. We take $F_i = s_i N_i - \sum_{j=1}^{L} c_{ij} N_i N_j$ in Eq. (1), where s_i is the growth rate, and $c_{ij} > 0$ represents the competitive interaction between type i and j [4]. Using the previously obtained bifurcation diagram [42] as a reference, we take $L = 3$, $(s_1, s_2, s_3) = (19, 3/2, 12)$, and

$$(c_{ij}) = \begin{pmatrix} 1 & 2 & 4 \\ c_{21} & 1/6 & 1/3 \\ 1 & 1 & 3 \end{pmatrix}.$$

Within a certain range of c_{21} and initial states, the limit cycle appears for $c_{21} < c_c$, while the steady-state coexistence of three types appears for $c_{21} \geq c_c$, where c_c is the supercritical Hopf bifurcation point, and the numerically found value is $c_c = 0.064163908$.

We used $c_{21} = 0.063833$ for Figs. 4(a) and (b), $c_{21} = c_c$ for Fig. 4(c) and Supplementary Fig. 4, and $0.999 c_c \leq c \leq 1.001 c_c$ for Fig. 4(d) and Supplementary Fig. 5, with the initial state $(N_1, N_2, N_3)|_{t=0} = (20, 5, 2)$. To solve the differential equations (1), we used a Julia package DifferentialEquations.jl [43].

Power-law decay at the saddle-node bifurcation. The normal form of the saddle-node bifurcation is given as $\partial_t x =$

$\mu - x^2$, where the stable fixed point ($x = \sqrt{\mu}$) appears only for $\mu > 0$ [1]. At the bifurcation point ($\mu = 0$), we can obtain a power-law decay as $x \sim t^{-1}$.

Considering a population dynamics that undergoes the saddle-node bifurcation as an abrupt change in the density and proportion of type 1, we should obtain $P_1 \sim \text{const.} + t^{-1}$ at the bifurcation point for a certain range of initial states. Then, the speed limit will follow $v_{\lim} = [\sum_i (\partial_i P_i)^2 / P_i]^{1/2} \sim t^{-\alpha^{\mathrm{SN}}_{\lim}}$ with $\alpha^{\mathrm{SN}}_{\lim} = 2$.

Acknowledgements

We thank the Information Theory Study Group and Biology Seminar members in RIKEN iTHEMS and Kyogo Kawaguchi for scientific discussions. We also thank Takashi Okada, Takaki Yamamoto, and Yohsuke T. Fukai for helpful comments. This work was supported by JSPS KAKENHI Grant Numbers JP20K14435 (to K.A.), JP19K22457, JP19K23768, JP20K15882 (to R.I.), and RIKEN iTHEMS.

Author contributions

K.A. and R.I. conceived the project. K.A., R.I., and R.H. performed the analytic calculations. K.A. performed the simulations and made all the plots. K.A. drafted the initial version of the manuscript. K.A., R.I., and R.H. discussed the results and wrote the manuscript.

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Reply to Reviewer #1

> *The authors derive a time-information uncertainty relation for evolutionary processes which they show places an upper bound on the speed in which observables for various ecological models can evolve. They purport that their bound is universal.*

We appreciate the referee for the time and effort spent in reviewing our work.

> *My only main concern has to do with wording. Eq. (3) is not new, in the sense that it is an application of the time information uncertainty relation, (Nicholson et.al. [17] in their work) where the distribution for type populations is playing the role of information rate. As they note, the fact the time information uncertainty relation is related to the price equation is also not new, as is noted in their citation Frank and Bruggeman Entropy 2020. It is my opinion that the wording around Eq. (3) could be modified in order to avoid confusion by readers coming from other fields.*

As the referee points out, the same type of inequality as Eq. (3) has been derived in [17] (Nicholson et al.), and the equivalence between the dynamical equation used in [17] and the Price equation has been pointed out in [19] (Frank and Bruggeman). As suggested by the referee, we added an explanation on this point just after Eq. (3) in the “Constraint on general population dynamics” section. Nevertheless, we would like to stress that we applied Eq. (3) to nonlinear population dynamics for the first time, as far as we know.

> *That said, in general I found this paper very exciting and interesting. The authors find scaling limits at the critical points for a set of ecological models. These rates come directly from the Fisher information and thus place speed limits on the rate that an observable can change around the critical point. Due to the Price equation being seen as placing limits on evolutionary Biology, these seems very novel and potentially impactful. Though scaling of the Fisher information has also been found before, see R. Hollerbach, D. Dimarche and E. Kim, Entropy, 20, (8) 2018 as one example, to my knowledge this has never been shown for evolutionary models and never in the context of non-equilibrium speed limits of the form shown here. I have several comments below, but otherwise I recommend for publication.*

Thank you for appreciating this work and suggesting an interesting paper.

We now mention the suggested paper (*R. Hollerbach et al.*) in the first paragraph of the “Universal constraint around transcritical bifurcation point” section.

> *1. While I found the results novel, perhaps the authors could expand on the consequences of limiting the speed for say, the growth of types? Or other physically relevant variables. These results are after all placing a constraint on the Price equation itself.*

According to the speed-limit inequality, if we assume that a quantity Ai itself is independent of time, the square of the temporal change rate of the average quantity is upper bounded by the product of the Fisher information and the variance of the quantity. Thus, as the variance of the quantity is larger, the average quantity can potentially change more quickly. For instance, if we take the typical length of type i as Ai (e.g., length of bacteria for several types of mutants), the average length can quickly change when the variance of the length is large.

We now add this example in the second paragraph of the “Relation to Fisher’s fundamental theorem” section.

2. The authors note that the velocity of the type dependent growth rate si saturates the speed limit. While they show this is true for their specific example of type growth rate. Could their be a more general explanation? With the rate Fi = siNi, this makes si be explicitly independent of time, i.e. the time dependence for the moments of si are in Pi. Since si is time independent, this is the special case of the Cramer-Rao bound, which is known to saturate when the distribution for the random variable in this case type number is Gaussian, see A. Cianchi, E. Lutwak, D Yang and G. Zhang et.al IEEE Transactions on Information Theory, 60, (1) 2014.

The referee kindly recommends a more general explanation about the saturation of the speed in the case of $F_i = s_i N_i$.

In the introduction part of the suggested reference (*A. Cianchi et al.*), the authors discuss the condition for the distribution function $f_\theta(x)$ to saturate the Cramer-Rao bound, where both of the variable x and the parameter θ are continuous. The authors (*A. Cianchi et al.*) show that, if we assume $f_\theta(x) = f(x - \theta)$, a Gaussian $f(x)$ saturates the Cramer-Rao bound. Though x, θ, and $f_\theta(x)$ correspond to i (label for types), t (time), and $P_i(t)$ in our study, respectively, we do not further assume $P_i(t) = f(i - t)$, and thus the Gaussian distribution does not appear for the saturation condition of the speed-limit inequality.

In the “Methods / Price equation and speed-limit inequality” section, we have generally shown that $A - < A >$ should be parallel or anti-parallel to $\partial_t P / P$ to saturate the speed-limit inequality. Specifically for the case of $F_i = s_i N_i$, by explicitly solving the equation for the proportion [Eq. (2) in the manuscript], we find that the proportion is given by the following softmax function:

$$P_i(t) = P_i(0) \exp(s_i t) / \left[\sum_{j=1}^{L} P_j(0) \exp(s_j t) \right].$$

Conversely, if $P_i(t)$ is given by the softmax function above, the saturation of the speed follows.

To explain the last points, which were inspired by the referee’s comment, we now add the second paragraph of the “Methods / Fisher’s fundamental theorem of natural selection” section.

3. Line 328/329 switch the order of we and here.

We have fixed the order of “we” and “here” as the referee suggests.

4. Line 299 is there a missing //?

We have confirmed that the place of || is correct. To avoid confusion, we have added parentheses before ||.

Reply to Reviewer #2

In their manuscript "Universal constraint on nonlinear population dynamics", the authors derive and discuss an upper bound on the evolution speed of general population dynamics. Their main result is the inequality (3), which relates the rate of change and standard deviation of a type-dependent quantity to the Fisher information associated with the population vector. This relation is then applied to three specific types of population dynamics and used to derive bounds on the scaling exponents near bifurcations.

The paper is very well written; the main results, their derivation and their consequences are explained clearly. The authors also provide concise summaries of the investigated models and their main features, as well as the consequences of their bound in each case.
The presented results are scientifically sound and novel, and well supported by the presented examples. As mentioned by the authors, population dynamics encompasses a very wide range of systems with wildly different phenomenology, so obtaining general bounds that are universally valid is certainly a valuable contribution to the field. The authors' conjecture that the bound should lead to universal constraints on the scaling exponents near bifurcations is very interesting and has the potential to inspire follow-up research.
In summary, I find this paper to be well-suited to Communications Physics and recommend publication as-is.

We appreciate the referee for the time and effort spent in reviewing our work. Thank you very much for appreciating this work.

Reply to Reviewer #3

This is an excellent paper, providing a very general theorem for the rate of change in a quantity in population dynamics. This can be thought of as a generalization of Fisher's Fundamental Theorem of Natural Selection; the more aligned a quantity is with the reproduction rates of the subpopulations, the closer the rate of change of the quantity can be to the limiting quantity.

The paper illustrates how generally this can be applied with an excellent variety of population models, and shows how this limiting rate is relevant to each situation, showing for example how extinction of a subpopulation relates to this limiting rate and a transcritical bifurcation.

We appreciate the referee for the time and effort spent in reviewing our work. Thank you very much for appreciating this work.

My only recommendation is that there is some research using the quasispecies-type models for Fishers FTNS that should be discussed, particularly because these address Fisher's FTNS in the presence of mutations in a model similar to that used in this paper. This work should be discussed (there are a few statements that are out of date in the paper - see comments in the attached pdf - which need to be updated). It would be very interesting to see if the limiting rate of this paper relates to the more general Fisher's Fund. Thm with Mutations, but I do not consider that a requirement for publication. I also had some comments where terminology or definitions could be modified to make this paper more generally accessible to readers in related fields - there should be at least a comment added to mention that the definitions in the paper differ than what is common in some fields.

Thank you for the recommendation related to Fisher’s fundamental theorem with mutation. In the following, we will reply to each comment written in the PDF file of the previous manuscript.

[Regarding l. 44 in the previous manuscript (“mutation processes have been outside the scope of the theorem”)]

Fisher's FTNS was derived incorporating mutations in:
"The fundamental theorem of natural selection with mutations"
https://link.springer.com/article/10.1007/s00285-017-1190-x

and the formula is simplified in:
Dynamical Systems and Fitness Maximization in Evolutionary Biology
https://link.springer.com/referenceworkentry/10.1007/978-3-319-70658-0_121-1

where it is shown that Fisher's thm becomes:
d_t<s> = (\delta s)^2 + \beta\mu\bar{s}
\beta = mean birth rate
\mu = mutation rate (per birth)
\bar{s} = mean affect of a single mutation on fitness

(NOTE: This is mixing notation between the two papers. d_t<s> = (\delta s)^2 is from the current paper under review and \beta\mu\bar{s} is using the notation from the paper referenced above.)

Fisher's Thm with mutations is counter to his origonal conclusion that mean fitness is always increasing because the mean affect of a mutation on fitness is in general negative (see "Fitness Is Strongly Influenced by Rare Mutations of Large Effect in a Microbial Mutation Accumulation Experiment" https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4096375/, although the distribution of the affects of mutations complex). Also see: "Rate, molecular spectrum, and consequences of human mutation" (https://www.pnas.org/doi/abs/10.1073/pnas.0912629107) The first sentance of the abstract is: "Although mutation provides the fuel for phenotypic evolution, it also imposes a substantial burden on fitness through the production of predominantly deleterious alleles,..."

As the referee points out, the suggested papers indeed extend Fisher's fundamental theorem of natural selection to the case with mutation.

We now corrected the misleading statements and added the references in the second paragraph of the "Introduction" section.

[Regarding l. 116 in the previous manuscript ("We take Fi = si Ni in Eq. (1), …")]

The referenced paper here Li expresses Fisher's FTNS in terms of gene frequencies, which is different to the subpopulation-(quasispecies-like) model you use here. The paper (https://link.springer.com/article/10.1007/s00285-017-1190-x) presents Fisher's FTNS with the same model you are using, so you should add that as a ref here.

Following the referee's suggestion, we added the reference in the first paragraph of the "Relation to Fisher's fundamental theorem" section.

[Regarding l. 131 in the previous manuscript ("For more general dynamics with mutation, Fisher's fundamental theorem does not hold.")]

As mentioned in line 45, Fisher's thm with mutations (with the usual assumptions of infinite population, no noise, no spatial effects, etc.) is
d_t<s> = (\delta s)^2 + \beta\mu\bar{s}

although the Right-hand-side isn't always positive, so Fisher's concept of increasing fitness is false.

We corrected the misleading statement and added the relevant references in the second paragraph of the "Relation to Fisher's fundamental theorem" section.

[Regarding l. 293 in the previous manuscript ("The equal sign in (3) is achieved when …")]

This is a beautiful description. Does it mean that the more correlated a quantity A is to the sub-population growth rate, the faster the increase in A?

Thank you for appreciating the description. Yes, as the correlation between A and the instantaneous growth rate is stronger, the speed of A becomes faster.

We added an explanation of this point in the third paragraph of the "Methods / Price equation and speed-limit inequality" section.

[Regarding l. 327 in the previous manuscript (“mutation rate from type j to i”)]

Often "mutation rate" means mutations per offspring/birth. I think mij here is the usual mutation rate times the birth rate, which is constant per type i so this formula is good but the definition and units should be clarified. Wilke uses Wij for your mij, and decomposes it as Wij = AjQij (see below). Recommendation: say something like "mij is the rate at which offspring from type i have genotype j; that is mij=siQij, where Qij is the probability that an offsping of genotype i has genotype j" This would be consistent with the quasispecies literature (surveyed below) and not cause confusion with genetics literature where mutation rate is mutations per offspring. [After further reading, maybe its fine to call this the 'mutation rate' but just mention its relation to mij=siQij.]

Here is a survey of how that term is defined in three other relevant papers (the first one is your reference 12, and the other two should probably be added as references - The Wilke paper because it discussed quasispecies in more of a population dynamics setting similar to your paper, and the Basener-Sanford paper because it does this, and then proves a version of Fisher's Thm with mutations related to your general goals.

On a more general note, the referenced paper "Quasispecies Made Simple" says:
"of those w1 offspring a fraction 1 − μ1 retain the A1 genotype"
so in that paper μ1 is the fraction of offspring from type 1 that have a mutation putting them in type 2. But then the paper say:
"The product w1(1 − μ1) is the number of A1 offspring of an A1 parent;"
so it seems fitness w1 in that paper is birth rate and no deaths are considered.

In the paper "Quasispecies theory in the context of population genetics"
https://pubmed.ncbi.nlm.nih.gov/16107214/, the author refers to the original equations from Eigen and Schuster and says:
"Wij = AjQij is the product of the replication rate (fitness) Aj of sequence j and the mutation probability Qij from sequence j to i,"

The paper "The fundamental theorem of natural selection with mutations"
https://link.springer.com/article/10.1007/s00285-017-1190-x
uses the same type of notation as in Wilke"
"Suppose now that Pi is the concentration of the ith genetic sequence, mi is the associated fitness, and that Qi j is the mutation probability from j to i ."

Thank you very much for the survey on how the terms related to mutation are used.

Following the referee’s suggestion, we added comments on the relation to the mutation probability Qij and the relevant references in the first paragraph of the “Methods / Evolutionary model with natural selection and mutation” section.

[Regarding l. 330 in the previous manuscript (“negligible”)]

Affects of population size and noise are considered for this equation using numerical simulations in:
Dynamical Systems and Fitness Maximization in Evolutionary Biology
https://link.springer.com/referenceworkentry/10.1007/978-3-319-70658-0_121-1

I am not sure noise and spatial effects are ever negligible in a biological population. I would phrase this more as "in a large and well-mixed population that can approximated by assuming the size is infinite and noise and spatial effects are zero."

If you are referencing biological popuatlions, its normal to refer to ODE models like the quasispecies as infinite models; the first sentence from Wilke "Quasispecies theory in the context of population genetics" is: "Quasispecies theory describes the evolution of an infinite population of asexual replicators at high mutation rate [1,2]"

As the referee suggests, we rephrased the expression and replaced the references in the first paragraph of the “Methods / Evolutionary model with natural selection and mutation” section.

Overall I recommend this paper highly for publication with the minor changes addressing some of the recent work in incorporating mutations in Fisher's Thm in the context of quasispecies-type models used in this paper.

Thank you for recommending the paper for publication. We hope that we have addressed the points raised by the referee.

REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

The author has addressed my concerns and improved the manuscript. I support publication.

Reviewer #3 (Remarks to the Author):

The paper is excellent. All my concerns have been addressed. The authors should be congratulated.