

Evolution in predator-prey systems

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Abstract We study the adaptive dynamics of predator prey systems modeled by a dynamical system in which the characteristics are allowed to evolve by small mutations. When only the prey are allowed to evolve, and the size of the mutational change tends to 0, the system does not exhibit prey coexistence and the parameters of the resident prey type converges to the solution of an ODE. When only the predators are allowed to evolve, coexistence of predators occurs. In this case, depending on the parameters being varied we see (i) the number of coexisting predators remains tight and the differences of the parameters from a reference species converge in distribution to a limit, or (ii) the number of coexisting predators tends to infinity, and we conjecture that the differences converge to a deterministic limit.

Keywords predator-prey, adaptive dynamics, branching random walk

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1 Introduction

We will consider predator-prey systems of the form

$$\begin{aligned}\frac{du_i}{dt} &= u_i \left(\beta_i \left(1 - \sum_k u_k \right) - \eta_i - \sum_j \alpha_{i,j} v_j \right) \\ \frac{dv_j}{dt} &= v_j \left(\sum_i \alpha_{i,j} u_i - \delta_j - \gamma_j v_j \right)\end{aligned}\tag{1}$$

where u_i , $1 \leq i \leq m$ are the densities of the prey, and v_j , $1 \leq j \leq n$ are the densities of the predators. These equations have the form of the mean-field equations of a particle

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systems in which the prey species occupy a grid with at most one particle per site and the predators roam the same grid with no limit on the number per site. If the number of prey of type i at x at time t is $\xi_i(x, t)$, with $\sum_i \xi_i(x, t) \leq 1$, and the number of predators of type j is $\zeta_j(x, t)$ then

- (i) prey of type i give birth onto vacant neighbors at rate β_i/k where k is the number of neighbors, die at rate η_i , and are eaten by predators at rate $\sum_j \alpha_j \zeta_j(x, t)$
- (ii) predators of type j are born at rate $\sum_i \xi_i(t, x) \alpha_{ij}$ and die at rate $\delta_j + \gamma_j(\zeta_j(x, t) - 1)$.

If we have fast stirring on the prey grid and the predators perform fast independent random walks then in the limit the prey states are a product measure and the predators are independent Poisson and we get the mean-field equation (1).

Interacting particle systems in which predators and prey share the same grid with at most one individual per site have been studied by Durrett (1992, 2002), but here we will be concerned with properties of the ODE. Our main interest is studying the effect of small mutations in the resident species on the equilibrium behavior of (1). While the co-evolutionary case in which both predator and prey are allowed to vary is certainly of interest (see Dieckmann, Morrow, and Law (1995) and Dercole, Irisson, and Rinaldi (2002)) and can lead to exotic behavior, we will here only consider the two cases of fixed predator/evolving prey and evolving predator/ fixed prey. Such examples are also of interest and have been studied in laboratory experiments (see, for example, Jones and Ellner (2007)).

Following the usual approach in adaptive dynamics, we shall assume that such mutations take place on a much slower time scale than the population dynamics reach equilibrium. To be precise, suppose that we are considering predator evolution and at time n we have k species of predator and one prey species coexisting in equilibrium. Then we pick one predator at random, introduce a small amount of a new species with a mutation in its traits, and let the densities evolve according to (1) until a possibly new equilibrium is reached before introducing the next mutation. By traits, we mean the parameters in (1) (birth, death, and consumption rates) that characterize each species' ability to survive and propagate. This approach has been considered before (see Champagnat and Lambert (2007) and the references therein), but most often in situations where evolution leads to a system in which the resident and mutant type cannot coexist in equilibrium.

Here, we will encounter examples where evolution leads to equilibrial coexistence of a growing number of species. This is somewhat different from the evolutionary branching found by Geritz et al. (1997). In that paper, and indeed in much of the evolutionary dynamics literature, the basic quantity is $g(x, y)$ the growth rate of species y when it is rare and type x is in equilibrium. This function has $g(x, x) = 0$ and the behavior of its partial derivatives indicate when an x is an evolutionarily stable strategy or when bifurcations can occur in the dynamics, see Geritz et al. (1997) for details. In this paper our prey evolution falls within this framework, but in our predator model we have $g(x, x) > 0$, i.e., due to our competition rules a copy of the resident can invade the resident. The biological relevance of this may be suspect but the mathematical consequences are interesting.

1.1 Prey Evolution

We begin with the case in which predator characteristics are held constant and the prey are allowed to evolve. To reduce the number of parameters, we will assume that

all prey have death rate 1 and consider mutations in birth rate β and the consumption rate α . Suppose we have a single species of prey and single species of predator with densities, u_1 and v governed by

$$\begin{aligned}\frac{du_1}{dt} &= u_1 (\beta_1(1 - u_1) - 1 - \alpha_1 v) \\ \frac{dv}{dt} &= v_1 (\alpha_1 u_1 - \delta - \gamma v)\end{aligned}$$

Our process evolves in discrete time with $(\alpha_\varepsilon(k), \beta_\varepsilon(k))$ being the characteristics, (α_1, β_1) , of the resident prey at time k . To move to time $k + 1$, a small density of some mutant predator with birth rate β_2 and consumption rate α_2 is introduced with (α_2, β_2) chosen uniformly from $B_\varepsilon(\alpha_\varepsilon(k), \beta_\varepsilon(k))$, the ball of radius ε around $(\alpha_\varepsilon(k), \beta_\varepsilon(k))$. The densities (u_1, u_2, v) then evolve according to (1). If the densities of u_1, u_2, v remain bounded away from 0 for all time, we say that coexistence occurs. Otherwise, one of the prey species will die out and we denote the “surviving” prey species by $(\alpha_\varepsilon(k + 1), \beta_\varepsilon(k + 1))$. Our first result says that coexistence of multiple prey species is unlikely in this system and mutations lead to “monomorphic dynamics” in which advantageous mutants replace residents while deleterious mutants die off.

Theorem 1 *Suppose at time n , we introduce mutations uniformly over the ball of radius ε around $y_\varepsilon(n)$, $B_\varepsilon(y_\varepsilon(n))$, where $y_\varepsilon(n) = (\alpha_\varepsilon(n), \beta_\varepsilon(n))$, $n < n_\varepsilon$, is the surviving species up to the first time n_ε that coexistence occurs. As $\varepsilon \rightarrow 0$, $\varepsilon n_\varepsilon \rightarrow \infty$ and $y_\varepsilon([t/\varepsilon]) \rightarrow y(t)$ where y is the unique solution to the ODE*

$$\frac{dy(t)}{dt} = \frac{2}{3\pi} \mathcal{N}(y(t)) \quad (2)$$

and $\mathcal{N}(\cdot)$ is explicitly calculable, see (14).

We will prove Theorem 1 in Section 2. The constant on the right hand side is EY^+ when (X, Y) is chosen at random from the ball of radius 1 and appears due to our choice of mutation distribution. (2) is essentially a special case of the “Canonical Equation of Adaptive Dynamics,” see (6.2) in Dieckmann and Law (1996), or (1) in Champagnat and Lambert (2007). Our algorithm corresponds to total mutation rate $N\mu = 1$. We do not have an explicitly defined fitness, but the infinitesimal drift in the traits is perpendicular to the region of values that cannot invade the resident, which is the direction of the fitness gradient.

Figure 1 gives a simulation of the process with $\varepsilon = 0.01$. The smooth curve is the boundary of the viable region $\beta_1 > \alpha_1/(\alpha_1 - 1)$ which is the set of (α_1, β_1) values of predators that can coexist with the prey. The trajectory wanders outside of the viable region because we do not run the dynamics in (1) but simply accept mutations that land in the correct half of the ball $B_\varepsilon(\alpha_\varepsilon(k), \beta_\varepsilon(k))$. The limiting result in Theorem 1 is not biologically sensible because the prey birth rate increases without bound. This could be remedied by restricting the permitted values of (α, β) to a curve, but we leave the details to the reader.

1.2 Predator Evolution

Suppose now that we have a single prey with death rate $\eta = 1$, growth rate $r = \beta - 1$, and density u and allow our predators to evolve. The first step is to develop a criteria

for determining coexistence of multiple predators. The next result, which is proved in Section 3, tells us that this can be done by checking a simple algebraic condition.

Theorem 2 *Predators with traits $x_1, \dots, x_N$ ordered by increasing ratios $\ell_i = \delta_i/\alpha_i$ can coexist with the prey (and if they do, they will converge to equilibrium) if and only*

$$\sum_{j=1}^N \alpha_j^2 (\ell_N - \ell_j) < r - \beta \ell_N \quad (3)$$

If (3) is not satisfied, we repeatedly drop the predator with largest ℓ until it is satisfied. This will give a unique, globally attracting equilibrium for initial densities in $\Gamma_{1,N}^+ := \{(u, v_1, \dots, v_N) \in \mathbb{R}^{N+1} : 0 < u \leq 1, v_i > 0\}$.

Suppose now that mutations of (α_k, δ_k) lead to a new species with $\alpha_{new} = \alpha_k + \varepsilon U_1$ and $\delta_{new} = \delta_k e^{\varepsilon U_2}$ where the U_i are uniform on $[-1, 1]$. Simulations suggest that we see a growing cloud of coexisting predators with some limiting shape and all predators have consumption rates α going off to infinity and $\log(\ell)$ going to $-\infty$ (see Figures 2 and 3). We have not been able to do a complete analysis of the full two parameter predator evolution model, so we specialize to the two cases where only α or δ varies and the other remains fixed.

1.3 Predator Evolution, I: Fixed δ

Our first result assumes $\delta = 1$ remains fixed and α changes. We use the following notation:

- N_n = number of coexisting predators at time n .
- $\alpha_j(n) = j^{th}$ largest α amongst all coexisting predators at time n with $\alpha_{\min}(n) := \alpha_{N_n}(n)$ and $\alpha_j(n) = \alpha_{\min}(n)$ if $j > N_n$.
- $d_j(n) = \alpha_j(n) - \alpha_{\min}(n)$ = differences between predator fitness levels.
- $\Delta_n = (d_1(n), d_2(n), \dots)$

In the case of fixed δ , writing N for N_n , the condition (3) simplifies to

$$\sum_{j=1}^N \frac{\alpha_j}{\alpha_N} (\alpha_j - \alpha_N) < r - \frac{\beta}{\alpha_N} \quad (4)$$

Since $\alpha_j/\alpha_N > 1$, this implies that all the differences $\alpha_j - \alpha_N$ must be $< r$ so we define $\mathcal{S} := [0, r]^{\mathbb{N}}$ and let $\|\cdot\|_{TV}$ denote the total variation norm on $\mathcal{M}_1(\mathcal{S})$ = space of probability measure on $\mathcal{S}$. We denote by P^α the law given an initial predator with trait α .

Theorem 3 *Suppose at time n , we choose predator $j \leq N_n$ at random and introduce a mutation uniformly over $(\alpha_j(n) - \varepsilon, \alpha_j(n) + \varepsilon)$ for some $\varepsilon > 0$. Let $\alpha > \beta/r$ be the trait of the initial predator. Then the sequence N_n is tight and $\alpha_{\min}(n) \rightarrow \infty$ a.s. as $n \rightarrow \infty$. In addition, there exists a measure π_ε on $\mathcal{S}$ and constant $a_\varepsilon > 0$ so that*

$$\|P^\alpha(\Delta_n \in \cdot) - \pi_\varepsilon(\cdot)\|_{TV} \rightarrow 0$$

and $\alpha_{\min}(n)/n \rightarrow a_\varepsilon > 0$ as $n \rightarrow \infty$.

The proof is given in Section 4. The reason for the difference from Theorem 1 is that a copy of the resident type can always invade (see Lemma 3) while in the case of prey evolution, a copy of the resident type cannot invade. To explain this, think of the resident predator as green and the invading predator as blue. The blue invaders only suffer density dependent killing from the other blue predators, and therefore can increase in number when rare. It is not clear that this choice is biologically reasonable but, as we will see, it does lead to some interesting dynamics.

The key to the proof of Theorem 3 is the observation that as $\alpha_N \rightarrow \infty$, the condition (4) becomes

$$\sum_{j=1}^N (\alpha_j - \alpha_N) < r$$

and we can show that the differences Δ_n are asymptotically a positive recurrent Harris chain with stationary distribution π_ε . A coupling argument shows that the nonhomogeneous chain also converges to π_ε . The linear growth of $\alpha_{\min}$ then follows from a standard result on functionals of positive recurrent Markov chains.

Figure 4 illustrates the tightness of N_n and linear growth of $\alpha_{\min}$. Figure 5 suggests that as the size of the perturbation $\varepsilon \rightarrow 0$, the spacings between species is $O(\varepsilon)$, and the number of coexisting species is $O(1/\varepsilon)$. We believe that if one converts the rescaled spacings Δ_n/ε into a measure by assigning each one mass ε then as $\varepsilon \rightarrow 0$, the distribution of this measure under π_ε converges to a deterministic limit in which the density of particles is roughly, but not exactly, exponential, see Figure 6.

1.4 Predator Evolution, II: Fixed α Case

If we instead fix α , but allow δ to vary, our condition for coexistence of $\delta_N > \delta_{N-1} > \dots > \delta_1$ becomes

$$\delta_N \left(\beta + \sum_{j=1}^N \left(1 - \frac{\delta_j}{\delta_N} \right) \right) < r. \quad (5)$$

In order to ensure positive death rates, we suppose that when δ_j is chosen to mutate, the new species has $\delta'_j = \delta_j e^U$ where U is uniform on $[-1, 1]$. We could multiply U by ε here, but since we study $X_j = -\log(\delta_j)$, there is no loss of generality in taking $\varepsilon = 1$.

It is more convenient to study this model in continuous time, so we suppose that each existing particle gives rise to mutants at rate 1. At time t , we have $N(t)$ particles at $X_1(t) > X_2(t) > \dots > X_{N(t)}(t)$ and particle j gives birth at rate one to a new particle uniformly distributed over $(X_j(t) - 1, X_j(t) + 1)$. Every time a new birth occurs, we reorder the particles in increasing order and check

$$e^{-X_{N(t)}} \left(\beta + \sum_{j=1}^N 1 - \exp(-[X_j(t) - X_{N(t)}]) \right) < r \quad (6)$$

with $N = N(t) + 1$. If the sum is satisfied, we keep all particles. If not, we repeatedly kill off the left-most particle until the condition is satisfied.

To get started in the analysis of this model, our first step in Section 5 is to prove a simple result which already shows that the behavior is much different from the case of fixed δ .

Lemma 1 As $t \rightarrow \infty$, $N_t \rightarrow \infty$ a.s.

Let S_t be a random walk starting at 0 that takes jumps at rate 1 uniform on $[-1, 1]$. The theory of large deviations tells us that

$$\Lambda(x) = \lim_{t \rightarrow \infty} \frac{1}{t} \log P(S_t > xt)$$

exists and can be calculated in terms of $E \exp(\theta S_t)$.

Theorem 4 Let $X_{\min}(t) = X_{N(t)}(t)$ and $X_{\max}(t) = X_1(t)$ be the positions of the leftmost and rightmost particles at time t . Then $X_{\max}(t)/t \rightarrow a$ and $X_{\min}(t)/t \rightarrow b$ a.s. as $t \rightarrow \infty$ where $a \approx 0.9053$ and $b \approx 0.5667$ satisfy the equations

$$\Lambda(a) = -1, \quad \Lambda(b) = -1 + b. \quad (7)$$

Furthermore, we have $\liminf (1/t) \log N_t \geq b$ a.s.

We will prove Theorem 4 in Section 5. To explain why it is true, let Z_t be the branching random walk in which particles give birth at rate 1 and their offspring are displaced by an amount uniform on $[-1, 1]$. A result of Biggins (1977) implies that the position of right-most particle in the branching random walk $r_t/t \rightarrow a$ and

$$\frac{1}{t} \log Z_t([xt, \infty)) \rightarrow 1 + \Lambda(x)$$

for $0 \leq x < a$ so $(1/t) \log Z_t([bt, \infty)) \rightarrow b$. Since we can construct Z_t in such a way that all the particles in $X(t)$ are in Z_t , we must have $\limsup X_{\max}(t)/t \leq a$ a.s. The definition of b and an argument by contradiction using (6) gives the upper bound $\limsup_{t \rightarrow \infty} X_{\min}(t)/t \leq b$ for the speed of the left-most particle.

To bound $\liminf_{t \rightarrow \infty} X_{\max}(t)/t$, we consider the following “toy” model: at any time t , we have M particles with positions $Y_1^M(t) > \dots > Y_M^M(t)$, all giving birth at rate one. Whenever a new particle is born, we reorder and delete the leftmost particle. Using techniques from Section 4, we could show that $Y_1^M(t)/t \rightarrow a_M$, but instead we complete the proof of the first result by showing

$$\lim_{M \rightarrow \infty} \liminf_{t \rightarrow \infty} Y_1^M(t)/t = a. \quad (8)$$

Nina Gantert has pointed out to us that Berard and Gouere (2008) have recently proved

$$a - a_M \sim C(\log(M))^2$$

for a related discrete time model in which all M particle split into two and then you take the right-most M . This confirms a slow rate of convergence, which was predicted much earlier by Brunet and Derrida (1997), and which we observed in our numerical attempts to verify the limit in (8), see Figure 7.

To bound $\liminf_{t \rightarrow \infty} X_{\min}(t)/t$, we study the branching random walk with killing at $-K + \gamma t$. Our result given in Lemma 12 is a cousin of a result of Kesten (1978) for branching Brownian motion on $[0, \infty)$ where during its lifetime, each particle moves according to Brownian Motion with drift $\mu < 0$ and variance σ^2 , all particles die at rate c and give birth to a mean m number of offspring upon death with particles killed when they hit 0. Kesten’s result states that the system has positive probability of survival when $\mu < \mu_0 = (2\sigma^2 c(m-1))^{1/2}$ (Theorem 1.1, (1.6)), and in this supercritical case,

if we start with one particle at x , then for every interval I , $Z_t(I)/E_x Z_t(I) \rightarrow W$ a.s for some finite random variables W (Theorem 1.1 (1.5)). However, Kesten's efforts are concentrated on the exotic behavior in the critical case $\mu = \mu_0$, and he says "so far we have only an ugly and complicated proof of the growth results in the supercritical case, and we shall therefore not prove Theorem 1.1." In section 5, we show that using ideas of Biggins (1977) it is easy to prove results for $(1/t) \log Z_t([ct, \infty))$.

The result $\limsup_{t \rightarrow \infty} X_{\min}(t)/t \leq b$ implies that if T is large and we start the branching random walk with one particle at $X_{\max}(T)$ at time T then all of the particles in the branching random walk with killing at $(b+\varepsilon)t$ are present in the $X_i(t)$. If $X_{\min}(t)$ is too far to the left then we would contradict (6). The last part of the proof suggests that most particles are near $X_{\min}(t)$. Simulations (see Figure 8) further suggest that:

Conjecture. *If we put mass $\exp(-X_{\min}(t))$ at $X_i(t) - X_{\min}(t)$ then this measure converges to a deterministic limit, which again is roughly but not exactly exponential.*

However, proving this seems to be a difficult problem.

The final conclusion $\liminf_{t \rightarrow \infty} (\log N_t)/t \geq b$ follows from the result for $X_{\min}(t)$ and the proof of Lemma 1. Since the result comes from replacing (6) by $e^{-X_N(t)}(\beta + N) < r$, it seems unlikely that b is the right constant, but finding the right constant would require proving the conjecture.

The proof of $\liminf_{t \rightarrow \infty} X_{\min}(t)/t \leq a$ leads to the following

Corollary. *If we run the predator evolution model with fixed δ in continuous time and let $a_\varepsilon^* = \lim_{t \rightarrow \infty} \alpha_{\min}(t)/t$, then $\lim_{\varepsilon \rightarrow 0} a_\varepsilon^* = a$.*

2 Prey Evolution

In this section we will prove Theorem 1, which assumes $\eta_i = 1$ in (1). The first step is to consider the case of one predator and one prey. The densities u_1, v of the prey and predator, respectively are governed by

$$\begin{aligned} \frac{du_1}{dt} &= u_1 (\beta_1(1 - u_1) - 1 - \alpha_1 v) \\ \frac{dv}{dt} &= v (\alpha_1 u_1 - \delta - \gamma v). \end{aligned}$$

To determine when the predator and prey can coexist, we note that if $\beta_1 > 1$ then in the absence of predators the prey reach an equilibrium density

$$u_1^* = (\beta_1 - 1)/\beta_1. \quad (9)$$

If the prey are in equilibrium then the predators can increase when v is small if

$$\alpha_1 u_1^* - \delta > 0. \quad (10)$$

Using the formula for u_1^* , we see that this holds if and only if $\alpha_1 > \delta$ and

$$\beta_1 > \frac{\alpha_1}{\alpha_1 - \delta} > 1. \quad (11)$$

We call this set of (α_1, β_1) the *viable region* for prey. See Figure 9.

A little algebra shows that when (11) occurs, there is a predator-prey equilibrium with

$$u_1^{**} = \frac{(\beta_1 - 1)\gamma + \alpha_1}{\beta_1\gamma + \alpha_1^2} \quad v^{**} = \frac{(\beta_1 - 1)\alpha_1 - \beta_1}{\beta_1\gamma + \alpha_1^2}. \quad (12)$$

To see when a second species of prey can coexist, we note that a prey species with parameters (α_2, β_2) can invade the first prey and the predator in equilibrium when

$$\begin{aligned} 0 &< \beta_2(1 - u_1^{**}) - 1 - \alpha_2 v^{**} \\ &= \beta_2 \frac{\gamma + \alpha_1^2 - \alpha_1}{\beta_1\gamma + \alpha_1^2} - 1 - \alpha_2 \frac{(\beta_1 - 1)\alpha_1 - \beta_1}{\beta_1\gamma + \alpha_1^2}. \end{aligned} \quad (13)$$

By interchanging the subscripts 1 and 2 we get the condition for the first prey to invade the second prey and predator in equilibrium. If both prey species are viable and the two invadability conditions hold, then Durrett (2002) showed (see Section 7.1) there is coexistence in the ODE, i.e., the three densities stay bounded away from 0.

Following Durrett (2002), we use the notation $\succ$ for “invades” (species j can invade species $1, \dots, j-1$ in equilibrium if its density will increase whenever $1, \dots, j-1$ are in equilibrium and a small initial density of j ’s is introduced). To make it easy to use this notation, our predator will be referred to as species 3. Using the new notation and defining

$$F(y_1, y_2) = \beta_2(1 - u_1^{**}(y_1)) - 1 - \alpha_2 v^{**}(y_1),$$

where $y_i = (\alpha_i, \beta_i)$, $i = 1, 2$, we have $2 \succ 1, 3$ if and only if

$$y_2 \in \{y : F(y_1, y) > 0\} =: \mathcal{L}_{y_1}$$

and $1 \succ 2, 3$ if and only if

$$y_2 \in \{y : F(y, y_1) > 0\} =: \mathcal{U}_{y_1}.$$

This describes a splitting of $\mathbb{R}^2$ into regions describing the outcome of the competition between the mutant and resident types, namely, if we restrict ourselves to values of y_1, y_2 in the viable region with $\beta_1, \beta_2 > 1$, then coexistence will occur if and only if $y_2 \in \mathcal{L}_{y_1} \cap \mathcal{U}_{y_1}$. We call the boundary curves $L_{y_1} = \{y : F(y_1, y) = 0\}$ and $U_{y_1} = \{y : F(y, y_1) = 0\}$ the invadability curves. The situation is depicted in Figure 9.

Calculus shows that the curve U_{y_1} is tangent to the curve L_{y_1} at y_1 . Let $\mathcal{N}(y_1)$ denote the corresponding unit normal vector:

$$\mathcal{N}(y_1) = c(-(1 - u_1^{**}(y_1)), v^{**}(y_1)) \quad (14)$$

With this notation in hand, we can complete the:

Proof of Theorem 1. If we introduce mutations that are chosen uniformly over the ball of radius ε around the current type (α, β) then the tangency of the invadability curves implies that the probability of coexistence is of order ε^2 and hence if n_ε is the first time coexistence occurs, $\varepsilon n_\varepsilon \rightarrow \infty$ in probability. Ignoring coexistence, mutations to points below the line $U_{y_\varepsilon(n)}$ will not invade, while those to points above $U_{y_\varepsilon(n)}$ will displace the current species $y_\varepsilon(n)$.

We claim that the infinitesimal mean

$$E((\alpha(1), \beta(1)) - (\alpha(0), \beta(0))) = \varepsilon \frac{2}{3\pi} \mathcal{N}(\alpha(0), \beta(0)). \quad (15)$$

To verify this, note that if we choose a point at random from the upper half of the ball of radius 1 in the (α, β) plane, then the β component has density $(4/\pi)\sqrt{1-\beta^2}$ and hence mean

$$\frac{4}{\pi} \int_0^1 \beta \sqrt{1-\beta^2} dy = \frac{4}{3\pi}.$$

(15) then follows by noting that choices from the half of the ball above $U_{y_\varepsilon(n)}$ occur with probability $1/2$.

It is clear from scaling that the entries in $\text{cov}[(\alpha(1), \beta(1)) - (\alpha(0), \beta(0))]$ are of order ε^2 . From this and the previous result we see that the infinitesimal mean and covariance of $y([t/\varepsilon])$ converge to $b(y) = (2/3\pi)\mathcal{N}(y(0))$ and $a(y) = 0$ respectively. To conclude weak convergence using Theorem 4.1 in Chapter 7 of Ethier and Kurtz (1986) now, we only have to show that the martingale problem for (a, b) is well posed. To do this we note that (i) b is Lipschitz continuous and (ii) on the boundary of the viable region, $\beta = \alpha/(\alpha - \delta)$ so the slope of L_{y_1} at y_1 is

$$\frac{\beta_1(\alpha_1 - \delta) - \alpha_1}{\gamma + \alpha_1(\alpha_1 - \delta)} = 0$$

implying the drift points straight up, and it is impossible for the ODE to leave the viable region. $\square$

3 ODE facts

To begin the study of predator evolution, we need to examine the limiting behavior of one prey/ multiple predator systems in which dynamics evolve according to (1). The goal of this section is the derivation of Propositions 1, 2, and 3, which together imply Theorem 2.

Continuing with earlier notation, we let v_j , $j = 1, \dots, N$ be the densities of N different predator species competing for a single prey with density u . For simplicity, we assume that $\eta = 1$ and all $\gamma_j = 1$, so our equation becomes:

$$\begin{aligned} \frac{du}{dt} &= u \left(\beta(1-u) - 1 - \sum_j \alpha_j v_j \right) \\ \frac{dv_j}{dt} &= v_j (\alpha_j u - \delta_j - v_j) \end{aligned}$$

on $\Gamma^N = \{(u, v_1, \dots, v_N) : 0 \leq u \leq 1, v_j \geq 0, \forall 1 \leq j \leq N\}$.

We suppose that $\beta > 1$ so that the prey have equilibrium density $\sigma_0 = (\beta - 1)/\beta$ in the absence of any predators, and let $r = \beta - 1$ be the intrinsic growth rate of the prey. Each predator is characterized by a vector of traits $x_j = (\alpha_j, \delta_j)$. If $n \leq N$ then on the face

$$\Gamma^n = \{v \in \Gamma^N : v_{n+1} = \dots v_N = 0\}$$

we can solve the equations $\alpha_j u - \delta_j - v_j = 0$ for v_j , $j = 1, \dots, n$ to get

$$\sigma_j^n = \alpha_j \sigma_0^n - \delta_j \quad (16)$$

and substitute these expressions into the equation $r - \beta u - \sum_{j=1}^n \alpha_j v_j = 0$ to conclude

$$r - \beta \sigma_0^n = \sum_{j=1}^n \alpha_j^2 \sigma_0^n - \sum_{j=1}^n \alpha_j \delta_j$$

Letting $T_n = \sum_{i=1}^n \alpha_i \delta_i$ and $S_n = \sum_{i=1}^n \alpha_i^2$, we have

$$\sigma_0^n = \frac{r + T_n}{\beta + S_n} \quad (17)$$

From these expressions, we can see that $\sigma_0^n > 0$. If $\sigma_j^n > 0$ for $1 \leq j \leq n$, then predators $x_1, \dots, x_n$ can coexist with equilibrium density σ^n on $\mathbb{R}^{n+1}$. Durrett (2002) derives conditions for coexistence in terms of invadability conditions. The next result shows that in our system, only the top level conditions are needed

Lemma 2 *Predators $x_1, \dots, x_n$ can coexist if and only if*

$$x_j \succ x_1, \dots, x_{j-1}, x_{j+1}, \dots, x_n, \quad \forall j = 1, \dots, n$$

i.e., predator x_j can invade the prey and the other $n-1$ predators in their equilibrium.

Proof Using (17) and indicating the dependence on the predator parameters in the notation we have

$$\alpha_j \sigma_0^n(x_1, \dots, x_n) = \frac{\alpha_j r + \alpha_j^2 \delta_j + \alpha_j \sum_{i \neq j} \alpha_i \delta_i}{\beta + S_n}$$

Adding $\delta_j - \delta_j(\beta + S_n)/(\beta + S_n)$, the above

$$\begin{aligned} &= \delta_j + \frac{\alpha_j r - \beta \delta_j + \sum_{i \neq j} (\alpha_j \alpha_i \delta_i - \alpha_i^2 \delta_j)}{\beta + S_n} \\ &= \delta_j + \frac{(\beta + \sum_{i \neq j} \alpha_i^2)(\alpha_j \sigma_0^{n-1}(x_1, \dots, x_{j-1}, x_{j+1}, \dots, x_n) - \delta_j)}{\beta + S_n} \end{aligned}$$

since $(\beta + \sum_{i \neq j} \alpha_i^2) \sigma_0^{n-1} = r + \sum_{i \neq j} \alpha_i \delta_i$. From this it follows that σ_j^n will be positive if and only if

$$\alpha_j \sigma_0^{n-1}(x_1, \dots, x_{j-1}, x_{j+1}, \dots, x_n) > \delta_j$$

which is the invadability condition.

Let $\ell_j = \delta_j / \alpha_j$. Dividing by α_j in the calculation in the previous lemma, and taking $j = n$

Lemma 3 *If $x_n \succ x_1, \dots, x_{n-1}$, then $\sigma_0^n(x_1, \dots, x_n) > \ell_n$.*

This implies that if x_n can invade then there is no limit to the number of copies of this species that can invade. The next result shows that ℓ_j is a good measure of the competitive ability of the predator.

Lemma 4 *Suppose that species $x_1, \dots, x_n$ coexist and let x_{n+1} be some other species. If $\ell_{n+1} < \ell_j$ for some $j = 1, \dots, n$, then $x_{n+1} \succ x_1, \dots, x_n$.*

Proof Without loss of generality, assume $\ell_{n+1} < \ell_n$. Suppose that x_{n+1} cannot invade. Then since $x_1, \dots, x_n$ coexist, $x_n \succ x_1, \dots, x_{n-1}$, and therefore, by the definition of invadability and Lemma 3, we have

$$\ell_{n+1} > \sigma_0^n(x_1, \dots, x_n) > \ell_n$$

a contradiction.

The next result greatly simplifies the process of determining which predators coexist in equilibrium.

Proposition 1 *Given any set $x_1, \dots, x_n$ of predators and any $k \leq n$, there is at most one set of k predators that can coexist and not be invaded by any other x_j , $j = k + 1, \dots, n$. Furthermore, if we assume that the x_i 's are labeled with increasing ℓ_i , this set is $x_1, \dots, x_k$.*

Proof Without loss of generality, suppose that the x_i 's are ordered by increasing ℓ_i and consider any set of k predators that is not predators $x_1, \dots, x_k$. If this set of k predators happens to coexist, then by Lemma 4, whichever of $x_1, \dots, x_k$ is not in the set, can invade the coexisting equilibrium.

Finally, we can prove convergence to equilibrium.

Proposition 2 *Suppose we have a collection of predators $x_1, \dots, x_N$ ordered by increasing ℓ 's and let $n \geq 0$ be the largest number of predators that can coexist on Γ in such a way that $x_j \not\prec x_1, \dots, x_n$ for $j = n + 1, \dots, N$. Then $\sigma^n = (\sigma_0^n, \sigma_1^n, \dots, \sigma_n^n)$ is a globally attracting fixed point on Γ^N with Lyapunov function*

$$V(u, v_1, \dots, v_N) = u - \sigma_0^n \log u + \sum_{i=1}^n (v_i - \sigma_i^n \log v_i) + \sum_{i=n+1}^N v_i.$$

Proof Differentiating V yields

$$\begin{aligned} \frac{dV}{dt} &= (u - \sigma_0^n)(r - \beta u - \sum_{i=1}^n \alpha_i v_i - \sum_{i=n+1}^N \alpha_i v_i) \\ &\quad + \sum_{i=1}^n (v_i - \sigma_i^n)(-\delta_i - v_i + \alpha_i u) + \sum_{i=n+1}^N v_i(-\delta_i - v_i + \alpha_i u) \\ &= -\beta(u - \sigma_0^n)^2 - \sum_{i=1}^n (v_i - \sigma_i^n)^2 - \sum_{i=n+1}^N v_i(\delta_i - \alpha_i \sigma_0^n) - \sum_{i=n+1}^N v_i^2. \end{aligned}$$

All terms except the second to last are obviously negative and this term is too since $x_j \not\prec x_1, \dots, x_n$ is by definition $\delta_j > \alpha_j \sigma_0^n$.

To complete the proof of Theorem 2, we need to show that the algebraic condition (3) is equivalent the n invadability conditions given in Lemma 2. This is done in the following proposition.

Proposition 3 *Suppose we have $x_1, \dots, x_N$ ordered by increasing ℓ_i . Then $x_1, \dots, x_N$ can coexist if and only if*

$$\beta \ell_N + \sum_{j=1}^N \alpha_j^2 (\ell_N - \ell_j) < r. \quad (18)$$

Proof We will show that condition (18) is equivalent to the condition $x_N \succ x_1, \dots, x_{N-1}$ and implies the other $n - 1$ invadability conditions necessary for coexistence. By definition, $x_N \succ x_1, \dots, x_{N-1}$ is true if and only if

$$\ell_N < \sigma_0^{N-1}(x_1, \dots, x_{N-1}) = \frac{r + \sum_{j=1}^{N-1} \alpha_j^2 \ell_j}{\beta + \sum_{j=1}^{N-1} \alpha_j^2} \quad (19)$$

where we have used $\ell_j = \delta_j / \alpha_j$ on the right. Multiplying both sides by the denominator of the right and then rearranging terms, we obtain (18) (since $\ell_N - \ell_N = 0$). Furthermore, since $\ell_N > \ell_k$, for all $k = 1, \dots, N - 1$, (18) implies that same equation holds if we replace ℓ_N by ℓ_k , $k < N$ on the left and reversing the algebra used to derive (18) from (19) shows that this is equivalent to $x_k \succ x_1, \dots, x_{k-1}, x_{k+1}, \dots, x_N$, proving the result.

4 Proof of Theorem 3

In this section, we assume that all predators have $\delta_j = 1$, and we use a mutation distribution $F_\varepsilon(\alpha)$ as uniform on $[\alpha - \varepsilon, \alpha + \varepsilon]$. In this case, our rule for coexistence (18) can be rewritten as:

$$\sum_{j=1}^N \frac{\alpha_j}{\alpha_N} (\alpha_j - \alpha_N) < r - \frac{\beta}{\alpha_N}. \quad (20)$$

We recall the following definitions from the introduction:

- N_n is the number of coexisting species at time n .
- $\alpha_j(n)$ is the j^{th} largest α amongst all coexisting species at time n with $\alpha_j(n) = \alpha_{N_n}(n)$, $j \geq N_n$.
- $\Delta_n = (d_1^n, \dots, d_{j^n}^n, \dots)$ with $d_j(n) = \alpha_j(n) - \alpha_{N_n}(n) \in [0, r]$.

We also set $\alpha_{\min}(n) = \alpha_{N_n}(n)$ and $Y_n = (\alpha_{\min}(n), \Delta_n)$. Clearly, Y_n is a Markov Chain. Our first step is to show

Lemma 5 *The sequence N_n is tight.*

Proof Define the sets $A^m = [0, r]^m \times \{0\}^{\mathbb{N}}$, for $m \in \mathbb{N}$. Then $\Delta_n \in A^m$ if and only if $N_n \leq m$. Let $M = M(r, \varepsilon) = \lceil \frac{4r}{\varepsilon} \rceil$ be the smallest integer $> 4r/\varepsilon$ and suppose that $Y_n = y \in \mathbb{R}^+ \times \mathcal{S}$. From (20), at most M of the $\alpha_j(n)$'s can be $\geq \alpha_{\min}(n) + \varepsilon/4$. With probability at least $1/4^M$, the next M mutants will be inserted to the right of $\alpha_{\min}(n) + \varepsilon/2$. But then none of the predators to the left $\alpha_{\min}(n) + \varepsilon/4$ can be in the coexisting set at time $n + m$ because otherwise, Proposition 1 would imply that any predator with $\alpha > \alpha_{\min}(n) + \varepsilon/2$ would also be in the set, and since there are at least M such predators,

$$\sum_{j=1}^{\infty} d_j(n + M) > M(\varepsilon/2 - \varepsilon/4) > r$$

contradicting (20). Therefore, we have the uniform lower bound

$$P(\Delta_{n+M} \in A^{2M} | Y_n = y) \geq 4^{-M} \quad (21)$$

which holds for all $y \in \mathbb{R}^+ \times \mathcal{S}$. Since this bound is uniform in y , tightness follows.

Lemma 6 As $n \rightarrow \infty$, the marginal transition probabilities for Δ_n :

$$p(\alpha_{\min}(n), \Delta, \cdot) := P(\Delta_{n+1} \in \cdot | Y_n = (\alpha_{\min}(n), \Delta))$$

converge in total variation to the transition probabilities for a time homogeneous Markov Chain X_n , in which (22) is used in place of (20) in the evolution algorithm of Theorem 2.

Proof Lemma 8 will show that $\alpha_{N_n}(n) \rightarrow \infty$ a.s. as $n \rightarrow \infty$. (The proofs of Lemmas 7 and 8 do not use the result of this lemma.) Combining $\alpha_{N_n}(n) \rightarrow \infty$ a.s. with the fact that $0 \leq \alpha_j(n) - \alpha_{N_n}(n) \leq r$ for all $n \geq 1$, $j \leq N_n$, we can see that (20) simplifies to

$$\sum_{j=1}^{N_n} d_j(n) < r \quad (22)$$

as $n \rightarrow \infty$. This implies that, in the limit, the differences evolve according to the following algorithm: pick a species $1 \leq k \leq N_n$ at random, insert a random mutation in $(d_k(n) - \varepsilon, d_k(n) + \varepsilon)$, and then modify the algorithm in Theorem 2 to use (22) instead of (20) with the rule that we shift the differences before calculating the sum if the new insertion is left of 0.

Before proving the required fact that $\alpha_{\min}(n) \rightarrow \infty$ a.s., we examine the limiting behavior of X_n .

Lemma 7 X_n is a positive recurrent, Harris Chain and hence, has a unique stationary distribution π .

Proof Following the arguments in Athreya and Ney (1978), it suffices to show that there exists a “regenerative” set $A \subset \mathcal{S}$ satisfying:

- (C1) $P^x(\tau_A < \infty) = 1$ for all $x \in \mathcal{S}$ where τ_A is hitting time of A .
- (C2) There exists a probability measure ρ on A , $\lambda > 0$, and $\kappa \in \mathbb{N}$ so that $p^\kappa(x, B) \geq \lambda \rho(B)$ for all $x \in A$, $B \subset A$.

The same calculation that led to (21) shows that A^{2M} satisfies the condition in (C1), but (C2) may not hold for this set. We therefore define a set G (for good) that will be reached from A^{2M} with probability 1 and satisfies (C2). To this end, let

$$\kappa = 1 + \sup \left\{ k : \sum_{j=1}^k j = \frac{k(k+1)}{2} < 2r/\varepsilon \right\}$$

and choose η small enough so that

$$\sum_{j=1}^{\kappa \kappa} j(\varepsilon/2 + \eta) < r. \quad (23)$$

Let $G = \{d_i - d_{i+1} \in (\varepsilon/2, \varepsilon/2 + \eta) \text{ for } i < \kappa \text{ and } d_i = 0 \text{ for } i \geq \kappa\}$. In other words, $d \in G$ corresponds to κ species coexisting with their α 's with spacings between $\varepsilon/2$ and $\varepsilon/2 + \eta$ units apart.

The first step in showing that (C1) and (C2) hold for $A = G$ is to show that if $X_n = x \in A^{2M}$, then we can get to A in κ steps by the following path: first, we

choose d_1 (the predator with the largest values of α) as our mutating predator at stage $n+1$ (which happens with probability at least $(2M)^{-1}$) and then mutate it to g_1 in $(d_1 + \varepsilon/2, d_1 + \varepsilon/2 + \eta)$ (which happens with probability $\eta/(2\varepsilon)$). The next step, we mutate g_1 (which happens with probability at least $(2M+1)^{-1}$) and then mutate to $g_2 \in (g_1 + \varepsilon/2, g_1 + \varepsilon/2 + \eta)$. If we continue for κ steps, then each g_j , $1 \leq j \leq \kappa$ will be at least as big as $d_1 + j\varepsilon/2$ so that by (22), no member of the coexisting set at time n will remain at time $n + \kappa$. Furthermore, by (23), the shifted set $d'_j = g_{\kappa-j+1} - g_1$, $1 \leq j \leq \kappa$ will satisfy (22) and therefore, $X_{n+\kappa} \in G$. It is clear from the construction that we have

$$p^\kappa(x, G) \geq \left(\frac{\eta}{2\varepsilon(2M+\kappa)} \right)^\kappa \quad (24)$$

To prove (C2) holds, let $B = \{d_i - d_{i+1} \in B_i \subset (\varepsilon/2, \varepsilon/2 + \eta) \text{ for } i < \kappa \text{ and } d_i = 0 \text{ for } i \geq \kappa\}$. Then if $x \in G$, taking the same path that led to (24) leads to

$$p^\kappa(x, B) \geq \frac{|B_1| \cdots |B_{\kappa-1}|}{(2\varepsilon)^{\kappa-1}} \quad (25)$$

which gives us (C2) by taking ρ to be the normalized, Lebesgue measure on the configurations in G .

To check positive recurrence, we let τ_A be the first hitting time of our regenerative set G . (21) and (24) tell us that there is a positive constant $\eta = \eta(r, \varepsilon)$ so that

$$p^{2M+\kappa}(x, G) \geq 2\eta > 0$$

for any $x \in \mathcal{S}$. Therefore, we have $E^x(\tau_A) \leq (2M + \kappa)/2\eta < \infty$, completing the proof.

Lemma 8 $\alpha_{\min}(n) \rightarrow \infty$ a.s. as $n \rightarrow \infty$.

Proof We can modify the construction in the previous Lemma to show that there exist constants $K, J \geq 1$, $\rho > 0$ so that

$$P(\alpha_1((n+1)K) - \alpha_1(nK) \geq J\varepsilon/2 | Y_{nK} = y) \geq \rho$$

for any $y \in \mathbb{R}^+ \times \mathcal{S}$ and $n \geq 0$. Therefore, $\alpha_1(n) \rightarrow \infty$ a.s. by the law of large numbers and the result follows since $\alpha_1(n) - \alpha_{\min}(n) < r$.

Theorem 5 As $n \rightarrow \infty$, $\|P^\alpha(\Delta_n \in \cdot) - \pi(\cdot)\|_{TV} \rightarrow 0$ for any initial $\alpha \in \mathbb{R}^+$.

Proof It suffices to prove the result for the subsequences $n = m\kappa + j$ for $0 \leq j < \kappa$, but then by using the Markov property at time j , it is enough to prove the result for $n = m\kappa$ and a general initial distribution. To prepare for the proof, recall that one can modify the state space of a Harris recurrent Markov chain to have a point ζ that corresponds to being distributed on the set A according to ρ with the exact position being independent of the past.

To prove the result, we will construct a process $(\tilde{X}_n, \tilde{\Delta}_n)$ on $\mathcal{S} \times \mathcal{S}$ so that the marginal law of $\tilde{\Delta}_n$ is the law of $\Delta_{n\kappa}$, the marginal distribution of $\tilde{X}_n$ is π for all n , and $\mathbb{P}(\tilde{X}_n \neq \tilde{\Delta}_n) \rightarrow 0$ as $n \rightarrow \infty$. Let $U_1, U_2, \dots$ and $V_1, V_2, \dots$ be independent and uniform on $[0, 1]$. To begin, let $q = p^\kappa$ and define $J_n : \mathcal{S} \times [0, 1] \rightarrow \mathcal{S}$ by

$$P(J_n(x, U_n) \in B) = q(\alpha_{\min}(n\kappa), x, B).$$

Suppose that $\tilde{X}_n$ has distribution π . Define $Z_{n+1} = J_n(\tilde{X}_n, U_n)$ and

$$\mu_n = P(Z_n \in A | \alpha_{\min}(n\kappa)) = \int q(\alpha_{\min}(n\kappa), x, A) \pi(dx)$$

Now conditional on the value of $\alpha_{\min}(n\kappa)$ we construct $\tilde{X}_{n+1}$ so that $(\tilde{X}_{n+1}, Z_{n+1})$ has measure

$$\mu_n \wedge \pi := \frac{1}{2}(\mu_n + \pi - |\mu_n - \pi|)$$

on the diagonal and $\tilde{X}_{n+1}$ has marginal distribution π . It follows that

$$\begin{aligned} \eta_{n+1} &\equiv \mathbb{P}(\tilde{X}_{n+1} \neq Z_{n+1}) = \|\mu_n - \pi\|_{TV} \\ &= \left\| \int q(\alpha_{\min}(n\kappa), x, \cdot) \pi(dx) - \int q(x, \cdot) \pi(dx) \right\|_{TV} \rightarrow 0 \end{aligned}$$

as $n \rightarrow \infty$ by Lemma 6.

When $\{\tilde{\Delta}_n = \tilde{X}_n\}$, we set $\tilde{\Delta}_{n+1} = J_n(\tilde{X}_n, U_n) = Z_{n+1}$ so that

$$P(\tilde{X}_{n+1} \neq \tilde{\Delta}_{n+1}, \tilde{X}_n = \tilde{\Delta}_n) \leq \eta_{n+1}$$

On $\{\tilde{X}_n \neq \tilde{\Delta}_n\}$, we take $\tilde{\Delta}_{n+1} = J_n(\tilde{X}_n, V_n)$. (25) implies that $q(x, \zeta) \geq \lambda$, so it follows from Lemma 6 that if $\alpha_{\min}(n\kappa) \geq \alpha_0$ then $q(\alpha_{\min}(n\kappa), x, \zeta) \geq \lambda/2$, and we have

$$P(\tilde{X}_{n+1} = \tilde{\Delta}_{n+1} | \tilde{X}_n \neq \tilde{\Delta}_n) > \lambda/2$$

so that if $\zeta_n = P(\tilde{X}_n \neq \tilde{\Delta}_n)$, then

$$\zeta_{n+1} \leq (1 - \lambda/2)\zeta_n + \eta_{n+1}.$$

Iterating, yields the inequality

$$\zeta_{n+1} \leq \sum_{i=1}^{n+1} (1 - \lambda/2)^{n+1-i} \eta_i \rightarrow 0$$

Since $\|P(\Delta_{n\kappa} \in \cdot) - \pi(\cdot)\|_{TV} \leq P(\tilde{X}_n \neq \tilde{Y}_n)$, this proves the result.

It remains to prove the result on the linear growth of $\alpha_{\min}(n)$. Since $\alpha_j - \alpha_{\min} \leq r$, it suffices to establish this for $\alpha_{\max}$. To do this, we look at the chain $Z_n = (\Delta_n, U_n, V_n)$ with U_n uniform on $[0, 1]$ giving the index $k = \lceil N_n U_n \rceil$ of the value to be mutated, and V_n independent uniform on $[-\varepsilon, \varepsilon]$ giving the change in the value due to mutation. If Δ_n follows the dynamics of the limiting chain, then it is clear that the distribution of Z_n will converge in distribution to $\tilde{\pi} = \pi \times \text{uniform}[0, 1] \times \text{uniform}[-\varepsilon, \varepsilon]$. Let $f(Z_n) = \alpha_{\max}(n) - \alpha_{\max}(n-1)$ be the amount shifted at the n^{th} step. Then f is non-negative and bounded above by ε so the strong law for functionals of Markov chains implies

$$\frac{\alpha_{\max}(n) - \alpha_{\max}(0)}{n} = \frac{1}{n} \sum_{m=1}^n f(Z_m) \rightarrow \int f(x) \tilde{\pi}(dx) = \bar{\alpha}$$

To conclude that $\bar{\alpha} > 0$ we note that $f > 0$ with positive probability. The last result was for the time homogeneous limiting chain, but can be extended to the real chain using the coupling in the proof of Theorem 5. This completes the proof of Theorem 3.

5 Proof of Theorem 4

Recall that the condition for coexistence is

$$\delta_N \left(\beta + \sum_{j=1}^N \left(1 - \frac{\delta_j}{\delta_N} \right) \right) < r. \quad (26)$$

Proof of Lemma 1. Let $X_i(t) = -\log(\delta_i(t))$ and $X_1(t) > \dots > X_M(t)$ be the rightmost M particles at this time. It should be clear from (26) that if

$$e^{-X_M(T)}(\beta + M) < r \quad (27)$$

then we will have $N_t \geq M$ for $t \geq T$. Let $y = -\log(r/(\beta + M))$. The right most particle is increasing in t . Since the number of particles changes by ≤ 1 each time and $\sum_{m=1}^{\infty} 1/m = \infty$ the right-most particle gives birth to the right of its current position plus $1/2$ infinitely many times. Thusd at some time T , we will have M points $\geq y$ and (27) will hold. $\square$

5.1 Asymptotics for X_{max}

By Lemma 1, we know there exists some time T so that $N_t \geq M$ for $t \geq T$. By the proof of the last lemma we can take T to be the first time $e^{-X_M(T)}(\beta + M) < r$, which is a stopping time, so the future behavior of the process is not affected.

Lemma 9 *If we start the toy model at time T with positions equal to the rightmost M particles at this time $X_1(T) > \dots > X_M(T)$, then the $X_i(t)$ and $Y_i^M(t)$ can be defined on the same space so that $X_i(t) \geq Y_i^M(t)$ for all $1 \leq i \leq M$ and $t \geq T$.*

Proof Couple the birth times of $X_i(t)$ and $Y_i^M(t)$ and the displacements of their offspring. Births of particles from $X_k(t)$ for $k > M$ may cause the X 's to get ahead of the Y 's, but coupled births for $i \leq M$ cause the vectors of X 's and Y 's to move in parallel.

For our next comparison consider the branching random walk started with one particle at $Y_1^M(0)$. Let T_k be the time of the k th birth, with $T_0 = 0$, and for $t \in [T_{k-1}, T_k)$ let $\zeta_1^k(t) > \zeta_2^k(t) > \dots > \zeta_k^k(t)$ be the locations of the particles present.

Lemma 10 *We can couple the branching random walk and the toy model so that for $t \in [T_{k-1}, T_k)$, $Y_j^M(t) \geq \zeta_j^k(t)$ for $1 \leq j \leq k$ and $k < M$.*

Proof Couple the birth times of $\zeta_j^k(t)$ and $Y_j^M(t)$ for $j \leq k$ and $t \in (T_{k-1}, T_k]$, i.e., there will be no births in (T_{k-1}, T_k) and the same particle will give birth at time T_k . Births of particles from $Y_j(t)$ for $j > k$ may cause the Y 's to get ahead of the ζ 's, but coupled births for $j \leq k$ cause the vectors of ζ 's and Y 's to move in parallel.

Let Z_t be a branching random walk started from one particle at 0, in which particles give birth at rate 1 and displacements are uniform on $[-1, 1]$. It is well known that the mean measure

$$EZ_t(A) = e^t P(S_t \in A) \quad (28)$$

where S_t is a continuous time random walk that jumps at rate one and takes step uniform on $[-1, 1]$. If we let $\phi(\theta) = (e^\theta - e^{-\theta})/2\theta$ be the moment generating function for the displacements, then

$$Ee^{\theta S_t} = \sum_{n=0}^{\infty} e^{-t} \frac{t^n}{n!} \phi^n(\theta) = \exp(t(\phi(\theta) - 1))$$

Chebyshev's inequality implies that if $\theta > 0$

$$P(S_t > xt) \leq \exp(-t(\theta x - \phi(\theta) + 1)) \quad (29)$$

and standard large deviations results imply that for $x \geq 0$,

$$\frac{1}{t} \log P(S_t > xt) \rightarrow \Lambda(x) = - \left(\sup_{\theta > 0} \{\theta x - \phi(\theta)\} + 1 \right) \quad (30)$$

where $\Lambda(0) = 0$ and Λ is strictly decreasing on $[0, \infty)$.

Biggins (1977), Theorem 2 shows that the right-most particle in the branching random walk $Z_{\max}(t)/t \rightarrow a$ a.s. where a , defined in (7), is the smallest $x > 0$ such that $\Lambda(x) \leq -1$.

Lemma 11 *Let B_M be the time of the M th birth in the branching random walk.*

$$\liminf_{t \rightarrow \infty} \frac{Y_1^M(t)}{t} \geq \frac{EZ_{\max}(B_M)}{EB_M} \rightarrow a \quad \text{as } M \rightarrow \infty$$

Proof Repeatedly applying the comparison in Lemma 10 to the right-most particle in the toy model, gives the first result. Biggins' result implies

$$Z_{\max}(B_M)/B_M \rightarrow a \quad \text{almost surely.}$$

Since $B_M = \xi_1 + \dots + \xi_M$ where the ξ_i are independent exponentials with mean $1/i$, it is easy to see that $B_M/EB_M \rightarrow 1$, so

$$Z_{\max}(B_M)/EB_M \rightarrow a \quad \text{almost surely.}$$

Therefore, the result will follow from the dominated convergence theorem if we can show that

$$E \left(\sup \frac{Z_{\max}(B_M)}{EB_M} \right) < \infty.$$

By Cauchy Schwartz, it suffices to show

$$E \left(\sup_{t \geq 1} \frac{Z_{\max}(t)}{t} \right)^2 < \infty \quad (31)$$

and

$$E \left(\sup \frac{B_M}{EB_M} \right)^2 < \infty. \quad (32)$$

To prove (31), we note that (28) and (29) imply that

$$P(Z_{\max}(t) > xt) \leq e^{t(1+\Lambda(x))}$$

and since Λ is concave with $\Lambda(0) = 0$ and $\Lambda(a) = -1$ with $a < 1$, it follows that for $x \geq 1$

$$P(Z_{\max}(t) > xt) \leq e^{t(1-x)}$$

Now if $Z_{\max}(t)/t > 2x$ for some t , then since $Z_{\max}(t)$ is non-decreasing, we must have $Z_{\max}(s)/s > x$ for some $s \in [t, t+1]$ and therefore, integrating t from 1 to ∞ , we see that if $x > 2$

$$P\left(\sup_{t \geq 1} Z_{\max}(t)/t > 2x\right) \leq e^{1-x}$$

which proves (31). To prove (32), we note that $EB_M = \sum_{i=1}^M 1/i$ and

$$E \exp(\theta B_M) = \prod_{i=1}^M \frac{1}{1 - \theta/i}$$

for $0 < \theta < 1$, so using Chebyshev

$$P(B_M > yEB_M) \leq \exp\left(-\theta y \sum_{i=1}^M \frac{1}{i} - \sum_{i=1}^M \log(1 - \theta/i)\right)$$

Taking $\theta = 1/2$ and choosing c so that $\log(1-x) \geq -x - cx^2$ when $0 < x < 1/2$, we have

$$\begin{aligned} P(B_M > yEB_M) &\leq \exp\left(\sum_{i=1}^M \frac{1}{2i}(1-y) + \frac{c}{4i^2}\right) \\ &\leq C \exp\left(\frac{1-y}{2} \log(M+1)\right) = C(M+1)^{(1-y)/2} \end{aligned}$$

Therefore if $y > 3$,

$$\sum_{M=2}^{\infty} (M+1)^{(1-y)/2} \leq \int_2^{\infty} x^{(1-y)/2} dy = \frac{2^{(3-y)/2}}{(y-3)/2}$$

which yields (32), completing the proof.

Since the particles $X_i(t)$ in our evolution model are a subset of those in the branching random walk, we have

$$\limsup_{t \rightarrow \infty} X_1(t)/t \leq a$$

which proves $X_{\max}(t)/t \rightarrow a$.

Proof of Corollary. If ε is small $\varepsilon M(M-1)/2 < r$. Using the coupling in Lemma 10 we can use the particles ζ_j^k , $j \leq k \leq M$, from the branching random walk started at $X_{\max}$ to get a lower bound on the right-most $k \leq M$ particles in the predator evolution with fixed δ . An induction argument shows that the spacings between the corresponding particles in the predator evolution are $\leq \varepsilon$ at all times. Since we have assumed $\varepsilon \sum_{j=1}^{M-1} j < r$ the right-most $k \leq M$ particles are never killed. The remainder of the proof is the same as before. $\square$

5.2 Asymptotics for $X_{\min}$

In order to get the speed of the leftmost particle, we will need the following result on a branching random walk with killing which is an adaptation of Biggins (1977), Theorems 1 and 2, which proves this result without killing.

Lemma 12 *Let $Z_t(\gamma, A)$ denote the number of particles in A under a branching random walk with birth rate one, displacements uniform on $[-1, 1]$, killing to the left of $-K + \gamma t$, and started with one particle at 0. Then for any $c > \gamma$ on the set of nonextinction*

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log Z_t(\gamma, [ct, \infty)) = I(c) \quad (33)$$

where $I(c) = 1 + \Lambda(c)$, and the probability of extinction tends to 0 as $K \rightarrow \infty$.

Proof Theorem 2 in Biggins along with (28) and (30) yields (33) in the case of no killing and since $Z_t(\gamma, [ct, \infty)) \subset Z_t([ct, \infty))$, we get the upper bound in (33). To get the lower bound, we recall that to prove the corresponding lower bound for the process without killing, Biggins lets Z_{m+1}^k be the points at time $(m+1)k$ that are at least kc units to the right of their ancestor in Z_m^k at time mk . $|Z_m^k|$ is a branching process with offspring distribution $|Z_1^k|$ so $(|Z_m^k|)^{1/m} \rightarrow E|Z_1^k|$ on the nonextinction set. Combining (28) and (30) implies $(1/k) \log E|Z_1^k| \rightarrow I(c)$ which yields the desired lower bound.

To extend this construction to the process with killing, let $\bar{Z}_{m+1}^k$ be the points at time $(m+1)k$ that are at least kc units to the right of their ancestor in $\bar{Z}_m^k$ at time mk and are not killed by going to the left of $-K + \gamma t$ of $mk \leq t \leq (m+1)k$. $|\bar{Z}_m^k|$ is a nonhomogeneous branching process, but for large m the killing has little effect so, on the set of nonextinction,

$$\frac{1}{m} \log |\bar{Z}_m^k| \rightarrow \log E|Z_1^k|$$

Using (28) and (30) again gives the desired lower bound.

With this result in hand, we can do the:

Proof of $X_{\min}(t)/t \rightarrow b$. When $X_{\min}(t)$ increases we must have

$$N_t e^{-X_{\min}(t)} \geq r.$$

Since the particles in X are a subset of the particles in the branching random walk, it follows that if $X_{\min}(t) \geq (b + \varepsilon)t$,

$$N_t e^{-X_{\min}(t)} \leq Z_t([(b + \varepsilon)t, \infty)) e^{-(b + \varepsilon)t} \rightarrow 0$$

as $t \rightarrow \infty$ since $I(c) < c$ for all $c > b$. Therefore, $\limsup X_{\min}(t)/t \leq b$ a.s.

To prove that $\liminf X_{\min}(t)/t \geq b$ a.s., let $c \in (b, a)$ and $\varepsilon > 0$. Choose K large enough so that the probability of extinction in the branching random walk with killing at $-k + bt$ is less than ε for all $k \geq K$ and then take T large enough so that $X_1(t) \geq ct$, for all $t \geq T$ (which is possible since $\lim X_1(t)/t = a$) and so that $bT > K$. Suppose that $X_{\min}(t) \leq (b - \rho)t$ for some $\rho > 0$. Then by comparing with a branching random walk with killing at $-X_1(T) + bt$, we have

$$\begin{aligned} F(t) &:= e^{-X_{\min}(t)} \sum_{j=1}^{N_t} (1 - e^{-X_j(t)/X_{\min}(t)}) \\ &\geq e^{-(b-\varepsilon)t} (1 - e^{-(c-b+\varepsilon)t}) Z_t(b, [ct, \infty)). \end{aligned} \quad (34)$$

But on the non-extinction set (which has probability at least $1 - \varepsilon$), we have

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log[e^{-(b-\varepsilon)t}(1 - e^{-(c-b+\varepsilon)t})Z_t(\gamma, [ct, \infty))] = I(c) - b + \rho \rightarrow \rho > 0$$

as $c \downarrow b$ and therefore, we must have $X_{\min}(t) > (b - \rho)t$ eventually or there would exist a sequence of points $t_i \rightarrow \infty$ for which $F(t_i) \rightarrow \infty$, contradicting (6). Therefore, $P(\liminf_{t \rightarrow \infty} X_{\min}(t)/t < b) < \varepsilon$ and since ε is arbitrary, this proves the result.

To conclude that $\liminf_{t \rightarrow \infty} (\log N_t)/t \geq b$ a.s., note that if $\varepsilon > 0$ then for large times there are at least $\exp((I(c) - \varepsilon)t)$ points of X to the left of ct . Picking c close to b and ε small gives the desired result. $\square$

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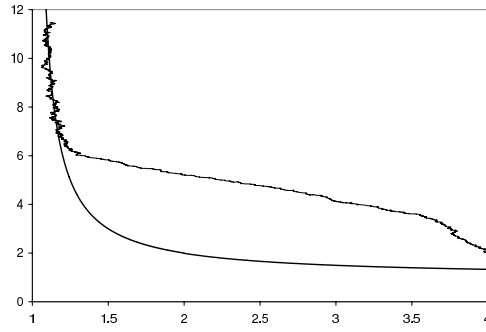


Fig. 1 Simulation of prey evolution with $\varepsilon = 0.01$ when $\alpha = 4$, $\beta = 2$, and $\delta = \gamma = 1$.

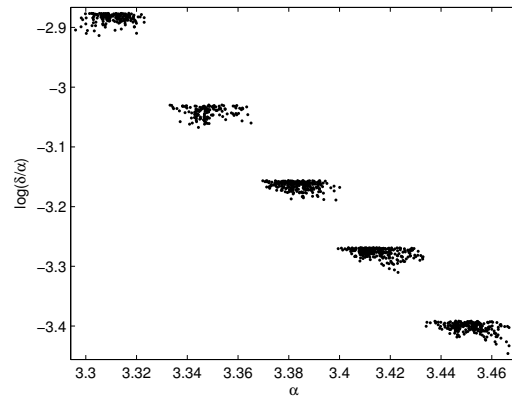


Fig. 2 Plots of points in two parameter predator evolution. The five clusters, from upper left to lower right, are the characteristics of the coexisting predators at times $n = 10^4, 1.25 \times 10^4, 1.5 \times 10^4, 1.75 \times 10^4$ and 2×10^4 . x -axis is the α values and y -axis is the corresponding values of $\log(\delta/\alpha)$. Parameters: $r = 1$, $\alpha(0) = 3$, $\delta(0) = .45$, $\varepsilon = .01$.

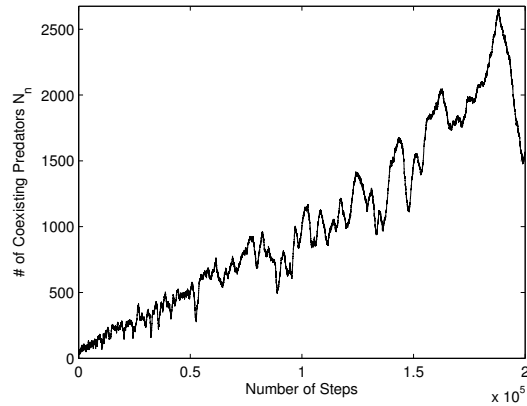


Fig. 3 Plot of N_n = number of species at time n in two parameter predator evolution model from Figure 2.

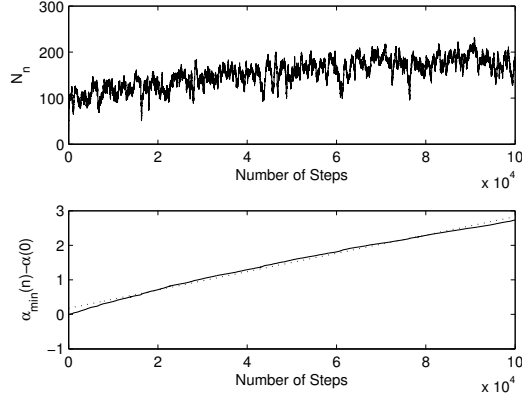


Fig. 4 Fixed death rate predator evolution model with $\varepsilon = .01$ and $r = 1$ starting with one predator at $\alpha(0) = 3$,

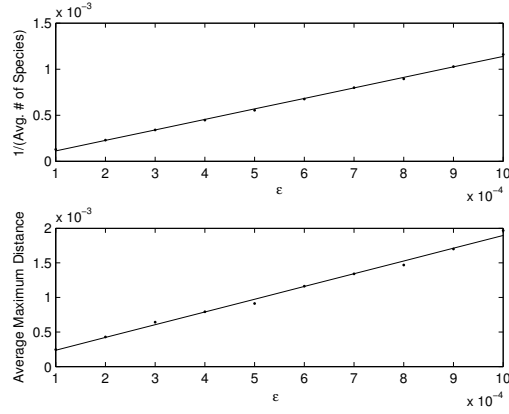


Fig. 5 Fixed death rate predator evolution model with $r = 1$, $\alpha(0) = 3$ and varying values of ε . Results are averages over last 25,000 iterations. Top panel shows the average number of species; the bottom panel the maximum distance between α 's.

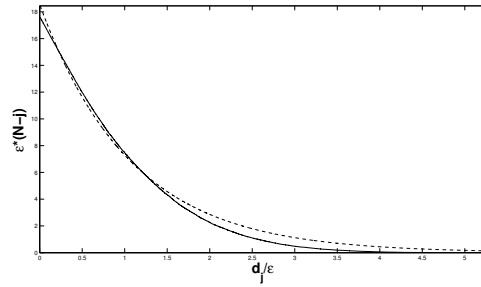


Fig. 6 Fixed death rate predator evolution model with $\varepsilon = .001$ and $r = 1$. Solid line shows d_j/ε vs. $\varepsilon(N_n - j)$ at time $n = 50,000$ when $N_n = 17626$. Dashed line gives an exponential approximation.

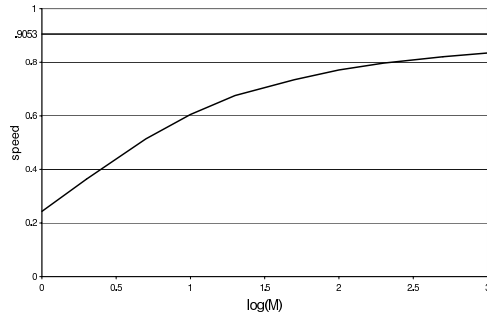


Fig. 7 Graph of speeds a_M versus $\log M$ showing slow convergence to limit.

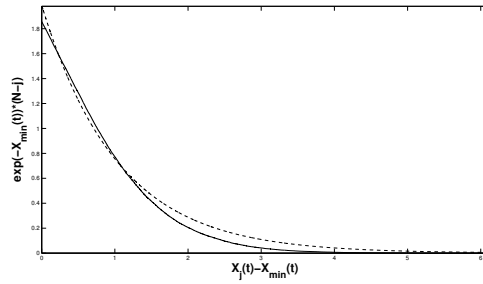


Fig. 8 Continuous time, fixed consumption rate predator evolution model with $r = 1$. Solid line shows $X_j(t) - X_{\min}(t)$ vs. $e^{-X_{\min}(t)}(N_t - j)$, for $j = 1, \dots, N_t = 25467$ at time $t \approx 20.25$ (after $n = 50,000$ insertions). Dashed line gives an exponential approximation.

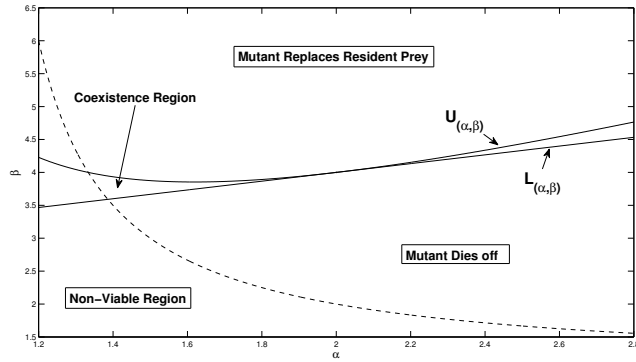


Fig. 9 Plot of invadability curves for $(\alpha_1, \beta_1) = (2, 4)$. For the predator, we set $\delta = \gamma = 1$. The dashed line gives the boundary of the viable region.