Rapid evolution promotes fluctuation-dependent species coexistence

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ABSTRACT

Recent studies have demonstrated that rapid contemporary evolution can play a significant role in regulating population dynamics on ecological timescales. Here we identify a previously unrecognized mechanism by which rapid evolution promotes species coexistence via temporal fluctuations and a trade-off between competitive ability and the speed of adaptive evolution. This is a special case of relative nonlinearity in coexistence theory, and given the propensity for both oscillatory dynamics and divergent rates of adaptation in the real world, we propose that this mechanism may operate widely in nature.

A wealth of empirical evidence has accumulated over the last few decades indicating that rapid contemporary evolution on ecological timescales[1] can be essential for understanding population dynamics[2,3]. More recently, evidence has begun to emerge that rapid evolution can also be a significant driver of community dynamics amongst competing species, and in particular play an important role in regulating species coexistence[4-12]. Rapid evolution can promote species coexistence when there is a trade-off between traits optimal for intraspecific and interspecific competition[4-6,8,12] or fine-tuning of prey defenses and predator foraging efforts[10,13]. Here we provide a previously unrecognized pathway for rapid evolution to promote coexistence via temporal fluctuations: differences in the rate of adaptation to fluctuating environments. Specifically, using model simulations, we show that rapidly evolving and non-evolving consumers can stably coexist even when they compete for a single resource.

How species coexist in nature has been a central topic in community ecology over the last century[14,15]. Independent of emerging interest into rapid evolution, a growing body of coexistence research has suggested that temporal fluctuations can promote diversity via two broad classes of mechanisms, the temporal storage effect and relative nonlinearity[16-20]. Although greater attention

has been given to the temporal storage effect[21-25], recent studies have shown that relative nonlinearity can be more important than previously thought for promoting coexistence[23-25]. In this paper, we also focus on relative nonlinearity, but we introduce rapid evolution as a previously neglected driver of relative nonlinearity.

Relative nonlinearity promotes coexistence when one species benefits from fluctuations in the intensity of competition (an opportunist or risk-seeking strategist) while the other species dominates in the absence of fluctuations (a gleaner or risk-avoiding strategist). In addition to their responses to fluctuations, for the two competing species to coexist, they need different impacts on fluctuations. If the opportunist species reduces the amplitude of fluctuations (by "consuming" the variance in the intensity of competition[26]) while the gleaner species increases it, each species produces a favorable environment for the competitor, resulting in negative frequency-dependence[27,28] (Fig. 1a-b).

As the name suggests, two species coexist via relative nonlinearity when consumer functional responses to a limiting resource differ in their degree of nonlinearity (Fig. 1c-d)[27-31]. The

responses to and impacts on fluctuations are clearly seen in the intermittent cycles (Fig. 1d), where the linear, competitively inferior species increases in abundance when the system oscillates but simultaneously dampens the consumer-resource cycles induced by the competitively superior species. In contrast, the nonlinear, competitively superior species increases when the system is stable but causes fluctuations (Fig. 1d). Because this criterion is perceived as being highly restrictive, relative nonlinearity has typically been assumed to play a minor role[21-25], but we propose that it may be more important than previously realized due to rapid evolution.

The basis for the mechanism presented here is that rapid evolution can enable populations to adapt to fluctuating environments (response) and to stabilize temporal fluctuations (impact)[32]. Thus, even when two species have the same curvature in their functional responses, they may have different responses and impacts of temporal fluctuations, facilitating coexistence. We consider a model of two consumers sharing a single resource with logistic resource growth and saturating consumer functional responses[27,31,33]. We assume a trade-off between the attack rate and mortality rate of consumers, and the evolving consumer invests more in resource uptake when resources are abundant, whereas it invests more in reduced mortality when resources are

scarce. We further assume that a competitively superior species (with the lower resource requirement) does not evolve, whereas an evolving, competitively inferior species grows faster than the competitively superior species when the resource is abundant (Fig. 2a) or scarce (Fig. 2b). Our parameter settings do not satisfy necessary conditions for coexistence identified in previous studies (Appendix S1, Fig. S1)[27,31] for any fixed trait values. Thus, when the speed of evolution in the competitively inferior species is slow, competitive exclusion ensues (Fig. S2). However, when evolution is faster, coexistence is possible (Fig. 2). This occurs because the rapidly evolving species benefits from resource fluctuations, but at the same time rapid evolution dampens the consumer-resource cycles (Appendix S2, Fig. S3) induced by the non-evolving superior competitor as shown in the intermittent cycles (Fig. 2f). Therefore, rapid evolution is working as a compensation mechanism for the competitively inferior species.

The mechanism for coexistence can be understood by looking at the very-rapid-evolution limit. When evolution is much faster than ecological processes, the evolving species always has the optimal trait values that maximize per-capita growth rate for a given resource concentration. The effect of very rapid evolution is to change the effective functional responses of the evolving

species from concave down (gray curves in Fig. 2a-b) to concave up (especially when the limiting resource is scarce: orange curves in Fig. 2a-b) and it is this change that allows coexistence. Although the realized per-capita growth rates when evolution is not much faster than ecology are different from those based on the optimal trait values due to the time lag in responses to changing environments (Fig. 2c-d), coexistence is still possible because of relative nonlinearity.

Mechanisms of rapid adaptative trait changes include rapid evolution and phenotypic plasticity. We showed that both types of rapid adaptation can promote consumer coexistence in exploitative competition (adaptive foraging and dormancy induction/reproduction suppression: Fig. 2, Appendix S3-4, Fig. S4-5)[34] as well as prey coexistence in apparent competition (defense evolution and inducible defense: Appendix S5, Fig. S6)[35]. Recently, Tan et al. showed that a competitively inferior consumer species with phenotypic plasticity can coexist with a superior species in synchronous cycles[34]. Although the authors discussed their findings in the context of game theory, our results indicate that they can also be explained as an outcome of relative nonlinearity. Furthermore, our work provides an explanation for previous simulation results

demonstrating coexistence of three prey types (asexually reproducing clones) with a shared predator and a shared resource[35]. According to classical R^* and P^* theory, only two species (or asexual clones) can coexist with a single predator and a single resource[36], but a third prey species with inducible defense can coexist with the two non-plastic (defended and undefended) prey by relative nonlinearity.

It will be valuable to conduct empirical studies that examine the effects of rapid evolution on species coexistence via relative nonlinearity. Previous studies on the consequences of rapid evolution have typically used a single clone for competition experiments *after* long-term experimental evolution[9]. However, it is rapid evolution itself during competition experiments that can promote coexistence via the mechanism outlined here, and a single clone cannot produce these kind of dynamics. Although it is difficult to control the presence/absence of rapid evolution, it may be possible by changing the amount of genetic variation in populations to see dynamical interactions[2,37]. While our model assumptions are quite general, one should note that rapid evolution does not always stabilize temporal fluctuations[32,37], in which case rapid evolution may result in priority effects via positive frequency-dependence[38].

With increasing evidence for rapid contemporary evolution on ecological timescales[1], there has been an interest in developing a broader theory of species coexistence that incorporates rapid evolution[8-10,12]. By allowing for rapid evolution in mechanistic resource competition models, we have identified a new mechanism by which relative nonlinearity of competition promotes coexistence. This mechanism may be important in competition between sexual and asexual species or species with different mutation rates. Alongside recent empirical work demonstrating relative nonlinearity across diverse systems[23-25], we hope that our findings will motivate a reappraisal of the perceived importance of relative nonlinearity in nature.

METHODS

Consider the dynamics of two consumers, N_1 and N_2, competing for a single resource, R, with quantitative traits, x_1 and x_2:

$$
\begin{aligned}
\frac{dR}{dt} &= R\left[r\left(1-\frac{R}{K}\right)-\sum_{j=1}^{2}\frac{a_j\left(x_j\right)N_j}{1+h_jR}\right],\\
\frac{dN_i}{dt} &= N_i\left[\frac{c_ia_i\left(x_i\right)R}{1+h_iR}-d_i\left(x_i\right)\right],\quad \left(i=1,2\right),\\
\frac{dx_i}{dt} &= V_i\left(x_j\right)\frac{\partial}{\partial x_i}\left(\frac{1}{N_i}\frac{dN_i}{dt}\right),\quad \left(i=1,2\right),
\end{aligned}
\tag{1}
$$

where r is the intrinsic growth rate, K is the carrying capacity, a_i is the attacking rate, h_i is the handling time, c_i is the conversion efficiency, d_i is the consumer mortality, and V_i is additive genetic variance of the trait x_i (i = 1, 2). We assume that increasing the trait value results in a larger attacking rate and mortality due to a trade-off ($a_i(x_i) = \alpha_i x_i$, $d_i(x_i) = \delta_{0i} + \delta_{1i}x_i + \delta_{2i}x_i^2$), the trait changes along the fitness gradient[32,39], and the function $V_i(x_i)$ bounds the trait value, $V_i(x_i) = v_i(x_{i\max} - x_i)(x_i - x_{i\min})$, where the minimum and maximum values of x_i are $x_{i\min}$ and $x_{i\max}$, respectively.

As the resource exhibits logistic growth and consumers exploit the resource with a Holling type II functional response, the system is the classical Rosenzweig-MacArthur model when there is a single consumer species[33]. When the system does not show fluctuations, the consumer with the smaller resource requirement (i.e., smaller R^*) reduces the resource level to the point (R_i^* =

$d_i/(a_i c_i - h_i d_i)$, $i = 1, 2$) where its competitor with a larger R^* cannot persist and is excluded. On the other hand, in the presence of endogenous limit cycles (e.g., with larger K values) the two consumers may coexist via relative nonlinearity[27,31]. The mechanism with rapid evolution further broadens the parameter space that allows coexistence mediated by temporal fluctuations.

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Conflict of Interest

The author declares no competing financial interests.

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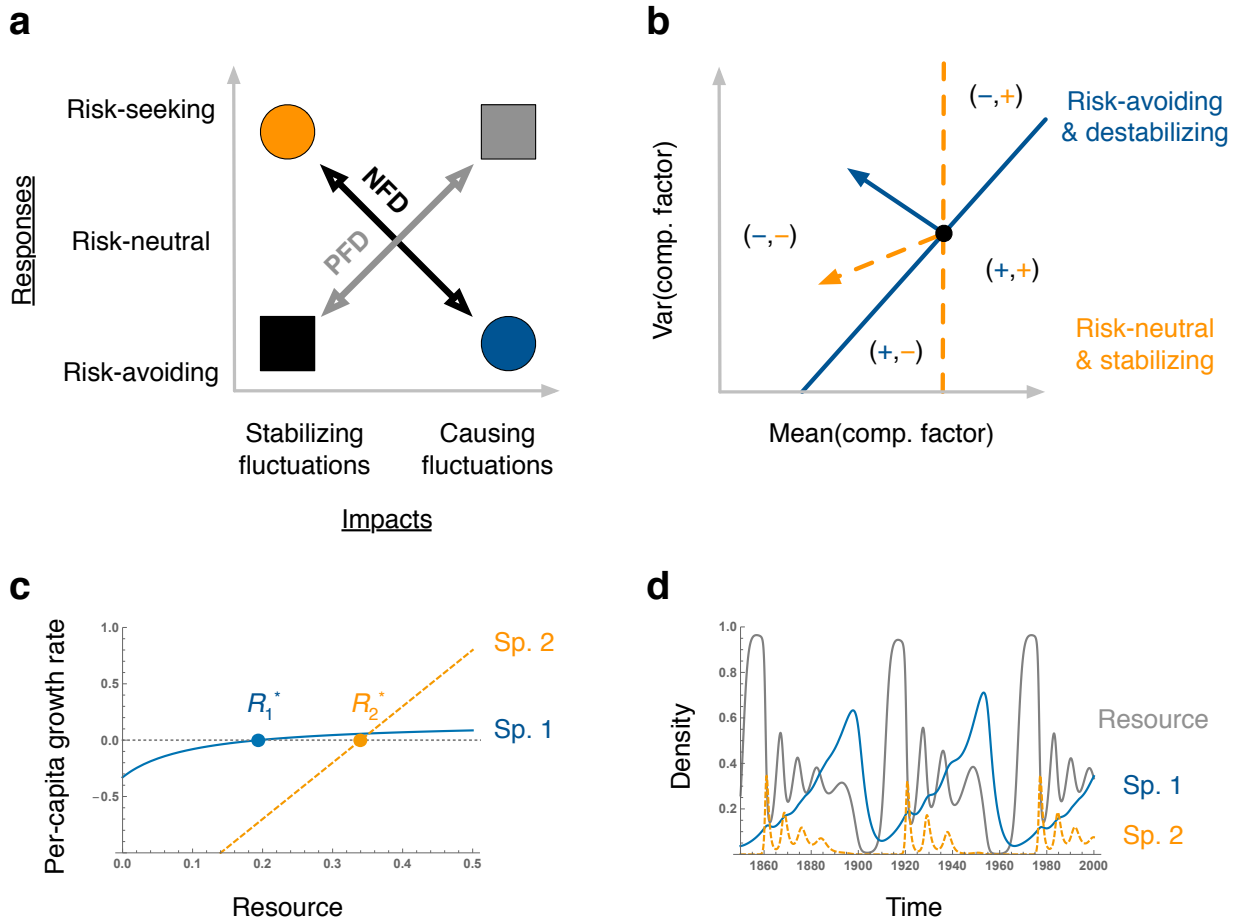

Figure 1 | Species coexistence by relative nonlinearity. a, Relative nonlinearity promotes coexistence with negative frequency-dependence (NFD) when one species stabilizes population cycles but benefits from fluctuating environments (risk-seeking), while the other species destabilizes dynamics but benefits from stable environments (risk-avoiding). Hence, we need to consider two aspects of the ecological niche: responses and impacts (the Grinnellian and Eltonian niches, respectively)[40]. Priority effects due to positive frequency-dependence (PFD) can arise when the risk-avoiding species stabilizes fluctuations while the risk-seeking species drive

fluctuations[38]. **b**, The concept of relative nonlinearity can also be expressed in terms of zero net growth isoclines (ZNGI)[40]. The risk-seeking (risk-avoiding) species has higher growth rates when the variance in the competitive factor (e.g., resource) is high (low), but when abundant reduces (increases) the variance as shown by the impact vector. **c-d**, Coexistence of species with linear and saturating functional responses[30]. Species 1 with a saturating functional response (blue line) has a smaller R^*, and causes limit cycles with the resource (grey line), which is disadvantageous due to nonlinear averaging. Species 2 with a linear functional response (the dashed orange line) has a larger R^* and stabilizes dynamics. Parameter values are $a_1 = a_2 = 5$, $h_1 = 10$, $h_2 = 0$, $d_1 = 0.33$, and $d_2 = 1.7$.

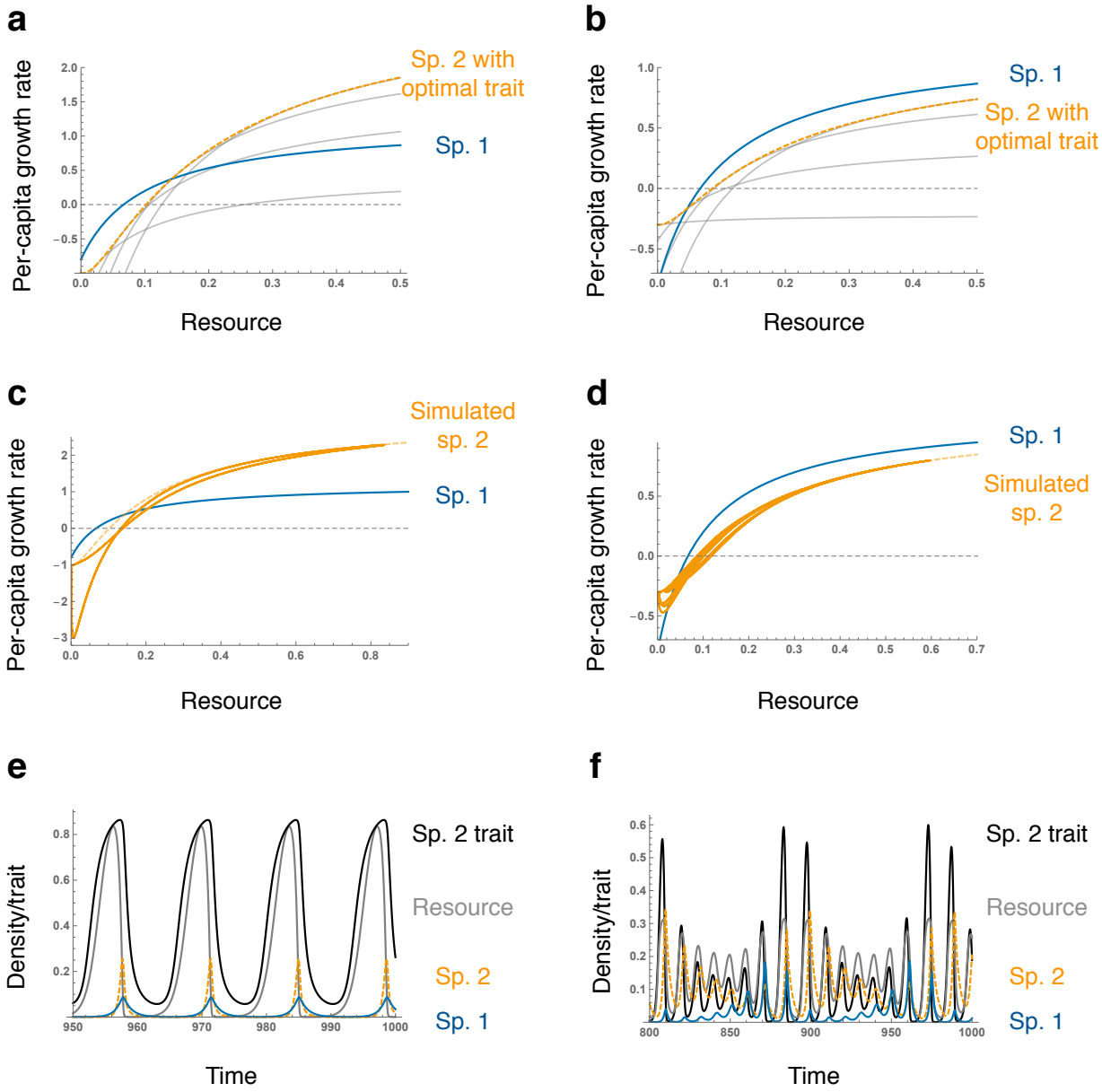

Figure 2 | Rapid evolution of a competitively inferior species promotes coexistence by relative nonlinearity. a-b, The per-capita growth rate of species 2 having the optimal trait (orange dashed line) is larger than that of species 1 (solid blue line) when the resource is abundant (**a**) or scarce (**b**). When the trait value is fixed (gray lines), species 2 is always

competitively inferior (Fig. S2). **c-d**, The realized per-capita growth rate of species 2 (orange solid line) is different from that with the optimal trait (orange dashed line) because of a time lag in adaptive evolution. **e-f**, Rapid evolution of species 2 results in coexistence with synchronous (**e**) or intermittent (**f**) cycles. Under intermittent cycles, the density of species 1 (blue solid line) increases when cycle amplitudes are small, whereas the density of species 2 (orange dashed line) increases under largely amplitude fluctuating. The trait value of species 2 is depicted in black, and resource abundance in gray. Parameter values are $a_1 = 20$, $\alpha_2 = 84$, $h_1 = h_2 = 10$, $d_1 = 0.8$, $\delta_{02} = 1$, $\delta_{12} = 0.24$, $\delta_{22} = 4$, $\beta_{\min} = 0$, $\beta_{\max} = 1$, $v_1 = 0$, and $v_2 = 0.5$ in a, c, and e, and $\delta_{02} = 0.3$ and $\delta_{22} = 11$ in b, d, and f.