

Supplemental Material:

Programmed death is favored by natural selection in spatial systems

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MODEL DETAILS

In this section we provide additional details for the reference model whose results are discussed in the main paper. The model dynamics is a sequence of synchronous updates of a two-dimensional spatial array of cells. At each time step, the following events simultaneously take place for each site in the array:

- An empty site has probability

$$P_{E \rightarrow R} = 1 - (1 - g)^{\mathcal{N}_R}$$

of transitioning to a resource-only site, where g is the probability per time step of a resource-only site reproducing into a given neighboring empty site, and \mathcal{N}_R is the number of resource-only sites among the empty site's four nearest neighbors. This expression is equivalent to the statement that each neighboring resource-only site has an independent probability g of "seeding" the empty site.

- A resource-only site has probability

$$P_{R \rightarrow C} = 1 - \prod_i^{\mathcal{N}_C} (1 - p_i)$$

of transitioning to a consumer site, where \mathcal{N}_C is the number of consumers among its four neighbors and the values p_i are the corresponding consumer reproduction probabilities. This expression corresponds to each neighboring consumer site i having an independent probability p_i of trying to reproduce into this site. If more than one consumer does so, one is chosen at random to be the parent, with equal probability for each. The offspring has p and q initialized equal to that of its parent; then with probability μ_p (μ_q), that value is increased by ϵ_p (ϵ_q), or decreased by that amount with equal probability.

- A consumer site has probability $P_{C \rightarrow E} = v + kc$ of transitioning to an empty site (all resources in the site are consumed, resulting in consumer death), where k is the number of offspring the consumer produces in this time step, and probability $P_{C \rightarrow R} =$

q of transitioning to a resource-only site (death due to intrinsic mortality).

Simulations were performed on lattices of size 250×250 , except for cases with immortal consumers where the population was not stable on a lattice of that size (quickly going to extinction in such cases). Accordingly, results for immortals shown in Figure 2 were run on the smallest of $\{250 \times 250, 500 \times 500, 750 \times 750\}$ for which a steady-state population of consumers could persist. Increasing the lattice size further does not change the steady-state values of p and q . Specifically, we used:

- 250×250 : $g = \{0.05, 0.1, 0.2\}, v = \{0.1, 0.2\}$
- 500×500 : $g = \{0.05, 0.1\}, v = \{0.005, 0.01, 0.05\};$
 $g = 0.2, v = \{0.01, 0.05\}$
- 750×750 : $g = 0.2, v = 0.005$

Mortal populations were stable on 250×250 arrays in all cases.

In most of the numerical studies presented in this work, we focus on the limiting case of no cost of reproduction ($c = 0$), due to the greater clarity of interpretation in that case: e.g., in immortal populations, the reproductive restraint that evolves cannot be attributed to an individual effort to conserve resources, since reproducing is free to the individual. Increasing c does not change the qualitative result that restraint is favored in the long term. We discuss the effect of nonzero values of c further in the section on mean-field analysis below.

In ascendance studies, we initialized the lattice randomly with each site having a 55% chance of being empty, a 40% chance of having resources only, and a 5% chance of having a consumer, with p and q in the latter case each randomly chosen from a uniform distribution between 0 and 1.

Values of p and q are only meaningful within a finite range, $[0, 1]$ and $[0, 1 - v]$ respectively. (The latter expression arises since starvation and intrinsic death are taken to be mutually exclusive possibilities.) Accordingly, mutants with values outside these ranges are set to the boundary values. To ensure that this operation does not cause artifacts in the steady-state value of q or p , we performed simulations that progressively reduced the

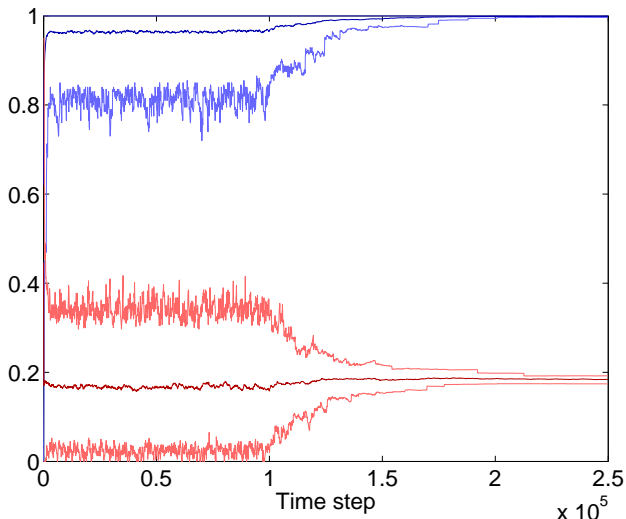


FIG. S1. Traces showing mean (dark) and maximum/minimum (light) values of p (blue) and q (red) over the full course of an ascendance study, with initial transient period ($t = 0$ – 100000) and intermediate period during which ϵ_p and ϵ_q are reduced ($t = 100000$ – 200000). Statistics reported in Figure 1 are based on the final 50000 time steps of each numerical trial.

size of mutations ϵ_p and ϵ_q . Following an initial 100,000 steps to achieve steady state, an additional 100,000 steps were performed during which ϵ_p and ϵ_q were halved every 10,000 steps, ending with a final 50,000 steps to obtain steady-state behavior (Figure S1). The resulting minimum value of q , as well as the mean, was significantly above 0 in all cases in Figure 2 (with the exception of the largest neighborhood sizes in panel E: see below), supporting the finding that finite lifespan is consistently favored. The mean values reported in Figure 2 are based on averages over those final 50,000 steps sampled once every 100 steps.

In invasion studies, we initialized the simulation with a steady-state configuration (following 200,000 time steps) of the “invaded” population. One consumer is then chosen at random and converted to an invader, with p unchanged, q set to 0, and μ_q set to 0.1275 or 0 according to whether the invader is mortal or immortal. If invaders succeed in taking over the entire consumer population, the model is reset on the next time step to a steady-state configuration of the invaded variant. If the invader’s offspring become extinct, or the steady state is reset following a successful takeover, a new consumer is chosen at random and converted to an invader. The trial continues for 100,000 introduction attempts, or 500,000 attempts for immortals invading mortals (due to such an invasion’s low chance of success). In control studies in which both invader and invaded are mortal, q is left unchanged when an invader is introduced. Studies for each (g, v) pair were conducted on arrays of the smallest size for which im-

mortal consumer populations could persist, as specified above. Table S1 gives probabilities of successful invasion for several values of g and v .

Competition studies are analogous to invasion studies without mutation. The simulation is initialized with a steady-state configuration for given values of parameters g, v, c ; all consumers have the corresponding equilibrium values of p and q , and mutation is turned off ($\mu_p = \mu_q = 0$). One consumer is chosen at random and converted to an invader, and its offspring followed as in invasion studies, with q set to a new value for invaders and μ_q still 0.

The contact rate ρ for consumers, defined as the mean number of resource-only sites in a consumer’s neighborhood, gives a measure of the resource availability in the local environment. However, it does not directly reflect the number of opportunities for the consumer to reproduce at that time step, because those neighboring resource sites may have other consumer neighbors of their own attempting to reproduce into them. Accordingly, we define the effective contact rate ρ' for a consumer by taking each of its resource-only neighbors j , dividing 1 by j ’s number of consumer neighbors, and adding those quantities: $\rho' = \sum_{j \in \text{nn in state } R} (1/\mathcal{N}_C(j))$. Thus $\rho'p$ is the expected number of offspring for a consumer at a given time step, and $\rho'pL = \rho'p/(v + q)$ its expected lifetime reproduction. The results shown in Figure 1D and 1E are based on competition studies with 10^5 introductions of invaders for each invading value of q .

In studies with increasing neighborhood size γ (Figure 2E), the neighborhood from which a resource can be chosen for reproduction into an empty site, or a consumer for reproduction into a resource-only site, is shown in Figure S2. In the studies of Figure 2E, the minimum value of q in the consumer population (following the reduction of ϵ_p and ϵ_q as described above) is greater than 0 in all trials for $\gamma \leq 32$ (intrinsic mortality remains favored); for $\gamma \geq 36$, the minimum value of q is 0 for all trials (consumers with unlimited intrinsic lifespan persist; intrinsic mortality is no longer evidently favored).

MEAN-FIELD ANALYSIS

In this section we present an analytic mean-field (spatially averaged) treatment of the model and show that it predicts the evolution of faster reproduction and longer lifespan under all circumstances. This is consistent with the expectation that homogenous systems do not allow evolution of shorter lifespan, even though the spatial model does.

Consider first a case without mutation and with a population of consumers all having a single value of p and of q . Let $\{n_R, n_C, n_E\}$ be the fraction of sites in each of the three possible states {resource-only, resource+consumer, empty}. For simplicity, we consider the case of small

$(g \cdot n_R)$ and $(p \cdot n_C)$, where the probability of multiple resources or consumers simultaneously trying to reproduce into a single site is small:

$$P_{E \rightarrow R} = 1 - (1 - g)^{N_R} \approx N_R g \approx n_R \gamma g$$

$$P_{R \rightarrow C} = 1 - \prod_i^{N_C} (1 - p_i) = 1 - (1 - p)^{N_C} \approx N_C p \approx n_C \gamma p$$

where the last step represents the spatial averaging, with γ equal to the number of neighbors of a site (4 in our model). At steady-state, for each of the three possible states, the number of sites making transitions to and from that state are equal:

$$\text{Resource-only: } n_E n_R \gamma g + n_C q = n_R n_C \gamma p$$

$$\text{Resource+consumer: } n_R n_C \gamma p = n_C r = n_C (v + r c + q)$$

$$\text{Empty: } n_C (v + r c) = n_E n_R \gamma g$$

where r is the renormalized consumer reproduction rate, i.e., the average number of offspring per consumer per time step. This system of equations can be solved to give these results:

$$\begin{aligned} r &= \frac{v + q}{1 - c} \\ n_R &= \frac{r}{\gamma p} \\ n_C &= \left(1 - \frac{r}{\gamma p}\right) \left(\frac{1}{1 + \frac{p}{g} \frac{v+q}{v+q}}\right) \\ n_E &= \left(1 - \frac{r}{\gamma p}\right) \left(\frac{1}{1 + \frac{g}{p} \frac{v+q}{v+q}}\right) \end{aligned}$$

These approximate mean-field equations can be useful in understanding the trends found in simulations of the spatial model as a function of model parameters (Figure S3) even though, as we will show, they predict incorrectly the outcome of evolution. For example, the actual consumer reproduction rate, r , is found to be independent of the probability p that a consumer tries to reproduce if given the opportunity. This counterintuitive result arises from compensating changes in the number of available resource sites into which consumers can reproduce.

In order to evaluate the predictions of mean-field theory for dominance of strains under mutation and selection, we consider a system with two consumer strains, having distinct parameter values $\{p_1, q_1\}$ and $\{p_2, q_2\}$. (The extension to larger numbers of strains is straightforward.) Site transition rates into the two consumer states are

$$\begin{aligned} n_{C1}^+ &= n_R n_{C1} \gamma p_1 \\ n_{C2}^+ &= n_R n_{C2} \gamma p_2 \end{aligned}$$

and away from these states are

$$\begin{aligned} n_{C1}^- &= n_{C1} (v + q_1 + r_1 c) = n_{C1} \left(\frac{v + q_1}{1 - c}\right) \\ n_{C2}^- &= n_{C2} (v + q_2 + r_2 c) = n_{C2} \left(\frac{v + q_2}{1 - c}\right) \end{aligned}$$

If $\frac{v+q_1}{(1-c)p_1} < n_R \gamma$, then $n_{C1}^+ > n_{C1}^-$ and the fraction of sites of consumer strain 1 increases. Similarly, if $\frac{v+q_2}{(1-c)p_2} > n_R \gamma$, then $n_{C2}^+ < n_{C2}^-$ and the fraction of sites of strain 2 decreases. Hence if

$$\frac{v + q_1}{p_1} < \frac{v + q_2}{p_2}$$

then strain 1 will dominate strain 2, driving it to extinction.

More exact mean-field calculations (not making the approximation of small gn_R and pn_C) do not change the essential conclusions. While the expressions for transition probabilities between states then have more complicated nonlinear dependences on g and p , it remains true that increasing p gives monotonically increasing probability of consumer reproduction at that time step. Moreover, the calculations make no approximations regarding q . As a result, it remains the case that higher p and lower q are always favored in the mean-field treatment.

Thus, in the mean-field approximation for two strains with equal g , the one with higher reproduction probability p always dominates; and for two strains with equal p , the one with lower intrinsic mortality probability q always dominates. These results can be immediately understood because in a homogenous (well-mixed) or mean-field system, all available resource sites can be equally reached for reproduction by any consumer, and thus the consumer that reproduces most—by reproducing fastest, or surviving to reproduce longest—dominates in all circumstances. The same argument does not hold in a spatial model.

VARIATIONS ON THE REFERENCE MODEL

In this section we briefly discuss how a number of qualitative changes to the reference model affect its behavior. We consider: deterministic rather than stochastic limitations to lifespan (explicit programmed mortality, or rapid senescence); increasing mortality with age (gradual senescence); spatial mixing within a consumer population and migration of consumers within resource areas; increased dispersal for reproduction of both consumers and resources; deterministic resource use with continuous-valued resources, rather than binary resource state and stochastic consumption; individual consumers' ability to adjust their "rate of living"; resources that regenerate spontaneously, rather than being spread only locally by existing resources; consumer reproduction supplanting others already present; resources that continue to regenerate even when exploited by consumers; and sexual reproduction by consumers.

All these model variants support the generality of the conclusion that finite lifespan is favored, when resources are limited and dispersion is local. For each variant, unless otherwise specified, we performed 10 independent nu-

merical trials on a 250×250 lattice with $g = v = 0.05$ and $c = 0$. Except where noted, in all cases p evolved to a value of 1 and q to a value significantly greater than 0, as in the reference model.

Deterministic lifespan

In this variant, the genotype specifies intrinsic lifespan directly as a fixed length of time: L time steps after a consumer is born, it dies, regardless of remaining resources. Including some variability in the lifespan, by choosing it from some distribution with mean at L and a moderate variance, does not change the results.

Increasing mortality with age

In this variant, a consumer's probability of death at each time step is given by the Gompertz equation [1] $m(t) = m_0 e^{qt}$, where m_0 is a constant (chosen here to be 0.1), t is the number of time steps since the consumer's birth, and q is a heritable value as in the reference model. In this case q is not restricted by the simulation to be nonnegative; still, it evolves to a limited value (for these parameter values, approximately 0.15).

Note that for other conditions, this model variant can predict the evolution of different senescence patterns. For instance, if intrinsic mortality is set to be initially much higher than the equilibrium found in the reference model (e.g., $m_0 = 0.5$), then negative senescence can evolve (for these parameter values, equilibrium $q \approx -0.23$).

Consumer migration

In this variant, we allow consumer mobility. For this purpose, we split each time step into three successive stages: first, reproduction of both resources and consumers; second, resource depletion and consumer death through both starvation and intrinsic mortality; and third, mobility, in which each consumer (asynchronously, in random order) is able to move.

We tested three types of mobility: (a) a consumer trades places with a randomly chosen neighboring consumer (if any exist); (b) a consumer moves to a neighboring, unoccupied resource site if such exists; (c) a consumer exchanges places with a nearby randomly chosen non-empty site of either type. In all three cases self-limited lifespan is favored; in cases (b) and (c) reproduction p sometimes evolves to an equilibrium value slightly below 1. Increasing the mobility distance to a limited extent (e.g., choosing the target site in version (c) from a 7×7 square centered at the consumer's original position) does not change the qualitative result.

Increased consumer or resource dispersal

In this variant, consumers or resources are not limited to reproducing into only the four neighboring sites. For ease of implementation, a modified version of the model was used for these studies: Instead of the reference model's synchronous update where each site was simultaneously updated based on its value and those of its neighbors, an asynchronous update was used in which sites were successively chosen in random order for updates of the following form: empty sites remained empty; resource sites remained resources, and had a probability g of also reproducing by converting one empty site to a resource site; consumer sites had a probability v of becoming an empty site and q of becoming a resource site ($v + q \leq 1$), and separately a probability p of reproducing by converting one resource site to a consumer site. For such resource or consumer reproduction, the offspring site was chosen randomly from all sites of the appropriate type such that both the row and column indices differed by at most R_R or R_C (for resources and consumers, respectively) from those of the parent. For $R_R = R_C = 1$, this model produces the same qualitative results as the reference model (p evolves to 1, q to nonzero values). (Note that these dispersal ranges are both effectively greater than those in the reference model: reproduction is possible there only in the 4-neighborhood, here in the 8-neighborhood.)

Increasing the consumer dispersal range R_C can disrupt the local neighborhood relationships that make it possible for selection to favor restraint. Large enough R_C makes the system effectively well-mixed. In such cases consumption increases through unchecked selection for faster reproduction and longer lifespan, until the consumer population exhausts all available resources and goes extinct. The dispersal range above which this occurs is a function of the ecological parameters g, v, c as well as the size of the simulation space. This is because g, v, c, R_C affect the length scale of the characteristic population structure; if that length scale is too large compared to the space, the spatial nature of the model breaks down. Thus a given value of R_C can result in extinction on lattices of a given size but allow evolution of restraint and a sustainable consumer population on larger lattices. For instance, with $g = v = 0.05$ and $c = 0$, a consumer population with $R_C = 1$ consistently goes extinct on a 50×50 lattice (in 5800 ± 6300 time steps), but survives (i.e., persists for at least 250,000 time steps, evolving intrinsic mortality) on a 100×100 lattice; $R_C = 2$ consistently gives extinction on a 200×200 lattice (in 60000 ± 37000 time steps) but survival on a 250×250 lattice; $R_C = 3$ results in consistent extinction on a 250×250 lattice (in 5400 ± 4900 time steps), survival in 3 of 10 trials on a 500×500 lattice (with extinction in 100000 ± 80000 time steps in the other trials), and consistent survival on a 750×750 lattice.

Increasing the resource dispersal range R_R increases the extent to which consumers generally have resources available, which affects the extent to which intrinsic mortality is favored. For instance, with $g = v = 0.05$, increasing R_R to 5 results in enough resource availability that intrinsic mortality is not favored; increasing the consumption rate v to 0.1 reduces resource availability and returns the model to the regime where intrinsic mortality is favored, and increasing v to 0.2 results in the evolution of still higher intrinsic mortality rates.

Continuous-valued resources and deterministic consumption

In this variant, we treat resources as continuous-valued and consumption as occurring with a fixed rate. All sites are characterized by the quantity of resources they contain, with a value from 0 to 1. Consumers deplete resources by an amount v per time step, and c per reproduction. When resources in a site reach 0, the consumer there dies. If the consumer dies prematurely due to intrinsic mortality, residual resources remain for future exploitation. When an empty site is converted to one containing resources, the resource value there is set to 1. Partially depleted resources are left unreplenished. Replenishing partially depleted resources slowly or quickly over time (to a maximum of 1) does not change the qualitative result.

Consumers can adjust rate of living in response to resource shortages

To consider the ability exhibited by many organisms to adjust rate of living in response to environmental conditions (e.g., dauer formation in *C. elegans*, dietary restriction [2]), we explored a variant based on the continuous-valued resource variant described above. In this variant, if a consumer is in a site with resource value below a threshold T , it adjusts its consumption v , reproduction p , and intrinsic mortality q all by a multiplicative constant k . Additionally, depleted resources are gradually renewed, by an amount D per time step, in both resource-only sites and those occupied by consumers. We conducted numerical trials with $g = 0.1, v = 0.2, D = 0.05, k = T = 0.5$.

Spontaneously generated resources

In this variant, we consider spontaneous appearance of resources at any location in space. This model corresponds to certain plant-herbivore systems, where a plant such as grass can be cropped down to its roots and regrow. Empty sites in this variant become resource

sites with probability g at each time step independent of whether other resources are located nearby. Resources are generated much more readily than in the reference model, and so a much lower value of g (we used 0.005) produces an overall level of resource production comparable to that in the reference model and a similar degree of lifespan control. For high values of g , the consumer population is not limited by resource availability and lifespan control does not evolve.

Reproduction supplants existing consumers

In this variant, we allow consumers to reproduce not only into sites with resources alone, but also those with consumers already present, replacing the previous consumer.

Resources reproduce even when exploited by consumers

In this variant, we explored the consequences of allowing resources to reproduce even when consumers are present—i.e., resource sites reproduce with probability g in the absence of consumers and g' in their presence (in the reference model, $g' = 0$).

A nonzero g' increases the overall level of resource availability. Hence this variant requires reducing g and/or increasing v to obtain results quantitatively comparable to those of the reference model. For example, for $g = g' = 0.05, v = 0.23$, the steady-state value of q is close to that of the reference model for $g = v = 0.05$ and for $g = v = 0.23$. For a given g and v , increasing g' leads to lower steady-state values of q (longer lifespan), just as increasing g for fixed v does in the reference model (Figure 2).

It is possible in this variant, if the level of resource growth is high enough compared to v , for consumers to have little enough impact on the spatial distribution of resources that selection does not limit reproduction probability (for immortals) or lifespan (for mortals). For example, with $g = v = 0.05$, reproduction and lifespan limits occur for $g' \leq g/3$ and not for $g' \geq g/2$.

Sexual reproduction by consumers

In this variant, when a consumer reproduces, a second consumer is randomly chosen to be the other parent of the offspring, with the values of p and q for the offspring being the average of those of the two parents plus mutation as in the reference model. When the second parent is chosen from nearby (e.g., from a 7×7 region centered on the offspring), finite lifespan is favored, as is reproductive restraint: q evolves to a value significantly greater than

0, and p to a value less than 1. When the second parent is drawn from the entire consumer population (i.e., a form of global dispersal), no restraint evolves: q evolves to 0 and p to 1.

CLASSIC PERSPECTIVES ON LIFESPAN CONTROL

Mainstream evolutionary theory considers it well-established that selection does not and cannot act in favor of decreased lifespan (unless more than compensated by a concomitant increase in early-life fitness, in the antagonistic pleiotropy framework [3]). This perspective is unambiguous and strongly stated throughout the literature, with characteristic statements about the impossibility of genes for aging or lifespan control and the error in thinking that aging could be adaptive or programmed (see, e.g., [2, 4–6]). The intuition is clear and often explicit: aging is disadvantageous to the individual and therefore should always be selected against when possible [2–5].

These views can be traced back to controversy in evolutionary theory in ca. the 1960s, in which in a broad rejection of the idea of group selection, it became standard practice to rule out explanations relying on selection above the individual level [7]. The corresponding argument in the context of the evolution of lifespan—that selection for shorter lifespan should not be considered if any alternative explanation exists—was explicitly stated

then [3], and continues to persist today. Such a view risks blinding evolutionary biology to an important explanatory process, particularly with increasing evidence that selection above the individual level is an important evolutionary force [8–12].

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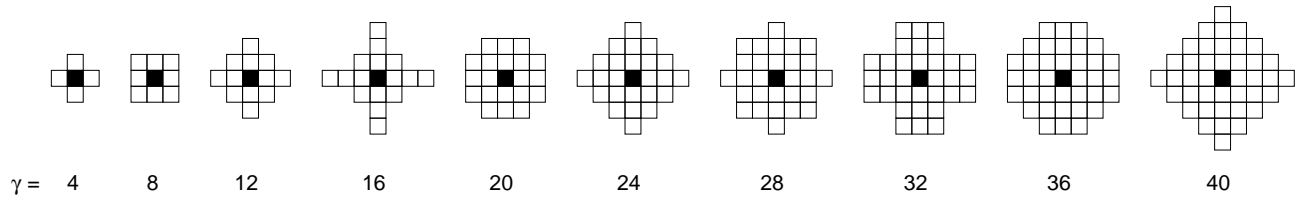


FIG. S2. Sites (white) considered to be in the neighborhood of a focal site (black), for the studies with increasing neighborhood size γ whose results are shown in Figure 2E.

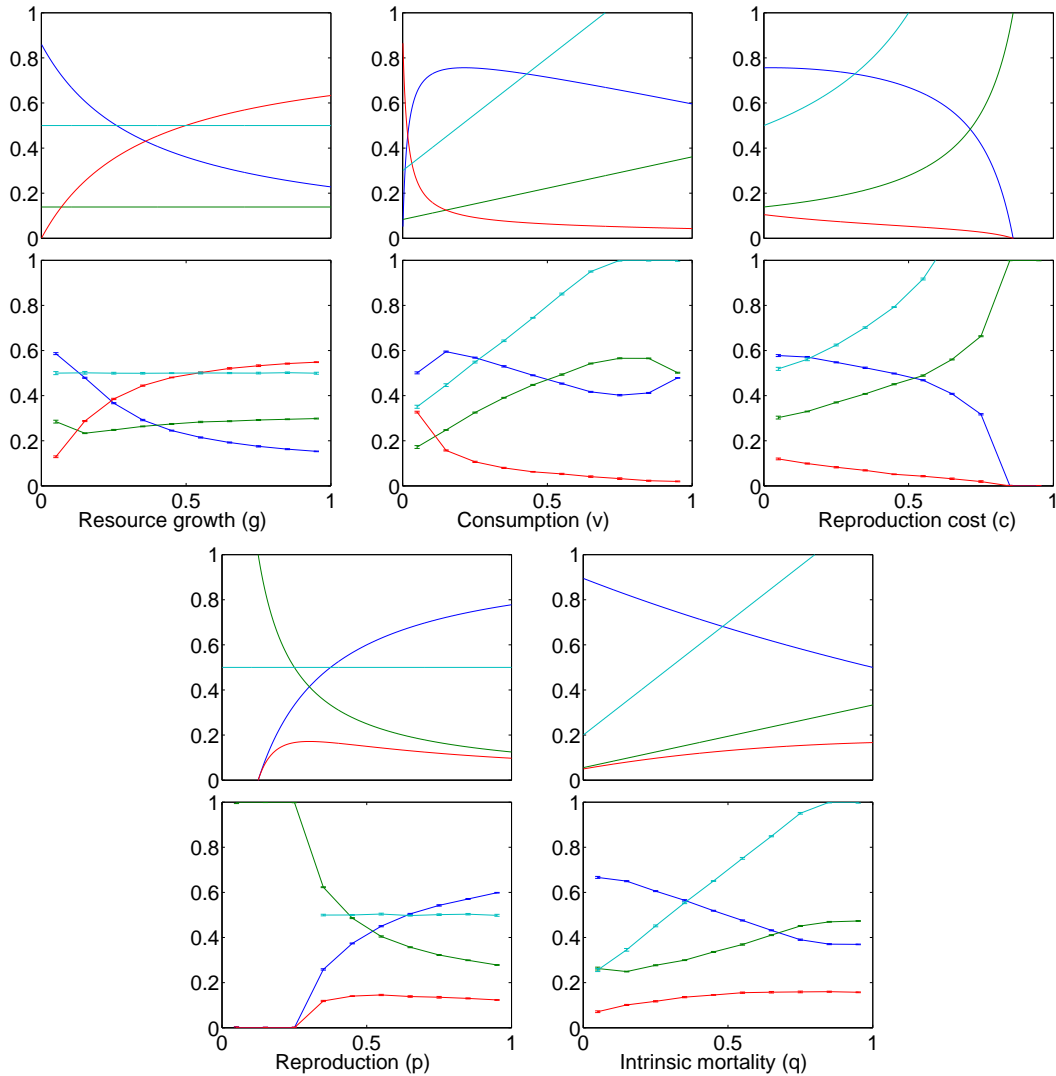


FIG. S3. Mean-field calculations generally predict trends in population levels and net reproduction. Each panel shows the effects of varying one of the five parameters $\{g, v, c, p, q\}$. Mean-field calculations are shown in the top panels, average results from ten independent spatial simulations are shown in the bottom panels. Green = fraction of array occupied by resource sites (n_r), red = fraction of consumers (n_c), blue = fraction empty (n_e), cyan = renormalized consumer reproduction rate (r). In panels other than the one in which they are varied, parameter values are $g = 0.05, v = 0.2, c = 0, p = 0.9, q = 0.3$.

TABLE S1. Mortals dominate immortals in invasion studies. Shown are probabilities of successful invasions for different values of resource growth rate g and consumption rate v (all with reproduction cost $c=0$), and for each combination of mortal and immortal invaders and invaded

$g = 0.05, v = 0.05$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.51 \pm 0.05) \times 10^{-2}$	$(1.0 \pm 0.7) \times 10^{-5}$
	Immortal	$(2 \pm 1) \times 10^{-5}$	0
$g = 0.05, v = 0.1$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(1.91 \pm 0.04) \times 10^{-2}$	$(1.1 \pm 0.3) \times 10^{-4}$
	Immortal	$(1.2 \pm 0.3) \times 10^{-4}$	0
$g = 0.05, v = 0.2$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(1.23 \pm 0.04) \times 10^{-2}$	$(1.6 \pm 0.4) \times 10^{-4}$
	Immortal	$(2.8 \pm 0.5) \times 10^{-4}$	0
$g = 0.1, v = 0.05$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.51 \pm 0.05) \times 10^{-2}$	$(2 \pm 1) \times 10^{-5}$
	Immortal	$(2 \pm 1) \times 10^{-5}$	0
$g = 0.1, v = 0.1$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.38 \pm 0.05) \times 10^{-2}$	$(5 \pm 2) \times 10^{-5}$
	Immortal	$(1.4 \pm 0.4) \times 10^{-4}$	0
$g = 0.1, v = 0.2$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(1.80 \pm 0.04) \times 10^{-2}$	$(1.1 \pm 0.3) \times 10^{-4}$
	Immortal	$(1.1 \pm 0.3) \times 10^{-4}$	0
$g = 0.2, v = 0.05$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.24 \pm 0.05) \times 10^{-2}$	$(2 \pm 1) \times 10^{-5}$
	Immortal	$(3 \pm 2) \times 10^{-5}$	0
$g = 0.2, v = 0.1$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.44 \pm 0.05) \times 10^{-2}$	$(5 \pm 2) \times 10^{-5}$
	Immortal	$(1.1 \pm 0.3) \times 10^{-4}$	0
$g = 0.2, v = 0.2$		Invaded:	
		Immortal	Mortal
Invader:	Mortal	$(2.12 \pm 0.5) \times 10^{-2}$	$(1 \pm 1) \times 10^{-5}$
	Immortal	$(7 \pm 3) \times 10^{-5}$	0