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Overcompensation of transient and permanent death rate increases in age-structured models with cannibalistic interactions

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ABSTRACT

There has been renewed interest in understanding the mathematical structure of ecological population models that lead to overcompensation, the process by which a population recovers to a higher level after suffering a permanent increase in predation or harvesting. Here, we apply a recently formulated kinetic population theory to formally construct an age-structured single-species population model that includes a cannibalistic interaction in which older individuals prey on younger ones. Depending on the age-dependent structure of this interaction, our model can exhibit transient or steady-state overcompensation of an increased death rate as well as oscillations of the total population, both phenomena that have been observed in ecological systems. Analytic and numerical analysis of our model reveals sufficient conditions for overcompensation and oscillations. We also show how our structured population partial integrodifferential equation (PIDE) model can be reduced to coupled ODE models representing piecewise constant parameter domains, providing additional mathematical insight into the emergence of overcompensation.

1. Introduction

Overcompensation, which describes the phenomenon in which the total population of a species increases after experiencing removal or culling [1], has become an increasingly important concept in ecology. This phenomenon, also termed the "hydra effect", states that a population increases in response to an *increased* death or removal rate [1–3]. These overcompensation effects have been shown to arise in European green crab [4], perch [5], and *Tribolium* beetles [6,7]. Overcompensation to selective harvesting is often seen in many tree [8] and fish populations [9,10]. Apical dominance in botany [11,12], whereby a central stem dominates secondary stems can also give rise to a type of pruning-induced overcompensation.

There are multiple hypotheses for the mechanism underlying overcompensation, including the removal of apical dominance [13–15] in plant stem populations, development of resistance to herbivory [16] in plant populations, reduction of competition or cannibalism in animal populations [4,17], and stage-specific interactions [6,7,18,19]. Other attempts to explain overcompensation also often rely on the interplay between multiple species, including consumer-resource competition. For example, a three-compartment consumer-resource model which tracks the amount of food, the number of predators, and the food consumption rate has been used to construct a model exhibiting "overcompensation" arising in the form of time-periodic increases and decreases of the total predator population [20]. Extensions of such consumer-resource models that incorporate intraspecific cannibalism in which adults prey on juveniles when food is scarce have also been used to demonstrate overcompensation [21]. Such consumer-resource models are constructed for animal populations and assume overcompensation arises when resources are abundant.

However, a recent biological/experimental report suggested that overcompensation can arise solely from intraspecific interactions, especially cannibalism [4,6,7,18,22]. This motivates us to provide a mathematical characterization of cannibalism-induced overcompensation. Single-species discrete-time stage-specific models have been proposed and shown to exhibit overcompensation as well as periodic and even chaotic dynamics [19,23]. Recently, [18] developed a continuous-time version of these models based on prior stage-specific models [24–26]. These models have been shown to exhibit nontrivial sustained oscillations through a Hopf bifurcation. But whether and how overcompensation may arise from such age-specific interactions are simply characterized.

Here, we generalize stage-specific models [24–26] by formulating a simple age-structured partial integrodifferential equation (PIDE) model

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with a general cannibalistic interaction that allows us to more formally study overcompensation. Our structured PIDE model will be developed from a high-dimensional kinetic/stochastic theory of age-structured cannibalistic interactions, which can formally be projected onto an age-structured logistic-growth-type PIDE model. Although continuous time and continuous-age PIDE models have been proposed [6,7], they have been lumped into discrete age bins before analysis. Population oscillations can arise in these lumped models, but they have not been analyzed in the context of overcompensation.

Our generalized PIDE model is easily solved numerically, allowing us to evaluate both its dynamics and how oscillations and overcompensation, transient or permanent, arise. Distinct from previous consumer-resource models [20,21,27,28], we show that our PIDE model can exhibit a rich variety of overcompensating dynamics that arises from intraspecific interactions alone, without being triggered by external factors such as an increase in resources. Mathematically, logistic-type discrete-stage self-inhibition models [29,30] have been shown to also give rise to undamped population oscillations.

Besides analyzing our age-structured PIDE model, we also reduce it to a set of coupled ODEs that more closely resemble multispecies or multistage ecological population models. We will discuss and compare the qualitative differences between an age-structured model and a stage-structured model in the overcompensation setting. For example, in [18], overcompensation is found to arise in a simple two-compartment–young and old populations–ODE model. In our structured population model, we show that a two-compartment ODE reduction does not admit overcompensation of an increase in death rate if the birth rates are kept constant, but that three or more compartments can.

In fact, our age-structured interacting model, as well as its ODE-system approximation, can exhibit rich behavior including dynamic and permanent overcompensation of increases in the death rate and the emergence of transient or permanent population oscillations following the loss of stability of a positive stable point [31]. These dynamics allow us to quantitatively distinguish *transient overcompensation*, where the total population temporarily increases following a *temporary* increase in death rate, from permanent, steady-state overcompensation, in which a permanent increase in death leads to a permanent increase in the total population.

In the next section, we develop a nonlinear single-species age-structured model that describes interactions such as cannibalism in animal populations. Numerical experiments are carried out in Section 3 to explore conditions under which overcompensation arises and to validate previous experimental findings. We also explicitly show how our age-structured PIDE model can be “discretized” into systems of ODEs, allowing us to derive additional corresponding conditions for overcompensation and oscillating populations. We give concluding remarks and discuss some future directions in the Summary and Conclusions section.

2. Age-structured intraspecies predation model

Motivated by the above real-world ecological examples, we formally construct a simple single-species age-structured population PIDE model for cannibalization that can lead to overcompensation. We start with a *linear* kinetic theory framework that was recently developed to describe the evolution of a probability density of proliferating cell populations [32–34]. To track all ages in a population, we define the vector $\mathbf{x}_s = (x_1, \dots, x_s)$ in which x_i is the age of the ith individual and s is the total number of individuals.

We denote the probability that an animal population has s individuals with ages $\mathbf{x}_s$ at time t to be $\rho_s(\mathbf{x}_s;t)$. Without loss of generality, we assume that the probability ρ_s is symmetric in the age variables, *i.e.*, for any permutation of $(x_1, \dots, x_s)$ denoted by $\mathbf{x}'_s$, $\rho_s(\mathbf{x}_s;t) = \rho_s(\mathbf{x}'_s;t)$. Normalization of $\rho_s(\mathbf{x}_s;t)$ also demands $\sum_{s=0}^{\infty}\int_0^{\infty}\rho_s(\mathbf{x}_s;t)\mathrm{d}\mathbf{x}_s \equiv 1,\ \forall\ t$. If we denote the birth rate and death rate for the ith individual in the population by β_i and μ_i respectively, $\rho_s(\mathbf{x}_s;t)$ satisfies the following PIDE [33]

$$\begin{aligned}
&\frac{\partial \rho_s(\mathbf{x}_s;t)}{\partial t} + \sum_{i=1}^{s}\frac{\partial \rho_s(\mathbf{x}_s;t)}{\partial x_i} = \\
&\qquad -\sum_{i=1}^{s}\big(\beta_i + \mu_i\big)\rho_s(\mathbf{x}_s;t) + \sum_{i=1}^{s+1}\int_0^{\infty}\mu_i\,\rho_{s+1}(\mathbf{x}_{s+1}[x_i = y];t)\mathrm{d}y \\
&\rho_s(\mathbf{x}_s[x_i = 0],t) = \frac{1}{s}\sum_{j=1}^{s-1}\beta_j\,\rho_{s-1}(\mathbf{x}_{s,-i};t),
\end{aligned} \tag{1}$$

where $\mathbf{x}_{s+1}[x_i = y] := (x_1, \dots, x_i = y, x_{i+1}, \dots, x_{s+1})$, $\mathbf{x}_s[x_i = 0] := (x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_s)$, and $\mathbf{x}_{s,-i} := (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_s)$. Details of the derivation of the linear kinetic equation (1) are given in [32–34].

The birth and death rates β_i and μ_i, may depend on the ages of individuals $x_{j\neq i}$ other than that of the ith one. Such multi-individual dependences of β_i, μ_i lead to correlations and ultimately nonlinear terms. Here, we assume the birth rate $\beta_i = \beta(x_i,t)$ of individual i depends on only the age x_i of that individual. The death rate can be decomposed into a natural death rate and a cannibalistic interaction term, *i.e.*,

$$\mu_i = \mu(x_i,t) + \sum_{j\neq i} K(x_j, x_i, t), \tag{2}$$

where $\mu(x_i,t)$ is the natural death rate of individual i and $K(x_j, x_i, t)$ is the cannibalizing rate of individual j on individual i. Note that $K(x_j, x_i, t)$ can depend on both the ages of the predator and the prey, which generalizes the previous model in [27] where K only depends on the prey’s age.

With these definitions, the PIDE satisfied by ρ_s becomes

$$\begin{aligned}
&\frac{\partial \rho_s(\mathbf{x}_s;t)}{\partial t} + \sum_{i=1}^{s}\frac{\partial \rho_s(\mathbf{x}_s;t)}{\partial x_i} = \\
&\qquad -\sum_{i=1}^{s}\left[\beta\big(x_i,t\big) + \mu(x_i,t) + \sum_{j\neq i}K(x_j,x_i,t)\right]\rho_s(\mathbf{x}_s;t) \\
&\qquad + (s+1)\int_0^{\infty}\left[\mu(y,t) + \sum_{i=1}^{s}K(x_i,y,t)\right]\rho_{s+1}(\mathbf{x}_s,y;t)\mathrm{d}y \\
&\rho_s(\mathbf{x}_s[x_i = 0],t) = \frac{1}{s}\sum_{j=1}^{s-1}\beta\big(x_j,t\big)\rho_{s-1}(\mathbf{x}_{s,-i};t),
\end{aligned} \tag{3}$$

and the argument $(\mathbf{x}_s, y)$ indicates an additional $(s+1)$st individual with age y.

The population density at age x can thus be defined as a sum over all possible numbers of individuals and marginalizing over all but one age:

$$n(x,t) := \sum_{s=0}^{\infty} s\int \rho_s(\mathbf{x}_s[x_1 = x];t)\mathrm{d}\mathbf{x}_{s,-1}. \tag{4}$$

We now show that the dependence of K on both x_j and x_i generates nonlinear population dynamics that can give rise to overcompensation of increased death as well as oscillations. Upon applying the marginalization and summation of Eq. (4) to Eq. (3), we obtain a PIDE satisfied by $n(x,t)$:

$$\begin{aligned}
&\frac{\partial n(x,t)}{\partial t} + \frac{\partial n(x,t)}{\partial x} \\
&\qquad = -\mu(x,t)n(x,t) - \int_0^{\infty}K(x',x,t)n^{(2)}(x',x,t)\mathrm{d}x', \\
&n(0,t) = \int_0^{\infty}\beta(x,t)n(x,t)\mathrm{d}x.
\end{aligned} \tag{5}$$

where

$$n^{(2)}(x',x,t) := \sum_{s=0}^{\infty}s(s-1)\int \rho_s(\mathbf{x}_s[x_1 = x', x_2 = x];t)\mathrm{d}\mathbf{x}_{s,-2}. \tag{6}$$

and $\mathbf{x}_{s,-2} := (x_3, \dots, x_s)$. Specifically, if the correlation between x and x' is small, and $s \gg 1$, we can approximate $n^{(2)}(x',x,t) \approx n(x',t)n(x,t)$

and obtain a closed-form PIDE for $n(x,t)$:

$$\begin{aligned}\frac{\partial n(x,t)}{\partial t}+\frac{\partial n(x,t)}{\partial x}&=-\left[\mu(x,t)+\int_0^\infty K(x',x,t)n(x',t)\mathrm{d}x'\right]n(x,t),\\ n(0,t)&=\int_0^\infty \beta(x,t)n(x,t)\mathrm{d}x.\end{aligned}\tag{7}$$

Eq. (7) is the most general form of a simple deterministic model that incorporates a continuously distributed predator–prey interaction within an age-structured population model [35,36]. Here, the quadratic interaction term couples predator and prey populations through the predation kernel $K(x',x,t)$. Previous analyses of (7) and related equations used them to model cannibalism [22,37], particularly egg–larvae interactions of the *Tribolium* beetle [6,7]; however, these studies did not derive the equations from the underlying kinetic theory as we have shown above nor did they analyze overcompensation in response to increased death as we will in the next section.

If $K(x',x,t)=0$, Eq. (7) reduces to the classical age-structured McKendrick model, which does not exhibit permanent overcompensation. If $K(x',x,t) := k(x,t)\delta(x'-x)$, where δ is the Dirac delta function, Eq. (7) coincides with previously studied age-structured growth models [29,30], reducing to

$$\begin{aligned}\frac{\partial n(x,t)}{\partial t}+\frac{\partial n(x,t)}{\partial x}&=-\Big(\mu(x,t)+k(x,t)n(x,t)\Big)n(x,t),\\ n(0,t)&=\int_0^\infty \beta(x,t)n(x,t)\mathrm{d}x.\end{aligned}\tag{8}$$

As we will be interested primarily in steady-state overcompensation, or population transients associated with instantaneous jumps in the death rate, we will restrict our analysis to time-independent $K(x',x)$ and instantaneous changes to otherwise time-independent $\beta(x)$ and $\mu(x)$. Dynamically, changing birth and death rates can be implemented by changing β and μ instantaneously to new values that subsequently remain constant (time-independent). Thus, we will henceforth assume time-independent β,μ (and K) after their abrupt change. If a steady-state population density $n^*(x)$ is reached, it will then satisfy

$$\begin{aligned}\frac{\mathrm{d}n^*(x)}{\mathrm{d}x}&=-\left[\mu(x)+\int_0^\infty K(x',x)n^*(x')\mathrm{d}x'\right]n^*(x),\\ n^*(0)&=\int_0^\infty \beta(x)n^*(x)\mathrm{d}x.\end{aligned}\tag{9}$$

Under this setup, we will show that for our model to display steady-state overcompensation associated with increased death rate, an interaction kernel $K(x',x)$ that varies with both x' and x is necessary.

Incidentally, we note that our PIDE model Eq. (9) can be simply extended to describe populations over structured variables x that represent quantities other than age. For example, if x represents organism size instead of age, it may follow a growth law

$$\frac{\mathrm{d}x}{\mathrm{d}t}=g(x,t).\tag{10}$$

Using a similar derivation starting from the multiparticle kinetic theory for the probability density, we obtain an equation for the population density $n(x,t)$ that is similar to Eq. (7)

$$\begin{aligned}\frac{\partial n(x,t)}{\partial t}+&\frac{\partial (g(x,t)n(x,t))}{\partial x}\\ &=-\left[\mu(x,t)+\int_0^\infty K(x',x,t)n(x',t)\mathrm{d}x'\right]n(x,t),\\ g(0,t)n(0,t)&=\int_0^\infty \beta(x,t)n(x,t)\mathrm{d}x.\end{aligned}\tag{11}$$

Thus, the dynamics of a population structured according to variables such as size or weight can be analyzed using Eq. (11).

However, if $\frac{\mathrm{d}x}{\mathrm{d}t}=g(x)$ (time-inhomogeneous growth), then by defining $y=\int_0^x \frac{1}{g(z)}\mathrm{d}z$, $\mathrm{d}y=\mathrm{d}t$, and the new structured variable y could be seen as an age. In this scenario, we shall obtain a differential equation for $n(y,t)$

$$\begin{aligned}\frac{\partial n(y,t)}{\partial t}+\frac{\partial n(y,t)}{\partial y}&=-\left[\mu(y,t)+\int_0^\infty K(y',y,t)n(y',t')\mathrm{d}y\right]n(y,t),\\ n(0,t)&=\int_0^\infty \beta(y,t)n(y,t)\mathrm{d}y.\end{aligned}\tag{12}$$

which is identical in form to Eq. (7). For simplicity and without loss of generality, we henceforth explore overcompensation in a population structured according to age or according to an attribute that grows in a time-inhomogeneous manner, allowing us to use Eq. (8) or (12).

3. Results and discussion

Overcompensation of the total population can be reflected as a transient increase in the overall population following a transient increase in μ, as a permanent change in the steady-state population and/or as a periodically fluctuating population following permanent increases in the death rate. Although the general conditions on $K(x',x)$ required for the model to exhibit overcompensation and/or oscillations cannot be analytically derived, we present several cases that preclude or allow overcompensation. We also present a piecewise constant function approximation to convert our PIDE model to a system of ODEs, further providing mathematical insight into the dynamical behavior of our model.

3.1. Specific interactions that preclude overcompensation

Here, we consider permanent changes in the birth and death rates β,μ and present simple interactions $K(x',x)$ for which permanent, steady-state overcompensation can be proven not to arise:

(*A.1*) $K(x',x)=k(x)\delta(x'-x), k(x)>0$. Correspondingly, Eq. (9) reduces to $\mathrm{d}n^*/\mathrm{d}x=-\mu(x)n^*-k(x)(n^*)^2$, $n^*(x=0)=\int_0^\infty \beta(x)n^*(x)\mathrm{d}x$.

(*A.2*) $K(x',x)=K(x')$ with constant β,μ. This interaction is independent of prey age x and the resulting model corresponds to an age-structured McKendrick model with a modified death rate $\mu\to\mu+\int_0^\infty K(x')n(x')\mathrm{d}x$ as proposed in [30].

(*A.3*) $K(x',x)=K(x)$ with constant β,μ. This case corresponds to predators of any age x' preferentially cannibalizing prey of age x according to $K(x)$. With this interaction kernel, Eq. (7) reduces to a self-consistent McKendrick equation, as in (ii), except with a modified death rate $\mu\to\mu+K(x)N^*$. A uniform interaction kernel (constant K) is a subcase.

Here, $\delta(x)$ is the Dirac delta distribution and $\theta(x>0)=1, \theta(x\le 0)=0$ denotes the Heaviside function. All of these cases admit simple, unique, nonzero steady states. The corresponding reduced models of cases (*A.1*), (*A.2*), and (*A.3*) all admit simple self-consistent solutions. For constant birth and death rates β and μ, we prove in Appendix A that interactions (*A.1*), (*A.2*), and (*A.3*) all preclude steady-state overcompensation; that is, the total steady-state population $N^*\equiv\int_0^\infty n^*(x)\mathrm{d}x$, where n^* is the steady-state solution of Eq. (9), does not increase when μ increases. Case (*A.1*) indicates that a more distributed kernel is required for overcompensation. Case (*A.2*) indicates that variation in predator age x' alone is insufficient to generate steady-state overcompensation. Case (*A.3*) represents an interaction kernel that varies only in prey age x and is also insufficient to generate steady-state overcompensation. These results imply that steady-state overcompensation requires $K(x',x)$ that varies to some degree in both the prey age x and predator age x'.

3.2. Specific interactions that may exhibit overcompensation

We have also found two simple forms for $K(x',x)$ that may exhibit steady-state overcompensation

Table 1

A list of analytic forms of $K(x',x)$ that we have investigated in the context of overcompensation under certain conditions.

Form of $K(x',x)$	Overcompensation	Analysis
$k(x)\delta(x'-x)$	Not possible	Analytical
$K(x')$	Not possible	Analytical
$K(x)$	Not possible	Analytical
$k\delta(x-a)\delta(x'-b)$	Possible	Analytical
$k\delta(x)\theta(x'-b)$	Possible	Analytical
$\theta(x'-X)\theta(X-x)$	Possible	Numerical
$x'\theta(x'-X)\theta(X-x)$	Possible	Numerical
$(x'-x)\theta(x'-X)\theta(X-x)$	Possible[a]	Numerical

[a] Indicates that the total population is fluctuating over time but that the time-averaged population exhibits overcompensation in response to increases in the death rate.

(*B.1*) $K(x',x) = k\delta(x-a)\delta(x'-b)$, with $\beta > \mu, k > 0$ constant. Under this point-source and point-sink interaction, the steady-state equation is $\mathrm{d}n^*/\mathrm{d}x = -\big[\mu + kn^*(b)\delta(x-a)\big]n^*$, which is solved by $n^*(x) = n^*(x=0)e^{-\mu x - kn^*(b)\theta(x-a)}$,

(*B.2*) $K(x',x) = k\delta(x)\theta(x'-b)$ with constant $\beta > \mu, k > 0$. The interaction describes adults with age $x \geq b$ feeding, with rate k on newborns or eggs. The steady-state ODE becomes $\mathrm{d}n^*/\mathrm{d}x = -\big[\mu + \int_b^\infty kn^*(x')\delta(x)\mathrm{d}x'\big]n^*(x)$, which is solved by $n^*(x) = n^*(0)e^{-\mu x - kN_\mathrm{b}}$ with $N_b := \int_b^\infty n^*(x)\mathrm{d}x$.

Appendix B provides detailed calculations of the total population under models (*B.1*) and (*B.2*). Further analysis shows the conditions (parameter regimes of μ, k, β) under which steady-state overcompensation, $\partial N^*/\partial\mu > 0$, arises.

Table 1 summarizes the different forms of the cannibalism rate functions $K(x',x)$ for which we have analytically or numerically demonstrated either the possibility or impossibility of overcompensation. All results are obtained using age-independent birth and death rates β and μ.

3.3. Existence and uniqueness of the positive steady state

The specific forms of $K(x',x)$ given above that either preclude or allow overcompensation provides some mechanistic insight into the interaction that can give rise to overcompensation. Roughly, the interaction kernel $K(x',x)$ should have a positive gradient in the x' direction and a negative gradient in the x direction. This asymmetry in $K(x',x)$ leads to sufficient suppression of the older, predating population such that a "killing of the killers" effect leads to larger total populations.

Henceforth, we consider a fairly general form for $K(x',x)$ that incorporates the dependencies on both x' and x that is compatible with overcompensation:

$$K(x',x) = 0, \ \ \forall x \geq X, \ \ \text{or} \ \ x' \leq x. \tag{13}$$

Here, X is an age threshold such that no individual above age X can be cannibalized. In Appendix C, we prove that given time-independent $\beta(x), \mu(x)$ our model (Eqs. (7) and (9)) admits one unique steady state n^* under some conditions. Thus, for a transient perturbation of the birth and death rates (which eventually return to their constant pre-perturbation values) permanent overcompensation of the population cannot arise. The system has no other accessible steady state and the total population returns to its unique steady-state value, provided it does not vanish during its transient evolution. However, abrupt, permanent increases in the death rate may lead to permanent overcompensation as the new steady state associated with higher μ may be associated with a higher total population $N^* = \int_0^\infty n^*(x,t)\mathrm{d}x$. In Appendix D, we discuss general characterization/conditions for existence of the positive steady state.

3.4. Overcompensation of increased death rates

Since analytically finding all conditions under which Eq. (7) or Eq. (9) exhibits overcompensation is difficult, we shall carry out numerical experiments to show how overcompensation arises for some simple forms of $K(x',x)$ after instantaneous changes in β and μ from one constant value to another. In general, we find that a cannibalism interaction K that decreases with x and increases with x' is more likely to exhibit larger overcompensation. We examine two simple forms of K: $K_1(x',x) = k\theta(x'-X)\theta(X-x)$ and $K_2(x',x) = kx'K_1(x',x) = k^2x'\theta(x'-X)\theta(X-x)$, both of which satisfy Eq. (13). Since k is a rate, we can measure β and μ in units of k and time t and ages x in units of $1/k$. In such units, we set $k=1$ without loss of generality and the dimensionless interactions take the forms

$$\begin{aligned} K_1(x',x) &\equiv \theta(x'-X)\theta(X-x), \\ K_2(x',x) &\equiv x'K_1(x',x) \\ &= x'\theta(x'-X)\theta(X-x). \end{aligned} \tag{14}$$

For concreteness, we choose $X=2$ and plot heatmaps of the dimensionless predation kernels K_1 and K_2 in Fig. 1(a) and (e). Subsequent results derived from using these interactions are displayed across each row.

The analysis of steady-state overcompensation boils down to investigating how the solution n^* obeying Eq. (9), and in particular, how the total population $N^* = \int_0^\infty n^*(x)\mathrm{d}x$ changes with β and μ. Fig. 1(b) and (f) are heatmaps of the total steady state population N^* as a function of birth rate β and death rate μ, for K_1 and K_2, respectively. These solutions $N^* = \int_0^\infty n^*(x)\mathrm{d}x$ are derived from the solution to Eq. (9). Note that when $\beta < \mu$, the only stable steady state is $n^*(x), N^* = 0$. The dashed curves in Fig. 1(b) and (f) are "phase boundaries" defined by $\partial_\mu N^* = 0$ that separate parameter space into regimes where $\partial_\mu N^* < 0$ from those where $\partial_\mu N^* > 0$. At larger values of μ (and smaller β) N^* decreases with μ, indicating the absence of overcompensation, or a normal response. However, at larger β and smaller μ, $\partial_\mu N^* > 0$ indicating overcompensation in response to increases in μ. Fig. 1(c) and (g) show the corresponding curves $N^*(\mu)$ for fixed values of β, quantitatively illustrating the different magnitudes of steady-state overcompensation through different values of the slope $\partial_\mu N^*$. These results, along with the interactions shown to preclude long-lasting overcompensation, indicate that permanent overcompensation in our model requires cannibalization of the young by the old and a $K(x',x)$ that increases in x' and decreases in x.

To interrogate the dynamics of the population following perturbations to the death rate, we now start the system at its steady state corresponding to specific values β_0, μ_0 and consider how the population $N(t)$ evolves after applying these two different perturbations:

$$\mu_1(t) = \mu_0 + (\log 2)\delta(t), \quad \mu_2(t) = \mu_0 + \theta(t)\Delta\mu. \tag{15}$$

To be specific, we take $\beta_0 = 2$, $\mu_0 = 1/2$, and $\Delta\mu = 1/2$. The death rate function $\mu_1(t)$ includes a delta function at $t=0$, which corresponds to an instantaneous removal of half the population from the steady state associated with β_0, μ_0 and the corresponding interaction K. A finite volume discretization [38] with $\Delta x = 0.02, x_{\max} = 10, \Delta t = 0.002$ was used to numerically solve Eq. (7) to find $n(x,t)$, which is then used to construct $N(t) = \int_0^\infty n(x,t)\mathrm{d}x$. Fig. 1(d) and (h) show damped oscillations in $N(t)$ associated with K_1 and $K_2 = x'K_1$, respectively. Although $\mu_1(t)$ immediately returns to the value $\mu_1(t>0) = \mu_0$, and $N(t\to\infty) \to N^*$, at shorter times, $N(t)$ oscillates and can exceed N^* at intermediate times. Thus, *transient overcompensation* can arise even though the population returns to the same value set by β_0, μ_0. If $\mu_2(t)$ is used, the death rate jumps from μ_0 to $\mu_0 + \Delta\mu$ at $t=0$, leading ultimately to a higher steady-state population. For μ_2, in addition to a higher steady-state population, initial oscillations can lead to even higher transient populations.

Motivated by these results showing that N^* can increase upon increasing μ for fixed values of β, we provide in Appendix E additional

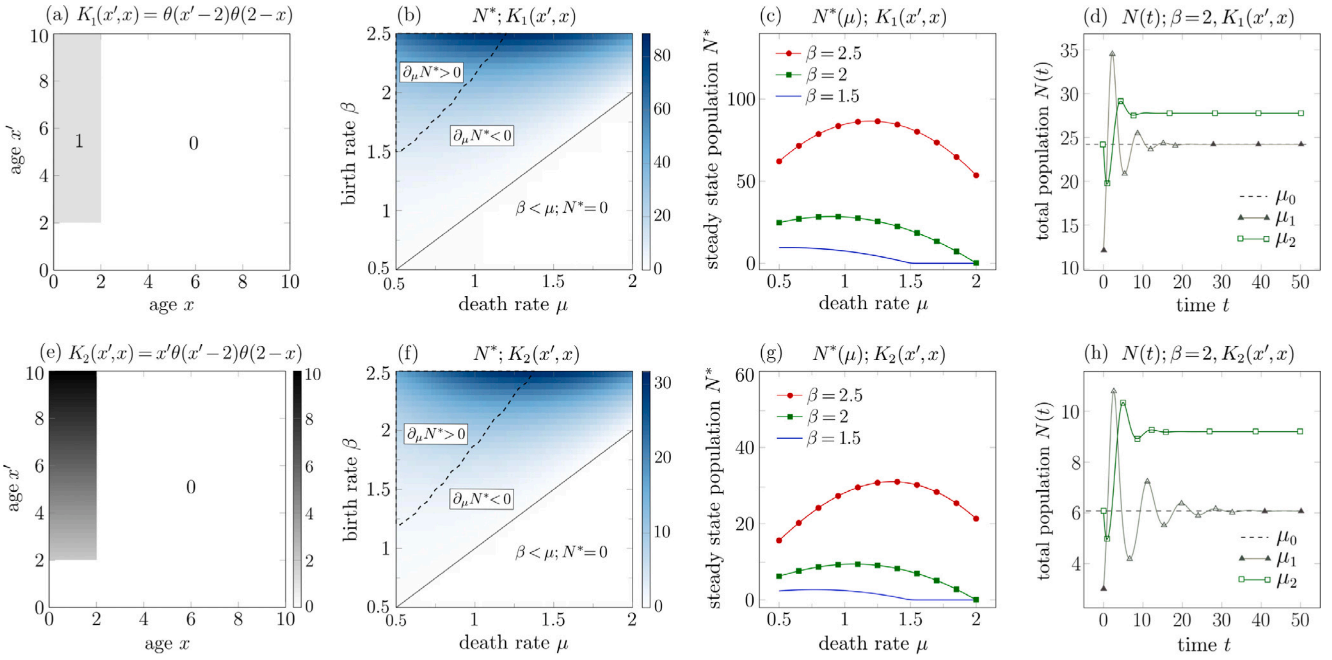

Fig. 1. (a) Heatmap of the dimensionless predation interaction $K_1(x',x) = \theta(x'-2)\theta(2-x)$. (b) Heatmap of the total steady-state population N^* as a function of constant β and μ. A nontrivial stable fixed point arises only for $\beta > \mu$. The region of no overcompensation, where $\partial_\mu N^* < 0$, is indicated while the parameters that admit steady-state overcompensation, where $\partial_\mu N^* > 0$ (not indicated), occur in the upper-left corner. The dashed curve delineates the phase boundary on which $\partial_\mu N^* = 0$. (c) N^* plotted as a function of μ for fixed values of $\beta = 2.5, 2, 1.5$. (d) Plots of $N(t)$ for $\beta = 2$ and death rate sequences $\mu_1(t)$ and $\mu_2(t)$ (Eq. (15)). For $\mu_1(t)$, damped oscillations yield transient overcompensation, while $\mu_2(t)$ results in a permanent, steady-state overcompensation, in addition to damped oscillations. (e-h) The corresponding results for $\beta = 2$ and the predation/cannibalization interaction $K_2(x',x) = x'K_1(x',x)$.

examples of mechanisms whereby a steady-state overcompensation can arise. First, we consider overcompensation in a model where resources are scare and predation can provide nourishment required for reproduction. This effect can be modeled by a predation-enhanced fecundity of the form $\beta(x) = \beta_0 + (\frac{1}{4})\int_0^\infty K(x,x')n(x',t)\mathrm{d}x'$. This model is shown to preserve overcompensation associated with increases in μ, as detailed in Appendix E.1.

We also show in Appendix E.2 that age-dependent harvesting can lead to overcompensation. Harvesting or culling of the population that is modeled via an additional removal term

$$\frac{\partial n(x,t)}{\partial t} + \frac{\partial n(x,t)}{\partial x} = -\left[\mu(x,t) + \int_0^\infty K(x',x)n(x',t)\mathrm{d}x'\right]n(x,t) - h(n;x,t), \qquad (16)$$

$$n(0,t) = \int_0^\infty \beta(x)n(x,t)\mathrm{d}x,$$

where $h(n;x,t)$ represents the rate of harvesting that may depend nonlinearly on the structured population. Increases in a realistic harvesting function $h(n;x,t)$ are shown to lead to permanent increases in the total population. Finally, we also prove in Appendix E.3 that for an interaction that satisfies Eq. (13), increasing a constant β will always lead to an increase in N^*; however, for asymmetric predation kernels that can be negative (a young-eat-old interaction), overcompensation in response to increased birth rates, where $\partial_\beta N^* < 0$ for fixed values of μ, can arise.

3.5. *Undamped oscillations*

The instantaneous changes in the death rate given by Eqs. (15) and the interactions K_1 and K_2 give rise to damped oscillations that eventually settle back to their corresponding unique values N^*. However, oscillations may be undamped and lead to *periodic overcompensation* when the fixed point loses stability and bifurcates to a stable limit cycle. Such oscillations have been observed, for example, in European green crabs populations [4]. Although the source of such oscillations may be difficult to disentangle from the effects of seasonality, they have been modeled in different contexts using a single-compartment *discrete-time* population model [31]. Overcompensation has also been described in consumer-resource models, as cycles of rising and falling populations [20], as in the classical predator–prey model.

Here, we use a simple, realistic old-eat-young cannibalization rate

$$K_3(x',x) = (x'-x)\theta(x'-2)\theta(2-x) \qquad (17)$$

in Eq. (7) and assume constant birth rate β and death rate μ. Upon using a finite volume discretization with $\Delta x = 0.01$ and initial condition $n(x,0) = e^{-2x}/2$, we numerically solve Eq. (7) in $t \in [0,T]$, $\Delta t = 0.002$ to investigate whether the total population $N(t)$ oscillates. Fig. 2(a) shows the heatmap of the interaction kernel $K_3(x',x) = (x'-x)\theta(x'-2)\theta(2-x)$, while Fig. 2(b) shows a heatmap of an oscillating structured population density $n(x,t)$ approximated by its local mean value $n(j,t) = (\Delta x)^{-1}\int_{j\Delta x}^{(j+1)\Delta x} n(y,t)\mathrm{d}y$. These oscillations lead to an oscillating total population $N(t)$, as shown in Fig. 2(c). Oscillations damp out when μ is large, but persist for smaller values of μ. The long-time amplitudes of oscillation shown in Fig. 2(d) indicate a sharp decrease as μ is increased. To better resolve the long-time average values of $N(t)$, we define its function average $\overline{N}(t) \equiv \frac{1}{t}\int_0^t N(s)\mathrm{d}s$ and plot them in Fig. 2(e). Besides oscillations that can lead to temporary overcompensation, increasing μ in the regime studied also led to increased averaged values of $N(t)$, and in particular, when oscillations are damped out at larger μ, permanent overcompensation can arise where the steady values N^* increase with μ. Thus, as μ increases, periodic overcompensation transitions to steady-state overcompensation. The phase diagram separating regimes of transient and permanent oscillations is shown in Fig. 2(f). As β increases and μ decreases, the dynamics transition from a monotonically converging one (to steady-state value N^*) to a periodically oscillating one, with a finite oscillation magnitude that arises when β exceeds a critical value $\beta_* \approx 1.87 + 0.93\mu$.

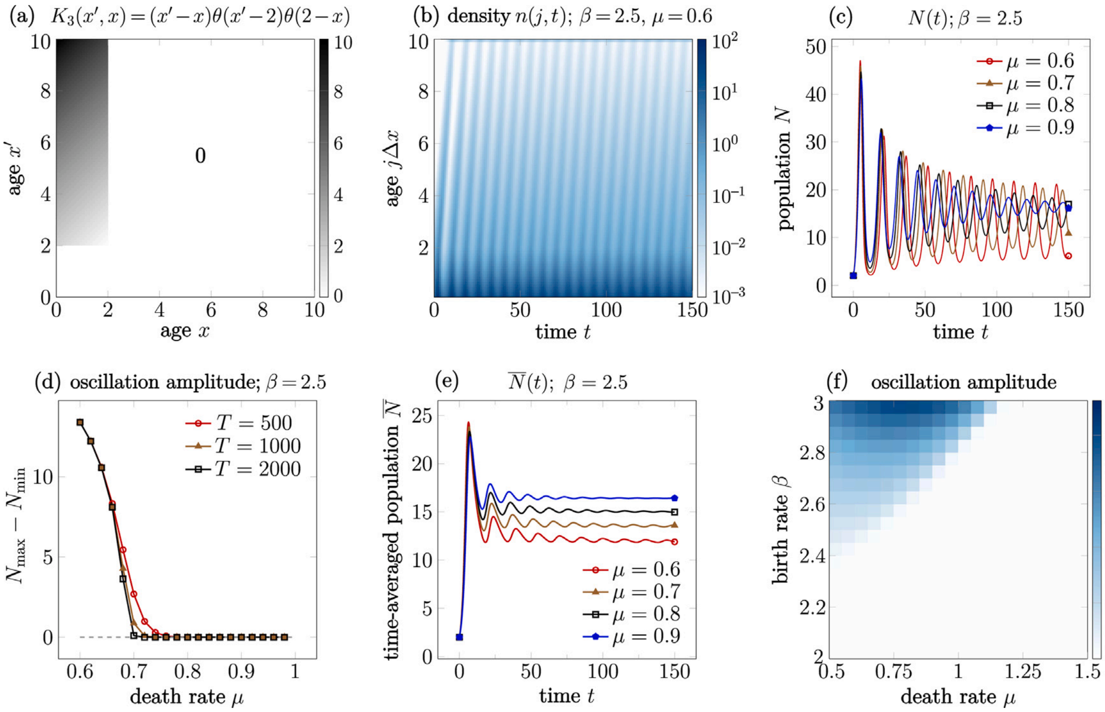

Fig. 2. (a) Heatmap of the interaction kernel $K_3(x',x) = (x'-x)\theta(x'-2)\theta(2-x)$ (Eq. (17)). (b) The population density computed using Eq. (17), $\beta = 2.5$, and $\mu = 0.6$, and approximated as $n(j,t) \equiv (\Delta x)^{-1}\int_{j\Delta x}^{(j+1)\Delta x} n(y,t)\mathrm{d}y$ with $\Delta x = 0.02$ displays persistent periodic oscillations. (c) The total population $N(t) = \int_0^\infty n(x,t)\mathrm{d}x$ also exhibits oscillations that persist(damp out) for small(large) values of μ. (d) The long-time oscillation amplitude $\max_{T-20\leq t\leq T} N(t) - \min_{T-20\leq t\leq T} N(t)$ near $T = 500$, $T = 1000$, and $T = 2000$, respectively, plotted as a function of μ ($\beta = 2.5$). As T is increased, the transition to oscillating states as μ is decreased becomes sharper These numerical results suggest that the transition at $\mu \sim 0.7$ has jump discontinuity in the first-order derivative. (e) Time-averaged populations $\overline{N}(t) \equiv \frac{1}{t}\int_0^t N(s)\mathrm{d}s$ for $\beta = 2.5, \mu = 0.6, 0.7, 0.8, 0.9$ that more clearly reveal the mean values of $N(t \to \infty)$. (f) Oscillation amplitude in β-μ space. As β increases from 2 to 3 and μ decreases from 1.5 to 0.5, undamped oscillations arise. Here, the oscillation amplitudes are measured by $\max_{480<t\leq 500} N(t) - \min_{480<t\leq 500} N(t)$. In the regime plotted, we find that undamped oscillations arise for $\beta \gtrsim 1.87 + 0.93\mu$.

3.6. Reduction of structured population PIDE to ODE systems

We have provided some numerical examples which explicitly show various types of overcompensation in response to variations in constant μ, β. However, our model can also be approximated via coarse-graining and discretization and formulated in terms of a system of coupled nonlinear ODEs. Systems of ODEs are typically used to describe multispecies models in which previous studies have found overcompensation. Multistage models in which, *e.g.*, adult or later-stage insect feed on eggs or early-stage individuals [39,40] can also be directly modeled by our discrete stage discretized ODEs.

Since the analysis of the general nonlinear PIDE model Eq. (7) or the steady-state integral–differential equation Eq. (9) is difficult and uniqueness only under Eq. (13) and a few specific proofs of cases that preclude overcompensation could be found (see Appendix A), related analyses of the ODE system can be more easily performed [18,41] if parameters and variables are considered to be piecewise constants. In addition to providing mathematical insight into the approximate, lower dimensional ODE system, the simplest numerical implementation of a finite volume method for the PIDE model Eq. (7) is conceptually similar to piecewise constant discretization in the age variable.

Here, we formally discretize our PIDE model and explore whether the resulting ODE models exhibit the analogous behaviors of the full PIDE model discussed above. We discretize the space of ages $[0,\infty)$ into $L+1$ bins: $[x_i, x_{i+1})$, $i = 0,\ldots,L$ where $x_i = i\Delta x$ if $i \leq L$, and $x_{L+1} = \infty$. Let the population on the ith bin $[x_i, x_{i+1})$ be denoted $n_i(t) = \int_{x_i}^{x_{i+1}} n(y,t)\mathrm{d}y$, $(x_{L+1} \to \infty)$. By integrating Eq. (7) over increments, each n_i obeys

$$\begin{aligned}\frac{\mathrm{d}n_i}{\mathrm{d}t} &= n(x_i,t) - n(x_{i+1},t) - \int_{x_i}^{x_{i+1}} \mu(x,t)n(x,t)\mathrm{d}x \\ &\quad - \int_{x_i}^{x_{i+1}}\mathrm{d}x \int_x^\infty \mathrm{d}x'\, n(x',t)K(x',x)n(x,t), \end{aligned} \tag{18}$$

$$n(0,t) = \sum_{i=0}^{L} \int_{x_i}^{x_{i+1}} \beta(x,t)n(x,t)\mathrm{d}x.$$

This reduction technique is similar to that used in [42] to reduce infinite dimensional PDE models for structured populations into a finite-dimensional set of ODEs.

We now take the coefficients β, μ, and K to be piecewise constant in each compartment, *i.e.*,

$$\begin{aligned}\beta(x,t) &= \beta_i(t), && x \in [x_i, x_{i+1}),\\ \mu(x,t) &= \mu_i(t), && x \in [x_i, x_{i+1}),\\ K(x',x) &= K_{j,i}(t), && x' \in [x_j, x_{j+1}),\ x \in [x_i, x_{i+1}),\end{aligned} \tag{19}$$

where $\beta(x,t) = \beta_i(t)$, $x \in [x_i, x_{i+1})$ if β is independent of cannibalism. Eq. (18) then simplifies to

$$\begin{aligned}\frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\mu_0(t)n_0(t) - n_0(t)\sum_{j=0}^{L} K_{j,0}n_j(t) + \sum_{j=1}^{L}\beta_j(t)n_j(t) - \frac{n_0(t)}{\Delta x},\\ \frac{\mathrm{d}n_i}{\mathrm{d}t} &= -\mu_i(t)n_i(t) - n_i(t)\sum_{j=i}^{L} K_{j,i}n_j(t) - \frac{n_i(t)-n_{i-1}(t)}{\Delta x},\\ \frac{\mathrm{d}n_L}{\mathrm{d}t} &= -\mu_L(t)n_L(t) - n_L(t)K_{L,L}n_L(t) + \frac{n_{L-1}(t)}{\Delta x}.\end{aligned} \tag{20}$$

$K_{i,i}$ represents the within-compartment competition introduced due to the discretization. In the following, we will assume that $K_{i,i} = 0$ and that $\beta_0 = 0$. Note that the ODE system Eq. (20) is also the discretized finite volume method we used to numerically solve the original PIDE

Eq. (7). We are particularly interested in whether the simplified ODE model Eq. (20) with time-independent coefficients gives rise to the rich dynamics observed in the original PIDE model, especially as L is varied. Our main results are: (i) the ODE system Eq. (20) has at most one positive steady state, (ii) the two-compartment ODE model (setting $L = 1$ in Eq. (20)) has a unique positive steady state and the steady-state populations n_0 and n_1 never increase with the death rate. This result differs from that of the two-stage ODE model in [18] because a different type of interaction was invoked, (iii) the three-compartment ODE model ($L = 2$) exhibits a unique, positive, stable steady state and can exhibit overcompensation of increased death rates, and (iv) higher-L ODE systems can exhibit long-term oscillations in addition to permanent overcompensation as the positive steady state destabilizes. The proofs for these results are detailed in Appendix F.

4. Summary and conclusions

In this paper, we use a linear kinetic population model to formally derive a bilinear, age-structured PIDE that incorporates a continuum of intraspecies cannibalistic interactions. Distinct from previous models that typically assume complicated interactions within multi-stage/multispecies populations or rely on complex consumer-resource interactions, we demonstrate mathematically that our single-species, bilinear interaction model, structured simply according to age, can give rise to a variety of dynamical behavior.

Although similar PIDEs have been previously proposed [6,7,22,37] and undamped population oscillations found, overcompensation in response to increased death were not treated. We used realistic forms of predation to show that this model can exhibit permanent, steady-state overcompensation of the total population in response to permanent increases in death rate. General forms of predation kernels $K(x', x)$ that preclude steady-state overcompensation were enumerated showing that gradients in both x' and x are necessary for static overcompensation (when β and μ are constants). Specifically, our analysis suggests that $K(x', x)$ that increases in x' and decreases in x are more likely to exhibit steady-state overcompensation. Using predation kernels $K_1(x', x)$ and $K_2(x', x)$, Eq. (7) was solved numerically using a finite volume method to show the emergence of steady-state overcompensation. Our PIDE model can also be numerically solved using recently developed spectral methods that adaptively decompose the solution $n(x, t)$ into spatial basis functions with time-dependent coefficients. These methods are detailed in [43–45] and are quite efficient at handling unbounded domains.

Our analyses also allowed us to quantitatively distinguish transient overcompensation from steady-state overcompensation. Dynamic, or transient overcompensation was defined in terms of oscillations in the total population that also arose under predation kernels K_1 and K_2 and abrupt changes in the values of μ and β (see Fig. 1). These cases exhibited damped oscillations in the total population that transiently exceeded their expected steady-state values. At long times, the total populations converged to steady values uniquely associated with their permanent values of μ. For μ that has permanently increased, steady-state overcompensation is not universal but arises only under certain values of β and μ. However, for values of β and μ under which steady-state overcompensation *does not* arise (for $K = K_1, K_2$), transient overcompensation may nonetheless arise following jumps in $\mu(t)$.

Using certain forms of K (see Fig. 1), dynamic or transient overcompensation was observed in terms of oscillations in the total population that eventually damps to steady values that could be lower or higher (steady-state overcompensation) following increases in $\mu(x)$. However, similar to predator–prey models that can exhibit periodic oscillations, we also found that an interaction such as $K_3(x', x) = (x' - x)\theta(x' - 2)\theta(2 - x)$ leads to undamped oscillations in total population for certain values of β and μ. Undamped oscillations typically arise from Hopf bifurcations, in which the stable fixed point of a dynamical system loses stability through a pair of conjugate eigenvalues λ cross the $\mathrm{Re}\,\lambda = 0$ line as a parameter (such as μ) is tuned. The Hopf bifurcation theorem, originally constructed for ODE systems [46] states that such a bifurcation always gives rise to a limit cycle. The Hopf bifurcation theorem has been extended to the general abstract setting of ODEs in Banach space [47] which includes age-structured and predator–prey problems [48–50]. While our model is framed in terms of a PIDE, it nonetheless falls under the scope of the generalized Hopf bifurcation theory in Banach spaces detailed in [48]. Therefore, we conjecture that our model, as explored in Fig. 2 exhibits a Hopf bifurcation. To further motivate this numerically, we show in Fig. 4 of Appendix F.4 the spectrum of a discretized version of the PIDE model. We find a pair of conjugate eigenvalues crossing the imaginary axis as μ is decreased below ~ 0.7, consistent with the value at which undamped oscillations emerge. Thus, the undamped oscillations in our model may arise from a Hopf bifurcation.

Besides formal proofs that certain simple predation interactions rule out permanent overcompensation, and numerical exploration of specific cases that exhibit dynamical (damped and undamped oscillations) and steady-state overcompensation, a rigorous analysis of our nonlinear structured population PIDE model remains elusive. However, simplification via coarse-graining and discretizing the age variable allowed the PIDE to be cast as a system of approximating ODEs for piecewise constant parameter functions $\beta(x), \mu(x)$, and $K(x', x)$.

Revutskaya et al. [51] has shown that a discrete-time, two-sex, three-compartment model exhibits multistability and overcompensation under harvesting. However, overcompensation of increased death does not require the presence of multistability. Under certain conditions, the ODEs derived from our original cannibalistic-interaction PIDEs showed at most one positive steady state, implying that permanent overcompensation of increases in the death rate in our model cannot be due to transitions from one steady state to another. In our formulation, steady-state overcompensation and permanent oscillations are also recapitulated in ODE systems of at least three and four dimensions, respectively. These results may provide insight into mathematical strategies for analyzing our PIDE model under age-dependent birth and death rates.

Our mathematical framework suggests a number of possible future avenues of investigation. For example, since chaotic behavior has been shown to arise in a three-dimensional, two-species predator–prey ODE model [52], an intriguing question is how chaotic solutions might arise in our single-species continuously structured model Eq. (7). Continuously structured PIDE models can also be combined within multicomponent/multispecies models where even richer behavior might arise. For example, multicompartment aging models with *symmetric* age-age interactions have been shown to give rise to waves in opinion dynamics [53]. How overcompensation or oscillatory behavior of the total population when it is structured according to and evolves in size (Eq. (10)) rather than age is also worthwhile modeling. Finally, in analogy with spatial predator–prey models [54,55], including age-dependent spatial diffusion within our continuum structured PIDE model may lead to intriguing behavior such as transport-mediated local and global overcompensation.

CRediT authorship contribution statement

Mingtao Xia: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Xiangting Li:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Tom Chou:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Mathematical Appendices

Appendix A. Interactions that preclude permanent overcompensation

Here, we consider a few explicit forms for the cannibalism rate $K(x', x)$ that are analytically tractable. We prove that these simple interaction terms preclude overcompensation of increases in death rate.

A.1. *Self-inhibition* $K(x', x) = k(x)\delta(x' - x)$ *(a special case of the Riccati equation)*

We first show that if cannibalization occurs within individuals of the same structured variable (age in this case), *i.e.*, $K(x', x) = k(x)\delta(x' - x), k(x) > 0$, no overcompensation can occur, even for age-dependent birth and death rates $\beta(x)$ and $\mu(x)$. The steady-state Eq. (9) becomes a Riccati equation with a specific boundary condition,

$$\begin{aligned} \frac{\mathrm{d}n^*(x)}{\mathrm{d}x} &= -\mu(x)n^*(x) - k(x)(n^*(x))^2, \\ n^*(0) &= \int_0^\infty \beta(x)n^*(x)\mathrm{d}x. \end{aligned} \tag{21}$$

After defining $q^*(x) := k(x)n^*(x)$, Eq. (21) simplifies to

$$\begin{aligned} \frac{\mathrm{d}q^*(x)}{\mathrm{d}x} &= -\hat{\mu}(x)q^*(x) - [q^*(x)]^2, \quad \hat{\mu}(x) := \mu(x) - \frac{k'(x)}{k(x)}, \\ q^*(0) &= \int_0^\infty \frac{k(0)}{k(x)}\beta(x)q^*(x)\mathrm{d}x. \end{aligned} \tag{22}$$

Substituting $q^*(x) = u'(x)/u(x)$ into Eq. (22), we obtain the linear ODE $\frac{\mathrm{d}^2u(x)}{\mathrm{d}x^2} + \hat{\mu}(x)\frac{\mathrm{d}u(x)}{\mathrm{d}x} = 0$ which admits the general solution

$$u(x) \propto \left(1 + C\int_0^x e^{-\int_0^z \hat{\mu}(y)\mathrm{d}y}\mathrm{d}z\right), \tag{23}$$

where C is an integration constant and it is assumed that $\hat{\mu}$ has a positive lower bound such that $e^{-\int_0^z \hat{\mu}(y)\mathrm{d}y}$ is integrable. The steady-state population density $n^*(x)$ is then reconstructed as

$$n^*(x) = \frac{1}{k(x)}\frac{e^{-\int_0^x \hat{\mu}(x')\mathrm{d}x'}}{\frac{1}{C} + \int_0^x e^{-\int_0^z \hat{\mu}(y)\mathrm{d}y}\mathrm{d}z}, \quad C = k(0)n^*(0). \tag{24}$$

Substituting Eq. (24) into Eq. (21), we find the constraint on $C = k(0)n^*(0)$

$$1 = \int_0^\infty \frac{k(0)}{k(x)}\frac{\beta(x)e^{-\int_0^x \hat{\mu}(x')\mathrm{d}x'}}{1 + C\int_0^x e^{-\int_0^z \hat{\mu}(y)\mathrm{d}y}\mathrm{d}z}\,\mathrm{d}x. \tag{25}$$

Suppose we have two different death rates $\mu_1(x) \geq \mu_2(x)$ (and thus $\hat{\mu}_1(x) \geq \hat{\mu}_2(x)$) with their corresponding steady-state solutions $n_1^*(x), n_2^*(x)$ defined by their integration constants $C(\mu_1), C(\mu_2)$. We first show that $C(\mu_1) > C(\mu_2)$. Define

$$F_\mu(C) = \int_0^\infty \frac{k(0)}{k(x)}\frac{\beta(x)e^{-\int_0^x \hat{\mu}(x')\mathrm{d}x'}}{1 + C\int_0^x e^{-\int_0^z \hat{\mu}(y)\mathrm{d}y}\mathrm{d}z}\,\mathrm{d}x, \tag{26}$$

which is a decreasing function of C when $C > 0$. Next, note that

$$\frac{e^{-\int_0^x \hat{\mu}_1(x')\mathrm{d}x'}}{1 + C\int_0^x e^{-\int_0^z \hat{\mu}_1(y)\mathrm{d}y}\mathrm{d}z} \leq \frac{e^{-\int_0^x \hat{\mu}_2(x')\mathrm{d}x'}}{1 + C\int_0^x e^{-\int_0^z \hat{\mu}_2(y)\mathrm{d}y}\mathrm{d}z} \tag{27}$$

if $\mu_1(x) \geq \mu_2(x)$. This is because $e^{-\int_0^x \hat{\mu}_2(x')\mathrm{d}x'} \geq e^{-\int_0^x \hat{\mu}_1(x')\mathrm{d}x'}$ and $e^{-\int_0^z \hat{\mu}_1(x')\mathrm{d}x'}e^{-\int_0^x \hat{\mu}_2(x')\mathrm{d}x'} > e^{-\int_0^z \hat{\mu}_2(x')\mathrm{d}x'}e^{-\int_0^x \hat{\mu}_1(x')\mathrm{d}x'}, \forall\, 0 < z < x$. Thus, $F_{\mu_1}(C(\mu_1)) = 1$ and $\mu_1(x) \geq \mu_2(x)$ imply $F_{\mu_2}(C(\mu_1)) > 1$. Together with the constraint $F_{\mu_2}(C(\mu_2)) = 1$ and monotonicity of F_{μ_2}, $F_{\mu_2}(C(\mu_1)) > 1$ implies $C(\mu_2) > C(\mu_1)$; in other words, $n_2^*(0) > n_1^*(0)$. Furthermore, we have for all $x \geq 0$

$$\begin{aligned} n_1^*(x) &= \frac{1}{k(x)}\frac{e^{-\int_0^x \hat{\mu}_1(x')\mathrm{d}x'}}{\frac{1}{C(\mu_1)} + \int_0^x e^{-\int_0^z \hat{\mu}_1(y)\mathrm{d}y}\mathrm{d}z} \\ &\leq \frac{1}{k(x)}\frac{e^{-\int_0^x \hat{\mu}_2(x')\mathrm{d}x'}}{\frac{1}{C(\mu_2)} + \int_0^x e^{-\int_0^z \hat{\mu}_2(y)\mathrm{d}y}\mathrm{d}z} = n_2^*(x). \end{aligned} \tag{28}$$

Thus, the total populations N_1^* and N_2^* satisfy $N_1^* = \int_0^\infty n_1^*(x)\mathrm{d}x \leq \int_0^\infty n_2^*(x)\mathrm{d}x = N_2^*$. We conclude that no overcompensation will be observed under an interaction of the form $K(x' - x) = k(x)\delta(x' - x)$.

A.2. x*-independent cannibalism rate* $K = K(x')$

We also show that an x-independent predation interaction (predators do not prefer prey of any age), $K(x', x) = K(x')$, precludes permanent overcompensation. In this proof however, we must assume age-independent birth and death $\beta(x) = \beta, \mu(x) = \mu$. For $K(x', x) = K(x')$, the solution to Eq. (9) satisfies

$$\begin{aligned} &n^*(x) = n^*(0)e^{-(\mu + K^*)x}, \quad K^* := \int_0^\infty K(x')n^*(x')\mathrm{d}x', \\ &n^*(0) = \beta N^* = \beta\int_0^\infty n^*(x)\mathrm{d}x. \end{aligned} \tag{29}$$

When $\mu \geq \beta$, no positive K^* in Eq. (29) can satisfy $N^* = \int_0^\infty n^*(x)\mathrm{d}x$ and no positive solution exists. Numerical integration of the full time-dependent model in Eq. (7) shows that the only steady state is $n^* \equiv 0$. When $\mu < \beta$, the solution to Eq. (29) is satisfied by $K^* = \beta - \mu$ which leads to $n^*(x) = \beta N^* e^{-\beta x}$. Upon using $n^*(x) = \beta N^* e^{-\beta x}$ in the expression $K^* = \beta - \mu = \int_0^\infty K(x')n^*(x')\mathrm{d}x' = \beta N^* \int_0^\infty K(x')e^{-\beta x'}\mathrm{d}x'$, we find

$$N^* = \frac{1 - \frac{\mu}{\beta}}{\int_0^\infty K(x')e^{-\beta x'}\mathrm{d}x'}, \tag{30}$$

which strictly decreases with μ. Thus, a predation kernel that is independent of prey age x cannot exhibit steady-state overcompensation.

A.3. x'*-independent cannibalism rate* $K(x', x) = K(x)$

For a predation/cannibalization rate of the form $K(x', x) = K(x)$, the steady-state Eq. (9) becomes

$$\begin{aligned} \frac{\mathrm{d}n^*(x)}{\mathrm{d}x} &= -\left[\mu + K(x)\int_0^\infty n^*(x')\mathrm{d}x'\right]n^*(x), \\ n^*(0) &= \beta N^*. \end{aligned} \tag{31}$$

We now prove that if μ, β are constants, then no permanent overcompensation will occur. Eq. (31) is solved by $n^*(x) = n^*(0)e^{-\mu x - N^*\tilde{K}(x)}$, where $\tilde{K}(x) \equiv \int_0^x K(y)\mathrm{d}y$. Upon integrating the solution and using the boundary condition $n^*(0) = \beta N^*$, eliminating $n^*(0)$, and using the definition $N^* = \int_0^\infty n(x)\mathrm{d}x$, we find an implicit solution for N^*:

$$1 = \beta\int_0^\infty e^{-\mu x - N^*\tilde{K}(x)}\mathrm{d}x \equiv F(\mu, N^*). \tag{32}$$

Eq. (32) is the specific form of Eq. (63) to be derived under a general condition later. To see how N^* varies with μ, we apply the implicit function theorem to obtain

$$\frac{\delta N^*}{\delta\mu} = -\frac{(\partial F/\partial\mu)}{(\partial F/\partial N^*)} = -\frac{\int_0^\infty x e^{-\mu x - N^*\tilde{K}(x)}\mathrm{d}x}{\int_0^\infty \tilde{K}(y)e^{-\mu y - N^*\tilde{K}(y)}\mathrm{d}y}. \tag{33}$$

For $\mu, N^* > 0$, the RHS above is negative. Thus, $\partial N^*/\partial\mu < 0$ and steady-state overcompensation cannot arise. This result implies that an interaction kernel $K(x', x)$ that varies only in x is insufficient for steady-state overcompensation and that variation in x' is necessary. This result, along with that in Appendix A.2, suggests that predation kernels $K(x', x)$ that vary in both x' and x are required for steady-state overcompensation, at least for age-independent β and μ.

Appendix B. Simple interactions that can exhibit steady-state overcompensation

Here, we consider some solvable examples of predation kernels $K(x', x)$ that *can* exhibit steady-state overcompensation.

B.1. Point source and sink

Consider the predation kernel defined as $K(x', x) = k\delta(x'-b)\delta(x-a)$, and β, μ assumed to be constant. The steady state solution of such a system satisfies:

$$\frac{\mathrm{d}n^*(x)}{\mathrm{d}x} = -\Big[\mu + kn^*(b)\delta(x-a)\Big]n^*(x). \tag{34}$$

For such a system, the steady-state expression for $n^*(x)$ can be written as:

$$n^*(x) = n^*(0)e^{-\mu x - kn^*(b)\theta(x-a)}. \tag{35}$$

Assuming $b > a$, we deduce from the boundary condition that

$$1 = \int_0^\infty \beta e^{-\mu x - kn^*(b)\theta(x-a)}\mathrm{d}x. \tag{36}$$

Since $n^*(b) > 0$, $(1 - e^{-kn^*(b)}) < 1$, and Eq. (36) can be satisfied if and only if

$$e^{-\mu a} > 1 - \frac{\mu}{\beta}. \tag{37}$$

Under this condition, $n^*(b)$ can be determined as

$$n^*(b) = -\frac{1}{k}\ln\Big(1 - \big(1 - \tfrac{\mu}{\beta}\big)e^{\mu a}\Big), \tag{38}$$

which, when used in conjunction with Eq. (35) determines $n^*(0)$, leading to the final expression for the steady state total population

$$N^* = -\frac{e^{\mu b}}{\beta k}\frac{\ln\Big(1 - \big(1 - \tfrac{\mu}{\beta}\big)e^{\mu a}\Big)}{\Big(1 - \big(1 - \tfrac{\mu}{\beta}\big)e^{\mu a}\Big)}. \tag{39}$$

One can see that the magnitude of interaction strength k does not change the sign of $\partial N^*/\partial\mu$. In the limit $a \to 0^+$, Eq. (39) reduces to

$$N^*(a \to 0^+) = \frac{e^{\mu b}}{\mu k}\ln\left(\frac{\beta}{\mu}\right). \tag{40}$$

Note that in this limit, the constraint Eq. (37) is always satisfied, although we still require $\beta > \mu$ to ensure that N^* is positive. Taking the derivative of Eq. (40) with respect to μ, we find

$$\frac{\partial N^*(a \to 0^+)}{\partial\mu} = \frac{e^{b\mu}}{\mu^2 k}\left[(b\mu - 1)\ln\Big(\frac{\beta}{\mu}\Big) - 1\right]. \tag{41}$$

In other words, $\partial N^*/\partial\mu$ is positive, with overcompensation, if and only if

$$(\mu b - 1)\ln\big(\tfrac{\beta}{\mu}\big) > 1. \tag{42}$$

Since $\mu \in (0, \beta)$, the lowest value of b that can still yield $\partial N^*/\partial\mu > 0$ (overcompensation) for some values of β, μ is

$$b_\mathrm{c} = \inf_{\mu\in(0,\beta)}\left(\frac{1}{\mu} + \frac{1}{\mu\ln\frac{\beta}{\mu}}\right) = \frac{e^{-\frac{1}{2}+\frac{\sqrt{5}}{2}}}{\beta} + \frac{e^{-\frac{1}{2}+\frac{\sqrt{5}}{2}}}{\beta\left(-\frac{1}{2} + \frac{\sqrt{5}}{2}\right)}. \tag{43}$$

Intuitively, large birth rate β and large interaction distance $b > b_\mathrm{c}$ are both favorable for overcompensation.

B.2. Predation on newborns/eggs

We now delve into a specific version of our older-predating-on-younger model, where the predation kernel K is given by

$$K(x', x) = \lim_{\varepsilon\to 0^+} k\delta(x-\varepsilon)\theta(x'-b), \tag{44}$$

where θ is the Heaviside function. In this scenario, the steady state solution $n^*(x)$ is solved by

$$n^*(x) = n^*(0)e^{-kN_b}e^{-\mu x}, \tag{45}$$

where

$$N_b := \int_b^\infty n^*(x)\mathrm{d}x \equiv \frac{n^*(b)}{\mu}. \tag{46}$$

The birth (boundary) condition can then be expressed as

$$1 = \tfrac{\beta}{\mu}e^{-kn^*(b)/\mu}. \tag{47}$$

Given the constraint $\beta > \mu$, the steady state population at $x = b$ becomes $n^*(b) = (\mu/k)\ln\big(\beta/\mu\big)$. Using this result in Eq. (45) allows us to determine $n^*(0)$ and total population N^*

$$N^* = \frac{e^{\mu b}}{k}\ln\Big(\frac{\beta}{\mu}\Big). \tag{48}$$

To demonstrate there exists an interval of μ for which overcompensation arises provided sufficiently large b, we examine when the condition

$$\frac{\partial N^*}{\partial\mu} = \frac{\left(\mu b\ln\left(\frac{\beta}{\mu}\right) - 1\right)e^{\mu b}}{\mu k} > 0 \tag{49}$$

holds. The threshold of b above which overcompensation is possible is thus

$$b_\mathrm{c} = \inf_{\mu\in(0,\beta)}\frac{1}{\mu\ln\Big(\frac{\beta}{\mu}\Big)} = \frac{e}{\beta}. \tag{50}$$

Appendix C. Uniqueness of the positive steady state of Eq. (7)

If the distributed interaction $K(x', x)$ satisfies Eq. (13), we shall prove uniqueness of a positive steady state under the assumption that the set $\{x : \exists x' > x > 0, K(x', x) > 0\} \cap \{x : \beta(x) > 0, x > 0\}$ has positive measure. We shall prove the following two statements. First, we assume two steady states, $m^*(x)$ and $n^*(x)$, and demonstrate that if $m^*(X) = n^*(X)$ at some age X, then $m^*(x)$ and $n^*(x)$ are precisely the same steady state everywhere. Second, without loss of generality, if $n^*(X) > m^*(X)$, we will demonstrate that $n^*(x) > m^*(x)\ \forall x \geq 0$. This dominance relation conflicts with the well-known Euler-Lotka equation, thereby demonstrating the uniqueness of the steady-state solution. These results indicate that although overcompensation can arise from transition to an alternative steady state upon increases in death or harvesting [51], multistability is not a necessary condition for overcompensation of increased death.

To show

$$m^*(X) = n^*(X) \Rightarrow m^*(x) = n^*(x),\ \forall x \geq X, \tag{51}$$

first note that since $K(x', x > X) = 0$, the interaction terms in Eq. (9) for both $m(x)$ and $n(x)$ vanish for $x > X$ and thus are linear first-order equations with identical decay rates $\mu(x)$ and coincident "initial conditions" $m^*(X) = n^*(X)$. Thus, the solutions for $x > X$ are identical.

What remains is to show that $m^*(X) = n^*(X) \Rightarrow m^*(x) = n^*(x), \forall x \geq 0$. To simplify notation, we set $\xi = X - x$, $\xi' = X - x'$ and define $f(\xi) \equiv n(X-x)$, $f^*(\xi) \equiv n^*(X-x)$, transforming the steady-state problem Eq. (9) into a general integral–differential equation with given initial data (using Eq. (51))

$$\begin{aligned} \frac{\mathrm{d}f(0 < \xi \leq X)}{\mathrm{d}\xi} &= \left[\mu(\xi) + \int_{-\infty}^{\xi} K(\xi', \xi)f(\xi')d\xi'\right]f(\xi), \\ f(\xi \leq 0) &= f^*(\xi), \end{aligned} \tag{52}$$

where we have reparameterized $\mu(x)$ such that $\mu(\xi) = \mu(x = X - \xi)$ and $K(x', x)$ such that $K(\xi', \xi) = K(x' = X - \xi', x = X - \xi)$. The goal is to march the steady-state uniqueness from $\xi < 0$ $(x > X)$ up to $\xi = X$ $(x = 0)$. Let us assume that uniqueness of $f(\xi)$ has been demonstrated up to ξ_0, *i.e.*, that $f(\xi) = f^*(\xi) \equiv n^*(X-\xi)$ has been uniquely determined in $(-\infty, \xi_0]$. Breaking up the integral term, we write

$$\begin{aligned}\frac{\mathrm{d}f(\xi > \xi_0)}{\mathrm{d}\xi} &= \left[\mu(\xi) + \int_{-\infty}^{\xi_0} K(\xi', \xi) f(\xi')\mathrm{d}\xi' \right. \\ &\qquad \left. + \int_{\xi_0}^{\xi} K(\xi', \xi) f(\xi')\mathrm{d}\xi' \right] f(\xi), \\ f(\xi \le \xi_0) &= f^*(\xi).\end{aligned} \tag{53}$$

We can march ξ_0 forward from 0 and consider a small region $(\xi_0, \xi_0+\varepsilon)$ successively. At each stage, since $f(\xi) = f^*(\xi_0 \le \xi < \xi_0+\varepsilon)$ has been uniquely determined, we can combine $\mu(\xi) + \int_{-\infty}^{\xi_0} K(\xi', \xi) f(\xi')\mathrm{d}\xi' \to \mu(\xi)$. If we start at $\xi_0 = 0$, it suffices to show that the solution to

$$\begin{aligned}\frac{\mathrm{d}f(\xi > 0)}{\mathrm{d}\xi} &= \left[\mu(\xi) + \int_0^{\xi} K(\xi', \xi) f(\xi')\mathrm{d}\xi' \right] f(\xi), \\ f(0) &= f^*(0)\end{aligned} \tag{54}$$

is unique in a small domain of $(0, \varepsilon)$.

Suppose that $\mu(\xi)$ is (locally) bounded by $\hat{\mu}$, $K(\xi', \xi)$ is bounded by $\hat{K}$, and g is the local solution to the associated differential equation

$$\begin{aligned}\frac{\mathrm{d}g(\xi > 0)}{\mathrm{d}\xi} &= \left[\hat{\mu} + \hat{K} \int_0^{\xi} g(\xi')\mathrm{d}\xi' \right] g(\xi), \\ g(0) &= f^*(0).\end{aligned} \tag{55}$$

The integral $G(\xi) \equiv \int_0^{\xi} g(\xi')\mathrm{d}\xi'$ then obeys the standard-form second-order ODE

$$\begin{aligned}\frac{\mathrm{d}^2 G(\xi > 0)}{\mathrm{d}\xi^2} &= \left[\hat{\mu} + \hat{K} G(\xi) \right] \frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}, \\ \left.\frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}\right|_{\xi=0} &= g(0) \equiv f^*(0), \quad G(0) = 0.\end{aligned} \tag{56}$$

The solution to Eq. (56) in the region $(0, \varepsilon)$ is unique and for any solution f of Eq. (54), $0 < f \le g$.

Now suppose that f_1 and f_2 are two solutions in the neighborhood of 0 that solve Eq. (54). We have

$$f_i(\xi) = f^*(\xi) + \int_0^{\xi} \left(\mu(\xi') + \int_0^{\xi'} K(\xi'', \xi') f_i(\xi'')\mathrm{d}\xi'' \right) f_i(\xi') d\xi' \tag{57}$$

for $i = 1, 2$. Note that

$$\begin{aligned}&\left| f_1(\xi') \int_0^{\xi'} K(\xi'', \xi') f_1(\xi'')\mathrm{d}\xi'' \right. \\ &\qquad \left. - f_2(\xi') \int_0^{\xi'} K(\xi'', \xi') f_2(\xi'')\mathrm{d}\xi'' \right| \\ &= \left| f_1(\xi') \int_0^{\xi'} K(\xi'', \xi') \Big(f_1(\xi'') - f_2(\xi'') \Big) \mathrm{d}\xi'' \right. \\ &\qquad \left. + \Big(f_1(\xi') - f_2(\xi') \Big) \int_0^{\xi'} K(\xi'', \xi') f_2(\xi'')\mathrm{d}\xi'' \right| \\ &\le 2\hat{K}\xi' \sup_{\xi \in (0,\varepsilon)} g(\xi) \sup_{\xi \in (0,\varepsilon)} \Big| f_1(\xi) - f_2(\xi) \Big|.\end{aligned} \tag{58}$$

Then, using Eq. (57), we conclude that

$$\sup_{\xi \in [0,0+\varepsilon]} \Big| f_1(\xi) - f_2(\xi) \Big| \le \left\{ \varepsilon \hat{\mu} + \varepsilon^2 \hat{K} \sup_{\xi \in (0,\varepsilon)} g(\xi) \right\} \sup_{\xi \in [0,0+\varepsilon]} \Big| f_1(\xi) - f_2(\xi) \Big|. \tag{59}$$

Since ε can be chosen sufficiently small such that $\left\{ \varepsilon \hat{\mu} + \varepsilon^2 \hat{K} \sup_{\xi \in (0,\varepsilon)} g(\xi) \right\} < 1$, we conclude $\sup_{\xi \in [0,0+\varepsilon]} \Big| f_1(\xi) - f_2(\xi) \Big| = 0$, proving the solution to Eq. (54) is unique in a neighborhood of 0. Under the assumption that the solution to Eq. (54) exists, we can replace the point $\xi = 0$ with $\xi \in (0, X)$ and conclude that the solution is unique in a small neighborhood of $\xi = X - x$. Therefore, the solution is globally unique in $(0, X)$, and the proof of the first statement is completed.

Next, we prove the second statement by showing that the case $n^*(X) > m^*(X)$ cannot not hold by first claiming that

$$n^*(X) > m^*(X) \Rightarrow n^*(x) > m^*(x), \ \forall x \ge 0. \tag{60}$$

We easily observe that the statement is true for $x \ge X$. Suppose for some x_0, $n^*(x_0) \le m^*(x_0)$. Then let $x^* = \sup_{x \ge 0}\{x : n^*(x) \le m^*(x)\}$. By continuity of m^* and n^*, we note that $x^* < X$.

Within the interval (x^*, X), $n^*(x) > m^*(x)$. Let $\xi = X - x$, and consider the functions m^* and n^* written as functions of ξ. The difference of Eq. (52) satisfied by m^* and n^* becomes

$$\frac{\mathrm{d}}{\mathrm{d}\xi} \left(n^*(\xi) - m^*(\xi) \right) \ge \mu(\xi) \left(n^*(\xi) - m^*(\xi) \right), \quad \forall \xi \in (0, \xi^*). \tag{61}$$

By integrating both sides of Eq. (61) from 0 to ξ^*, we conclude that $n^*(\xi^*) - m^*(\xi^*) > 0$, which demonstrates the dominance relation $n^*(x) > m^*(x)$, $\forall x \ge 0$.

We can now exploit the equilibrium form of the Euler-Lotka equation [56,57]. Let $\tilde{\mu}(x) = \mu(x) + \int_x^{\infty} K(x', x) n^*(x') dx'$ be the effective death rate and $s(x) = \exp\left(-\int_0^x \tilde{\mu}(x')\mathrm{d}x' \right)$ be the survival probability of any individual up to age x. The overall steady-state rate of new births defined by

$$n(0, t) \equiv B(t) = \int_0^{\infty} \beta(x) n(x, t)\mathrm{d}x \tag{62}$$

can be formally written in terms of $s(x)$ and the form of the method of characteristics solution $n(x < t, t) = n(0, t-x)s(x) = B(t-x)s(x)$. Using this form of $n(x < t, t)$ in the integrand in Eq. (62), we find in the $t \to \infty$ limit $B(t) = \int_0^{\infty} \beta(x) B(t-x) s(x)\mathrm{d}x$. Since in the $t \to \infty$ steady state limit all quantities are independent of time, $B(t) = B$ and

$$1 = \int_0^{\infty} \beta(x) s(x)\mathrm{d}x \equiv \int_0^{\infty} \beta(x) e^{-\int_0^x \tilde{\mu}(x')\mathrm{d}x'}\mathrm{d}x, \tag{63}$$

which means that at steady state, the population $n^*(x)$ and effective death rate $\tilde{\mu}(x')$ settles to value such that the effective reproductive number $R_0 \equiv \int_0^{\infty} \beta(x) s(x)\mathrm{d}x = 1$.

Eq. (63) must be satisfied at steady state but allows us to compare different $\tilde{\mu}$s associated with different steady state solutions. For different steady states m^* and n^* such that $m^* > n^*$ at all ages, the effective death rates satisfy $\tilde{\mu}^{(m)} \ge \tilde{\mu}^{(n)}$. Since β remains the same, the survival probability satisfies $s^{(m)} \le s^{(n)}$, where the inequality should hold on a positive measure interval. Because $\{x : \exists x' > x > 0, K(x', x) > 0\} \cap \{x : \beta(x) > 0, x > 0\}$ has positive measure, we will conclude

$$1 = \int_0^{\infty} \beta(x) e^{-\int_0^x \tilde{\mu}^{(m)}(x')\mathrm{d}x'}\mathrm{d}x < \int_0^{\infty} \beta(x) e^{-\int_0^x \tilde{\mu}^{(n)}(x')\mathrm{d}x'}\mathrm{d}x = 1. \tag{64}$$

This contradiction shows that if K is continuous and compactly supported and if $\{x : \exists x' > x > 0, K(x', x) > 0\} \cap \{x : \beta(x) > 0, x > 0\}$ has positive measure, then Eq. (7) admits at most one positive steady state.

Appendix D. Existence of a positive steady state of Eq. (7)

If a predation kernel satisfies Eq. (13), we can also obtain the criterion for the existence of a positive steady state, which is equivalent to finding a positive solution $n^*(x)$ to Eqs. (9) under certain additional assumptions.

In Appendix C, we showed that any solution $n^*(x)$ to Eqs. (9) must satisfy Eq. (54) with the transformed coordinate $\xi = X - x$ and $f(\xi) = n^*(X-x)$. For the existence arguments, we first investigate the condition under which Eq. (54) has a positive solution. Formally, we pick the initial condition $n_X := f(0) > 0$ as the parameter of interest, and consider the domain of n_X such that the solution to Eq. (54) exists up to $\xi = X$. Define $f_{-1}(\xi) \equiv 0$ and $f_{n+1}(\xi)$ as solutions to the ODE

$$\begin{aligned}\frac{1}{f_{n+1}(\xi)} \frac{\mathrm{d}f_{n+1}(\xi)}{\mathrm{d}\xi} &= \mu(\xi) + \int_0^{\xi} K(\xi', \xi) f_n(\xi')\mathrm{d}\xi', \ \forall \xi \in (0, X), \\ f_{n+1}(0) &= n_X,\end{aligned} \tag{65}$$

where $n \ge -1$. In particular, $f_0(\xi) = n_X e^{\int_0^{\xi} \mu(\xi')\mathrm{d}\xi'} > 0 = f_{-1}(\xi)$ for all $\xi \in (0, X)$. For each n, an iterative argument shows that f_n is bounded, continuous, and nonnegative on $[0, X]$. In addition, $f_0(\xi) > f_{-1}(\xi), \forall \xi \in (0, X)$ implies that $\{f_n(\xi)\}$ is a monotonically increasing sequence in both ξ and n. Therefore, $f(\xi) := \lim_{n\to\infty} f_n(\xi) \in$

$(0,\infty]$ exists and satisfies Eq. (54) up to the moment of blowup $\xi^* \equiv \sup\{\xi \in (0,X) : f(\xi) < \infty\}$, thanks to the monotone convergence theorem.

We also observe that $f(\xi)$ depends monotonically on the initial value n_X. For sufficiently regular μ and K, we also observe that $f(\xi)$ depends continuously on the initial condition n_X. Define the upper limit for n_X by $n_X^* \equiv \sup\left\{n_X : \xi^*(n_X) > X\right\}$ with the convention that $\sup\emptyset = 0$, and we find an open domain $(0, n_X^*)$ of n_X such that $f(\xi) < \infty$ for all $\xi \in [0,X]$ with the initial value n_X. In particular, the continuity assumption implies $\lim_{n_X\to n_{X-}^*} f(X) = \infty$. The marginal case $n_X^* = \infty$ is covered by this equation because $f(X) \geq f(0) = n_X \to \infty$.

Now, we recover $n^*(x)$ from $f(\xi)$ and denote n^* by $n_{n_X}^*$ to emphasize the dependence on n_X. For the sake of simplicity, we assume the upper limit $n_X^* = +\infty$ in the following discussion. This can be achieved by imposing proper restrictions on μ and K, such that the existence of the solution to Eq. (56) on the interval $(0,X)$ is guaranteed.

We proved that there is a unique solution $n_{n_X}^*(x)$ to the first equation in Eqs. (9) when $n_{n_X}^*(X) = n_X$ provided that μ and K are bounded on $[0,X]$, there exist positive constants $\mu_0, K_0 > 0$ such that $\mu \geq \mu_0, K \geq K_0$, and K vanishes for $x > X$. We shall show that the solution to Eqs. (9) exists under the following two conditions: (i) in the cannibalism-free environment ($K = 0$), the expected number of offspring that an individual will give birth to is larger than 1

$$\int_0^\infty \beta(x) e^{-\int_0^x \mu(x')\mathrm{d}x'}\mathrm{d}x > 1, \tag{66}$$

and (ii) given any $\left.\frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}\right|_{\xi=0} := n_X$, the second order ODE Eq. (56) can be solved up to $\xi = X$, and that $\frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}$, $\xi \in (0,X)$ depends continuously on the initial $\frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}|_{\xi=0}$.

Note that the existence of the solution to Eqs. (9) requires a proper n_X such that $n_{n_X}^*(0)$ is suitable for the second equation in Eqs. (9), *i.e.*, the boundary condition representing the newborn cells. So we need to show that $\left.\frac{\mathrm{d}G(\xi)}{\mathrm{d}\xi}\right|_{\xi=X} = n_{n_X}^*(0)$ satisfies the boundary condition in Eqs. (9). Note that as long as $n_X > 0$, $n_{n_X}^*(x) > 0$, $\forall x \geq 0$. Let $\tilde{\mu}_{n_X}$ denote the effective death rate $\tilde{\mu}_{n_X}(x) = \mu(x) + \int_x^\infty K(x',x) n_{n_X}^*(x')\mathrm{d}x'$, then the second equation in Eqs. (9) is equivalent to

$$n_{n_X}^*(0)\left\{1 - \int_0^\infty \beta(x) e^{-\int_0^x \tilde{\mu}_{n_X}(x')\mathrm{d}x'}\mathrm{d}x\right\} = 0. \tag{67}$$

We define the Euler-Lotka functional as

$$\mathrm{EL}\left[n_{n_X}^*\right] = \int_0^\infty \beta(x) e^{-\int_0^x \tilde{\mu}_{n_X}(x')\mathrm{d}x'}\mathrm{d}x, \tag{68}$$

Then, the second equation in Eq. (9) is equivalent to the famous Euler-Lotka equation $\mathrm{EL}\left[n_{n_X}^*\right] = 1$ for positive solutions $n_{n_X}^*$. We have shown that $n_X < n_X' \Rightarrow \tilde{\mu}_{n_X}(x) \leq \tilde{\mu}_{n_X'}(x)$, $\forall x \geq 0$. Therefore, the function $n_X \mapsto \mathrm{EL}\left[n_{n_X}^*\right]$ is monotonically decreasing. Because $n_{n_X}^*(x)$, $x \leq X$ depends continuously on $n_{n_X}^*$, the functional Eq. (68) also depends continuously on $n_{n_X}^*$. Consequently, we conclude that the existence of the positive steady state is equivalent to

$$\begin{aligned}
&\lim_{n_X\to\infty}\int_0^\infty \beta(x) e^{-\int_0^x \tilde{\mu}_{n_X}(x')\mathrm{d}x'}\mathrm{d}x < 1;\\
&\lim_{n_X\to 0+}\int_0^\infty \beta(x) e^{-\int_0^x \tilde{\mu}_{n_X}(x')\mathrm{d}x'}\mathrm{d}x > 1.
\end{aligned} \tag{69}$$

When $n_X = 0$, $n_{n_X}^*(x) \equiv 0$. Furthermore, for $x < X$, $n^*(x) \geq n^*(X)$, which implies $\lim_{n_X\to\infty} n_{n_X}^*(x) = \infty, x < X$. Since we have assumed that both μ and K have positive lower bounds on their support and that the solution $n_{n_X}^*$ is continuously dependent on the initial condition n_X, we could conclude that

$$\begin{aligned}
\lim_{n_X\to 0+}\tilde{\mu}_{n_X}(x) =& \mu(x) + \int_x^\infty K(x',x) n_0^*(x')\mathrm{d}x' = \mu(x);\\
\lim_{n_X\to\infty}\tilde{\mu}_{n_X}(x) =& \mu(x) + \int_x^\infty K(x',x) n_\infty^*(x')\mathrm{d}x = \begin{cases}\mu(x) & x \geq X\\ \infty & \text{otherwise.}\end{cases}
\end{aligned} \tag{70}$$

The first equation in Eq. (69) is satisfied as

$$\lim_{n_X\to\infty}\int_0^\infty \beta(x) e^{-\int_0^x \tilde{\mu}_{n_X}(x')\mathrm{d}x'}\mathrm{d}x = 0 \tag{71}$$

because $\lim_{n_X\to\infty}\tilde{\mu}_{n_X}(x) = \infty, x \in (0,X)$. Furthermore, the second equation in Eq. (69) is satisfied by the assumption Eq. (66). Therefore, there must exist an n_X such that $\mathrm{EL}\left[n_{n_X}^*\right] = 1$, and thus the corresponding $n_{n_X}(x)$ satisfies the two equations in Eqs. (9).

Appendix E. Additional examples of overcompensation

E.1. Cannibalism-related birth rate

In the main discussion, we assumed that cannibalism only modifies the death rate. Here, we provide a numerical example in which preying on juveniles can increase birth rates. This limit may arise when food is not abundant and cannibalism provides nourishment for reproduction. In this case the birth rate can be a function of the amount of cannibalism measured by $\int_0^\infty K(x,x')n(x',t)\mathrm{d}x' \equiv \phi[n;x]$, which is a functional of $n(x)$. We will assume that $\beta(x,\phi[n;x])$ takes the form

$$\begin{aligned}
\beta(x,\phi[n;x]) &= \beta_0 + \tfrac{1}{4}\phi[n;x]\\
&= \beta_0 + \frac{1}{4}\int_0^\infty K(x,x')n(x',t)\mathrm{d}x',
\end{aligned} \tag{72}$$

where β_0, μ are constants. Using Eq. (72) along with $K(x',x) = K_1(x',x) \equiv \theta(x'-2)\theta(2-x)$ in Eq. (7), we compute and plot the total population at steady-state as a function of β_0 and μ in Fig. 3(b). When β_0 is fixed, the total population is found to first increase with the death rate μ until $\mu \to \beta_0^+$ when the population starts to diminish. This implies that for the cannibalism-rate-dependent birth rate β defined in Eq. (72), overcompensation can arise.

E.2. Harvesting-induced overcompensation

Populations can also overcompensate selective harvesting [8–10] which we can model by incorporating, as shown by Eq. (16), an age-dependent harvesting term $h(n;x,t)$ that can be a nonlinear function of n [58].

We explore age-dependent harvesting $h(n;x,t)$ that preferentially removes older populations and show numerically that overcompensation can arise for the two forms of harvesting

$$\begin{aligned}
h_1 &= \min\{n(x,t), h\}\theta(x-2),\\
h_2 &= \frac{hn(x,t)}{n(x,t)+n_{1/2}}\theta(x-2),
\end{aligned} \tag{73}$$

where h is the intrinsic maximum harvesting rate and $n_{1/2}$ is a constant half-saturation density. Both effective harvesting rates h_1 and h_2 vanish with the population densities $n(x,t)$, saturate to h when $n(x,t) \gg n_{1/2}$, and increase with the parameter h. We set all other dimensionless coefficients in Eq. (16) to $K(x',x) = K_4(x',x) = (x'-x)\theta(x'-x)$, $\beta = 1$, $\mu = 0.5$, $n_{1/2} = 1$. In Fig. 3(a), we plot the plot steady-state population N^* for scenarios h_1 and h_2 as a function of h. The total population N^* is seen to increase with h for both harvesting strategies, indicating overcompensation in response to increased harvesting rate.

E.3. Overcompensation following changes in birth rate

The usual "hydra effect" overcompensation is described by a steady state total population that increases with the *death* rate. In all of our examples, the total population at the steady-state increased with birth rate β. One can show that if $K(x',x) \geq 0$ and $K(x',x) = 0$ for $x > X$ or $x' \leq x$, the steady-state solutions to Eq. (9) that correspond to birth rates $\beta_1(x) > \beta_2(x)$, $n_{\beta_1}^*(x)$ and $n_{\beta_2}^*(x)$, are such that the total steady-state total populations

$$N_{\beta_1}^* := \int_0^\infty n_{\beta_1}^*(x)\mathrm{d}x > N_{\beta_2}^* := \int_0^\infty n_{\beta_2}^*(x)\mathrm{d}x. \tag{74}$$

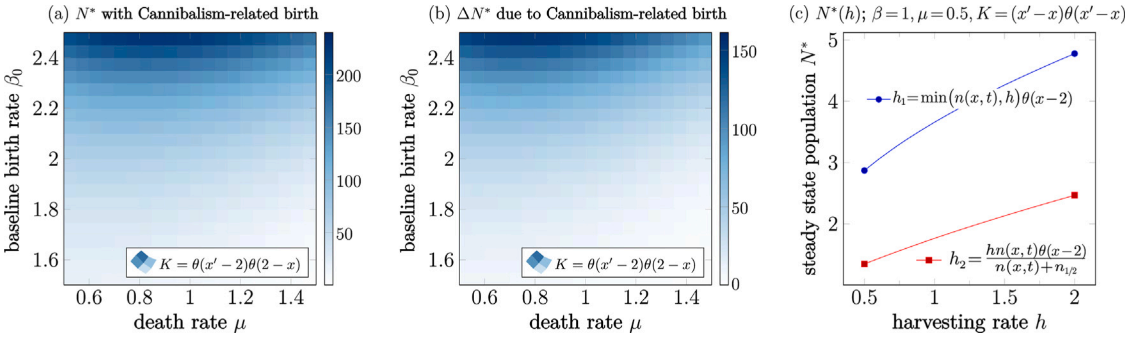

Fig. 3. (a) The steady-state total population $N^*(\beta(x, \phi[n; x]))$ that displays overcompensation with a constant death rate for the cannibalism-dependent birth rate Eq. (72), where cannibalism has a positive effect on the birth rate. (b) The difference in the steady-state population $N^*(\beta(x, \phi[n; x])) - N^*(\beta_0)$, where $N^*(\beta(x, t))$ is the steady-state total population with a constant birth rate $\beta := \beta_0$. Because $\beta(x, \phi[n; x]) > \beta_0$ for n^*, the difference is always positive. Furthermore, for some fixed β_0, the difference $N^*(\beta(x, \phi[n; x])) - N^*(\beta_0)$ also "overcompensates" by first increase then decrease with $\mu := \mu_0$. (c) The steady-state total population for h_1, h_2 in Eq. (73) for the harvesting model Eq. (16). Overcompensation is observed with increasing harvesting rates. Furthermore, since $h_1 > h_2$ if h is the same, for a fixed h, the total population under the harvesting rate h_1 is greater than that under h_2.

In fact, steady-state solution $n^*(x), x \geq 0$ to Eq. (9) can be expressed in terms of $n^*(X)$

$$\begin{aligned} n^*(x \leq X) =& n^*(X) e^{\int_x^X \mu(x')\mathrm{d}x'} e^{\int_x^X \int_{x'}^\infty K(y,x') n^*(y)\mathrm{d}y\mathrm{d}x'}, \\ n^*(x \geq X) =& n^*(X) e^{-\int_X^x \mu(x')\mathrm{d}x'}. \end{aligned} \tag{75}$$

We conclude from Eq. (75) that if $n^*_{\beta_1}(X) > n^*_{\beta_2}(X)$ then $n^*_{\beta_1}(x) > n^*_{\beta_2}(x), x \geq 0$ and therefore Eq. (74) still holds.

On the other hand, if $n^*_{\beta_1}(X) \leq n^*_{\beta_2}(X)$, we conclude from Eq. (75) that $n^*_{\beta_1}(x) \leq n^*_{\beta_2}(x), x \geq 0$. However, from Eq. (63), we have

$$\int_0^\infty \beta_i(x) e^{-\int_0^x \tilde{\mu}_i(x')\mathrm{d}x'} \mathrm{d}x = 1, \quad i = 1, 2 \tag{76}$$

where

$$\begin{aligned} \tilde{\mu}_1(x) = \mu(x) + \int_x^\infty K(x', x) n^*_{\beta_1}(x')\mathrm{d}x' \leq \tilde{\mu}_2(x) \\ = \mu(x) + \int_x^\infty K(x', x) n^*_{\beta_2}(x')\mathrm{d}x'. \end{aligned} \tag{77}$$

Therefore,

$$\begin{aligned} 1 = \int_0^\infty \beta_1(x) e^{-\int_0^x \tilde{\mu}_1(a)\mathrm{d}a}\mathrm{d}x \\ > \int_0^\infty \beta_2(x) e^{-\int_0^x \tilde{\mu}_2(a)\mathrm{d}a}\mathrm{d}x = 1 \end{aligned} \tag{78}$$

is a contradiction, which implies that the steady-state population density $n^*_{\beta_1}(x) > n^*_{\beta_2}(x)$ and that the total steady-state population $\int_0^\infty n^*_{\beta_1}(x)\mathrm{d}x > \int_0^\infty n^*_{\beta_2}(x)\mathrm{d}x$ always increases with birth rate when $K \geq 0$ and the predation is unidirectional (old-eat-young).

In scenarios in which the younger population can prey on the older population, and K can be negative, steady-state total populations *can* decrease with the birth rate, *i.e.*, the steady-state total population "overcompensates" as the birth rate decreases. As an example, we assume a dimensionless predation rate of the form

$$\tilde{K}(x', x) \equiv 2\theta(X - x') - 1, \tag{79}$$

set X, μ, and β to be dimensionless constants, and investigate how the population varies with β. Here, the young population $x' < X$ suppresses the whole population as $\tilde{K}(x', x) = 1 > 0, x' < X$, while the old population $x' \geq X$ has a positive effect on the whole population since $\tilde{K}(x', x) = -1$, $x' \geq X$, possibly through intraspecific collaboration. The explicit solution for the steady-state population is

$$\begin{aligned} n^*(x) =& \frac{\beta(\beta - \mu)e^{-\beta x}}{\left(1 - 2e^{-\beta X}\right)}, \\ N^* =& \int_0^\infty n^*(x)\mathrm{d}x = \frac{(\beta - \mu)}{\left(1 - 2e^{-\beta X}\right)}. \end{aligned} \tag{80}$$

Upon taking the derivative $\partial_\beta N^*$, we find

$$\frac{\partial N^*}{\partial \beta} = \frac{1 - 2e^{-\beta X} - 2(\beta - \mu) X e^{-\beta X}}{\left(1 - 2e^{-\beta X}\right)^2}, \tag{81}$$

and specifically, $\left(\partial N^*/\partial \beta\right) < 0$ if $2 + 2(\beta - \mu)X > e^{\beta X}$. Therefore, if the interspecific interaction K allows younger individuals to suppress the overall population, the steady-state population can overcompensate by decreasing as the birth rate β is increased.

Appendix F. Analysis of the discretized ODE system Eq. (20)

F.1. Uniqueness of the positive equilibrium of the ODE Eq. (20)

We shall first show that there is at most one positive steady-state solution $\{n_i^*\}$ of the discretized ODE Eq. (20). We will prove by contradiction and assuming two distinct positive equilibria. The positive steady-state solution to Eq. (20), if it exists, satisfies the backward difference equation

$$n^*_{i-1} = \Big(1 + \Delta x \mu_i + \Delta x \sum_{j \geq i} K_{j,i} n_j^*\Big) n_i^*, \quad 1 < i \leq L - 1 \tag{82}$$

$$n^*_{L-1} = \Delta x \left(\mu_L + K_{L,L} n_L^*\right) n_L^* \tag{83}$$

$$\sum_{i=1}^L \beta_i n_i^* = \mu_0 n_0^* + n_0^* \sum_{j=0}^L K_{j,i} n_j^* + \frac{n_0^*}{\Delta x}. \tag{84}$$

We proceed by showing that if $\{m_i^*\}$ and $\{n_i^*\}$ are two positive steady states, then $m_L^* = n_L^*$. If $m_L^* = n_L^*$, then by induction, $m_i^* \equiv n_i^*$. If $n_L^* > m_L^*$, then $n^*_{L-1} > m^*_{L-1}$ by Eq. (83). Since $K_{i,j} \geq 0$, we observe that $K_{L-1,L} n_L^* \geq K_{L-1,L} m_L^*$. This inequality further demonstrates that $n^*_{L-2} > m^*_{L-2}$ combined with Eq. (82). Thus, by induction, $n_L^* > m_L^*$ leads to $n_i^* > m_i^*$ for all $i \in \{0, 1, \ldots, L\}$.

Next, let $n_i(t)$ be solutions to Eq. (20) with the initial value equal to the steady state n_i^*. Let $B(t) := \sum_i \beta_i n_i(t)$ be the newborn population at time t. Then, for any compartment i, the population $n_i(t)$ at time t is composed of two parts: the survivors from the initial $t = 0$ population and those who were born in $(0, t)$. In order to characterize survival, we define $\{s_{i,j}(t)\}_{i,j=0}^L$ to be the solution of

$$\begin{aligned} \frac{\mathrm{d}s_{i,0}(t)}{\mathrm{d}t} =& -\mu_0 s_{i,0}(t) - s_{i,0}(t) \sum_{j=0}^L K_{j,0} n_j(t) - \frac{s_{i,0}(t)}{\Delta x}, \\ \frac{\mathrm{d}s_{i,j}(t)}{\mathrm{d}t} =& -\mu_j s_{i,j}(t) - s_{i,j}(t) \sum_{\ell=j}^L K_{\ell,j} n_\ell(t) \\ &+ \frac{s_{i,j-1}(t) - s_{i,j}(t)}{\Delta x}, \quad 0 < j < L, \\ \frac{\mathrm{d}s_{i,L}(t)}{\mathrm{d}t} =& -\mu_L s_{i,L}(t) - s_{i,L}(t) K_{L,L} n_L(t) + \frac{s_{i,L-1}(t)}{\Delta x}, \end{aligned} \tag{85}$$

with the initial condition $s_{i,j=i}(0) = 1$ and $s_{i,k\neq i}(0) = 0$.

Note that an initial condition $n_i(0) = n_i^*$ implies that $n_i(t) = n_i^*$. Since death rates and interaction terms do not explicitly depend on time, the survival fraction is time-translation invariant, *i.e.*, the survival from compartment i at time $t = 0$ to the compartment j at time $t = T - \tau$ is the same as survival from compartment i at time $t = \tau$ to the compartment j at time $t = T$. Therefore, the solution to Eq. (20) can be written as

$$n_i(t) = \sum_{j=0}^{L} n_j(0) s_{j,i}(t) + \int_0^t B(\tau) s_{0,i}(t-\tau)\mathrm{d}\tau, \tag{86}$$

where $B(t) := \sum_{i=0}^{L} \beta_i n_i(t)$ is the total birth rate at time t. Since every individual eventually dies, we have $\lim_{t\to\infty} s_{i,j}(t) = 0$ for all i, j. Therefore, using the solution in Eq. (86) in $B(t)$, the birth rate can be decomposed into contributions from the initial population and from the population born within time $(0, t)$:

$$B(t) = \sum_{i,j=0}^{L} \beta_j n_i(0) s_{i,j}(t) + \int_0^t B(t-\tau) \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau. \tag{87}$$

At steady state, we introduce the lower and upper bounds of $B(t)$:

$$\begin{aligned} &\int_0^t B(t-\tau) \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau \le B(t) \\ &\le \int_0^t B(t-\tau) \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau + \sum_{i,j=0}^{L} n_i^* \max_i\{\beta_i\} s_{i,j}(t), \end{aligned} \tag{88}$$

where the left-hand side represents the birth rate at time t generated by individuals born within $(0, t)$ and the right-hand side are the birth rate of newborns at time t that are offspring of individuals born within $(0, t)$, plus the maximum possible number of offspring that the initial population could have given birth to up to time t. When $n_i(0) = n_i^*$, $B(t) := B$ is a constant and the limit $t \to \infty$ forces the lower and upper bounds to converge yielding

$$B = B \int_0^\infty \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau, \tag{89}$$

which is the discrete analogue of the $R_0 = 1$ condition of Eq. (63) where the factor $\int_0^\infty \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau$ on the right-hand side is the expected offspring that one individual has during its lifetime.

Similar to the proof of uniqueness in Appendix C, it is intuitively clear that $s_{0,i}(a)$ as well as $\int_0^\infty \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau$ monotonically decreases with increasing effective death rate $\tilde{\mu}_i$. We demonstrate this by explicitly computing

$$\begin{aligned} 1 &= \int_0^\infty \sum_{i=0}^{L} \beta_i s_{0,i}(\tau)\mathrm{d}\tau \\ &= \sum_{i=1}^{L-1} \prod_{j=0}^{i-1} \frac{1}{(1+\Delta x \tilde{\mu}_j)} \int_0^\infty \left(\tilde{\mu}_i + \tfrac{1}{\Delta x}\right) \beta_i t e^{-(\tilde{\mu}_i + 1/\Delta x)t}\mathrm{d}t \\ &\qquad + \prod_{j=0}^{L-1} \frac{1}{(1+\Delta x \tilde{\mu}_j)} \int_0^\infty \mu_L \beta_L t e^{-\tilde{\mu}_L t}\mathrm{d}t, \\ &= \sum_{i=1}^{L-1} \frac{\beta_i \Delta x}{(1+\Delta x \tilde{\mu}_i)} \prod_{j=0}^{i-1} \frac{1}{(1+\Delta x \tilde{\mu}_j)} + \frac{\beta_L}{\mu_L} \prod_{j=0}^{L-1} \frac{1}{(1+\Delta x \tilde{\mu}_j)}, \end{aligned} \tag{90}$$

where $\tilde{\mu}_i := \mu_i + \sum_{j>i} K_{j,i} n_j^*$. The first term on the right-hand side of Eq. (90) is the summation of the expected number of offspring that an individual gives birth to while in the i^{th}, $i < L$ stage multiplied by the probability that it will survive until the ith stage. The second term on the right-hand side is the expected number of offspring that an individual gives birth while in the Lth stage multiplied by the probability that it survives to the Lth stage. If $n_i^* > m_i^*$, $i = 0, \dots, L$ and there exists at least one $K_{j,i} > 0$, then $\tilde{\mu}_i^n > \tilde{\mu}_i^m$ and Eq. (90) cannot be satisfied by two distinct steady-state solutions $\{m_i^*\} \neq \{n_i^*\}$.

F.2. Permanent overcompensation is precluded in two-compartment ODE models

In the following discussion, we will exclude the artificial self-inhibition term $K_{i,i}$ as a result of binning the age structure into a finite number of compartments. We start by considering the simplest two-compartment model by imposing some additional assumptions on the coefficients. Setting $L = 1$ (two compartments) in Eq. (20), we find

$$\begin{aligned} \frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\mu_0 n_0 - K_{1,0} n_1 n_0 + \beta_1 n_1 - \frac{n_0}{\Delta x}, \\ \frac{\mathrm{d}n_1}{\mathrm{d}t} &= -\mu_1 n_1 + \frac{n_0}{\Delta x}. \end{aligned} \tag{91}$$

Eq. (91) admits a unique steady state at

$$(n_0^*, n_1^*) = \left(\frac{\beta_1 - \mu_1 - \mu_0\mu_1\Delta x}{K_{1,0}}, \frac{\beta_1 - \mu_1 - \mu_0\mu_1\Delta x}{K_{1,0}\mu_1\Delta x} \right), \tag{92}$$

which, as is the total population $n_0^* + n_1^*$, monotonically decreasing with either μ_0 or μ_1, indicating that steady-state overcompensation cannot arise. The Jacobian matrix at the fixed point is

$$\mathbf{J} = \begin{bmatrix} -\mu_0 - K_{1,0}n_1^* - \frac{1}{\Delta x} & -K_{1,0}n_0^* + \beta_1 \\ \frac{1}{\Delta x} & -\mu_1 \end{bmatrix}. \tag{93}$$

which has two negative eigenvalues if the equilibrium $(n_0^*, n_1^*) > 0$. Therefore, the steady state is stable and we do not expect periodic oscillations in a small neighborhood around this fixed point. Additionally, $\nabla \cdot (-\mu_0 n_0 - K_{1,0} n_1 n_0 + \beta_1 n_1 - \frac{n_0}{\Delta x}, -\mu_1 n_1 + \frac{n_0}{\Delta x}) < 0$. Thus, from Dulac's criterion, there does not exist a limit cycle in the first quadrant $n_0 > 0, n_1 > 0$. Note that the oscillations demonstrated for a two-compartment model studied in [6] arose from a different form of the birth rate, which we keep constant.

F.3. Undamped oscillations are precluded in a three-compartment model

Setting $L = 2$ in Eq. (20), we obtain

$$\begin{aligned} \frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\frac{n_0}{\Delta x} - \mu_0 n_0 - K_{1,0} n_1 n_0 - K_{2,0} n_2 n_0 + \beta_1 n_1 + \beta_2 n_2, \\ \frac{\mathrm{d}n_1}{\mathrm{d}t} &= -\frac{n_1}{\Delta x} + \frac{n_0}{\Delta x} - \mu_1 n_1 - K_{2,1} n_2 n_1, \\ \frac{\mathrm{d}n_2}{\mathrm{d}t} &= \frac{n_1}{\Delta x} - \mu_2 n_2. \end{aligned} \tag{94}$$

First, we demonstrate that this three-compartment model can exhibit overcompensation by considering a simple specific set of parameters: $\beta_2 = \beta_2' + \mu_2$, $\beta_2' \ge 0$, $\mu_0 = \mu_1 = 0$, $K_{1,0} = K_{2,1} = 0$. Eqs. (94) then simplify to

$$\begin{aligned} \frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\frac{n_0}{\Delta x} - K_{2,0} n_2 n_0 + (\beta_2' + \mu_2) n_2 + \beta_1 n_1, \\ \frac{\mathrm{d}n_1}{\mathrm{d}t} &= \frac{n_0 - n_1}{\Delta x}, \\ \frac{\mathrm{d}n_2}{\mathrm{d}t} &= \frac{n_1}{\Delta x} - \mu_2 n_2 \end{aligned} \tag{95}$$

which admits the positive steady state

$$(n_0^*, n_1^*, n_2^*) = \left(\frac{\beta_1\mu_2\Delta x + \beta_2'}{K_{2,0}}, \frac{\beta_1\mu_2\Delta x + \beta_2'}{K_{2,0}}, \frac{\beta_1\mu_2\Delta x + \beta_2'}{\Delta x \mu_2 K_{2,0}} \right) \tag{96}$$

and the total steady-state population

$$N(\mu_2) := n_0^* + n_1^* + n_2^* = 2\frac{\beta_1\mu_2\Delta x + \beta_2'}{K_{2,0}} + \frac{\beta_1\mu_2\Delta x + \beta_2'}{\Delta x \mu_2 K_{2,0}}. \tag{97}$$

Therefore, $\partial N(\mu_2)/\partial\mu_2 = \frac{2\beta_1\Delta x}{K_{2,0}} - \frac{\beta_2'}{K_{2,0}\mu_2^2\Delta x}$ indicates that the total population at equilibrium $N(\mu_2)$ will increase with the death rate of the oldest population μ_2 if $\mu_2 > \sqrt{\frac{\beta_2'}{2\beta_1\Delta x^2}}$. So in order to observe overcompensation, at least three compartments are needed.

Next, we show that the positive steady state of the three-compartment model Eqs. (94), if it exists, is stable. This statement holds for general parameter values in Eqs. (94). The steady-state populations n_i^* obey the relationships

$$\begin{aligned} n_1^* &= \Delta x \mu_2 n_2^*, \\ n_0^* &= \left(\Delta x + \mu_1 \Delta x^2 + \Delta x^2 K_{2,1} n_2^*\right) \mu_2 n_2^*, \\ \Delta x\, \beta_1 \mu_2 + \beta_2 &= \mu_2 \Big(\mu_0 + \Delta x K_{1,0} \mu_2 n_2^* + K_{2,0} n_2^* + \tfrac{1}{\Delta x} \Big) \\ &\qquad \times \Big(\Delta x + \Delta x^2 \mu_1 + \Delta x^2 K_{2,1} n_2^* \Big). \end{aligned} \tag{98}$$

Therefore, this system contains one real positive fixed point whenever a positive root for n_2^* satisfies the last equation in (98). This occurs for parameters values for which

$$\beta_1 \mu_2 \Delta x + \beta_2 > \mu_2 \left(\mu_0 \Delta x + 1\right)\left(\mu_1 \Delta x + 1\right). \tag{99}$$

The Jacobian matrix at this fixed point is

$$\mathbf{J} = \begin{bmatrix} -\mu_0 - K_{1,0} n_1^* - \frac{1}{\Delta x} - K_{2,0} n_2^* & -K_{1,0} n_0^* + \beta_1 & -K_{2,0} n_0^* + \beta_2 \\ \frac{1}{\Delta x} & -\frac{1}{\Delta x} - \mu_1 - K_{2,1} n_2^* & -K_{2,1} n_1^* \\ 0 & \frac{1}{\Delta x} & -\mu_2 \end{bmatrix} \tag{100}$$

whose eigenpolynomial $f(\lambda) \equiv \det(\lambda \mathbb{I} - \mathbf{J})$ is

$$\begin{aligned} f(\lambda) = &\left(\lambda + \mu_0 + K_{1,0} n_1^* + \tfrac{1}{\Delta x} + K_{2,0} n_2^*\right)\left(\lambda + \tfrac{1}{\Delta x} + \mu_1 + K_{2,1} n_2^*\right)\left(\lambda + \mu_2\right) \\ &+ \tfrac{1}{\Delta x^2}\left(K_{2,0} n_0^* - \beta_2\right) + \tfrac{1}{\Delta x} K_{2,1} n_1^* \left(\lambda + \mu_0 + K_{1,0} n_1^* + \tfrac{1}{\Delta x} + K_{2,0} n_2^*\right) \\ &+ \tfrac{1}{\Delta x}\left(\lambda + \mu_2\right)\left(K_{1,0} n_0^* - \beta_1\right), \end{aligned} \tag{101}$$

where $\mathbb{I}$ is the identity matrix. To simplify this expression, define the effective death rates to be $\tilde{\mu}_0 = \mu_0 + n_1^* K_{1,0} + n_2^* K_{2,0}$ and $\tilde{\mu}_1 = \mu_1 + n_2^* K_{2,1}$. Then, the eigenpolynomial can be expressed as

$$\begin{aligned} f(\lambda) &= \lambda^3 + C_2 \lambda^2 + C_1 \lambda + C_0, \\ C_2 &= \mu_2 + \tilde{\mu}_0 + \tilde{\mu}_1 + \tfrac{2}{\Delta x} \\ C_1 &= K_{1,0} n_1^* \left(\tilde{\mu}_1 + \tfrac{1}{\Delta x}\right) + K_{2,1} n_2^* \mu_2 + \mu_2 C_2 + \tfrac{\beta_2}{\Delta x^2 \mu_2} \\ C_0 &= \tfrac{\mu_2}{\Delta x} \left(K_{1,0} n_1^* \Delta x \tilde{\mu}_1 + K_{1,0} n_1^* + K_{2,0} n_2^* \Delta x \tilde{\mu}_1 \right. \\ &\qquad \left. + K_{2,0} n_2^* + K_{2,1} n_2^* \Delta x \tilde{\mu}_0 + K_{2,1} n_2^* \right) \end{aligned} \tag{102}$$

Here, we have employed Eq. (98) to replace n_0^*, n_1^*, and β_1 by simple terms involving n_2^*. Note that our parameters are all non-negative. We may reasonably parameterize our model such that at least one $K_{i,j} > 0$, at least one $\mu_i > 0$, at least one $\beta_i > 0$, and all $n_i^* > 0$. Under such assumptions, $C_0, C_1, C_2 > 0$. We denote $D_0 = C_1 C_2 - C_0 > 0$. To see that $D_0 > 0$, we just claim that every term in C_0 can be written as one term in the product $C_1 C_2$. For example, the first term $K_{1,0} n_1^* \tilde{\mu}_1 \mu_2$ in C_0 can be written as the product of the $K_{1,0} n_1^* \tilde{\mu}_1$ term from C_1 and the μ_2 term from C_2. Also note that every term in C_1 and C_2 is positive. Thus, we have $D_0 > 0$. Then, by applying the Routh–Hurwitz criterion, the roots of $f(\lambda)$ are all in the open left half-plane, and thus the positive stable equilibrium is stable.

Combining the previous uniqueness statement and the stability analysis, the system Eq. (94) admits at most one positive steady state which must be stable. Therefore, a three-compartment model precludes oscillatory solutions in a close neighborhood around the steady state in the total population since the positive steady state is stable.

F.4. Higher-order reduced ODE models

Next, we consider ODE models with more than two compartments. Previously, each compartment is intended to represent a stage in the life-cycle of the animal, e.g., larva, pupa, adult. In the general case, the birth and death rate of an individual varies across ages, which motivates the consideration of multiple compartments with each compartment representing a small age window, say, one year. From a mathematical perspective, discretization of the age structure is almost necessary to numerically solve the PIDE model, unless other methods like spectral methods are used. The more compartments there are, the more accurate the discretized approximation is.

For higher-order ODE models with $L+1, L \geq 2$ compartments, we can consider the special case

$$\begin{aligned} \frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\frac{n_0}{\Delta x} - K_{L,0} n_0 n_L + \beta_1 n_1 + (\beta_L' + \mu_L) n_L, \\ \frac{\mathrm{d}n_i}{\mathrm{d}t} &= \frac{n_{i-1} - n_i}{\Delta x}, \ i = 1, 2 \ldots, L-1, \\ \frac{\mathrm{d}n_L}{\mathrm{d}t} &= \frac{n_{L-1}}{\Delta x} - \mu_L n_L. \end{aligned} \tag{103}$$

which has the equilibrium

$$\begin{aligned} n_i^* &= \frac{\beta_1 \mu_L \Delta x + \beta_L'}{K_{L,0}}, \ i = 0, \ldots, L-1; \\ n_L^* &= \frac{\beta_1 \mu_L \Delta x + \beta_L'}{K_{L,0} \mu_L \Delta x}. \end{aligned} \tag{104}$$

The total population at equilibrium as a function of μ_L is $N^*(\mu_L) := \sum_{i=0}^{L} n_i^* = L \frac{\beta_1 \mu_L \Delta x + \beta_L'}{K_{L,0}} + \frac{\beta_1 \mu_L \Delta x + \beta_L'}{K_{L,0} \mu_L \Delta x}$. Therefore, $\frac{\mathrm{d}N(\mu_L)}{\mathrm{d}\mu_L} = \frac{L \beta_1 \Delta x}{K_{L,0}} - \frac{\beta_L'}{K_{L,0} \mu_L^2 \Delta x}$, indicating that the total population at equilibrium is increasing with μ_L as long as $\mu_L > \sqrt{\frac{\beta_L'}{L \beta_1 \Delta x^2}}$. Thus, for ODE models with larger number of compartments, overcompensation of the total equilibrium population in response to increases in death rate of certain subpopulations is always possible.

The equilibrium of multi-compartment ODE models, if it exists, could be unstable. We now switch back to the model discussed in the main text in Section 3.5. The numerical solution of the structured population obtained by the finite volume method, which is a 500-compartment ODE Eq. (20) with $L = 499$ displays undamped oscillatory behavior. We numerically analyzed the stability of the positive equilibrium of the PIDE Eq. (7) with the cannibalism rate $K(x', x)$ defined by Eq. (17) and the same age-independent birth rate β and death rate μ as used in Section 3.5. As a surrogate of the PIDE Eq. (7), we numerically analyzed the derived ODE system Eq. (20) in Section 3.5 with $\mathrm{d}x = 0.02$, $L = 499$. In Eqs. (82) and (83), n_{i-1}^* is completely determined by $\left\{ n_j^* : j \geq i \right\}$. Therefore, the steady-state solution $n_i^*, i = 0, \ldots, L-1$ can be parameterized by the value of n_L^*, *i.e.*, $n_i^* = n_i^*(n_L^*)$. Considering the newborn individuals, we employed the bisection method to find a proper positive n_L^* such that Eq. (84) is satisfied.

We then consider the Jacobian matrix $\mathbf{J}(n^*)$ of the dynamical system at the steady state and numerically find its eigenvalues. We denote the principle eigenvalue of $\mathbf{J}(n^*)$ with the largest real part by λ_0. The eigenvector corresponding to λ_0 decays (grows) slowest for $\mathrm{Re}\,\lambda_0 < 0$ ($\mathrm{Re}\,\lambda_0 > 0$) and characterizes the long-term local dynamical behavior of the system. Near the steady state, we found that, corresponding to the region of oscillation described in Fig. 2(f), there is also a region of linearly unstable steady states with $\mathrm{Re}\lambda_0 > 0$ shown in Fig. 4(a).

To better understand the correspondence between oscillation and unstable steady states, we examined real and imaginary parts of λ_0 as a function of β in detail, as shown in Fig. 4(b). When $\beta = 2.5$ is fixed, the real part of the principal eigenvalue $\mathrm{Re}\,\lambda_0$ increases as μ is decreased, vanishing at about $\mu \approx 0.7$. At this point λ_0 (and λ_0^*) become purely imaginary, indicative of a Hopf-type bifurcation. As μ is further decreased, λ_0 and λ_0^* acquire positive real parts. This regime corresponds to the numerical result plotted in Fig. 2(c.d) where undamped oscillations are found to arise when $\beta = 2.5, \mu \leq 0.7$.

Generalizing to more compartments, if the Jacobian matrix $\mathbf{J}_L$ of the positive equilibrium $(n_0^*, \ldots, n_L^*)$ of the $(L+1)$-compartment reduced ODE model Eq. (20) has an unstable equilibrium, we can assume that

$$\mathbf{v}_L \in \mathbb{R}^{L+1}, \ \mathbf{J}_L \mathbf{v}_L = \lambda \mathbb{I} \mathbf{v}_L = (v_1, \ldots, v_L) \neq 0, \ \mathrm{Re}\lambda > 0. \tag{105}$$

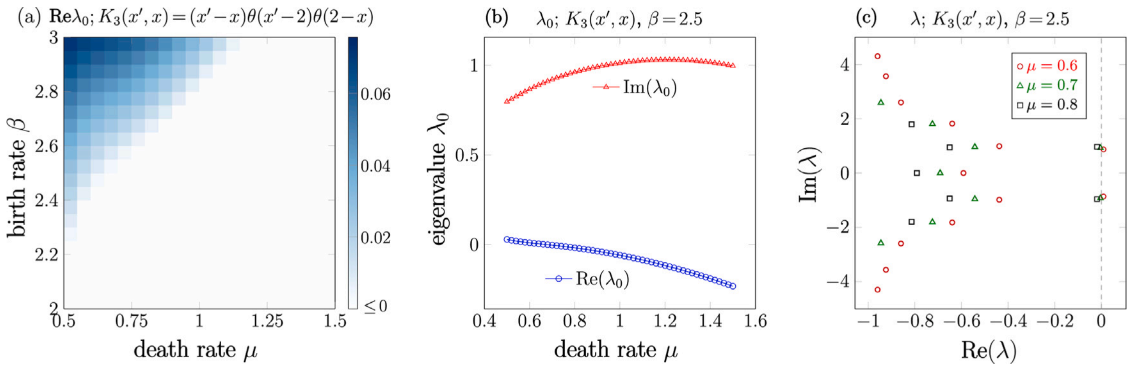

Fig. 4. (a) Heatmap of the real part of the principle eigenvalue λ_0 associated with the Jacobian matrix of the discretized, 500 ODE system Eq. (20) (with $L = 499$) at its fixed point. The top left region takes positive real values. (b) Dependence of the largest eigenvalue λ_0 on μ for $\beta = 2.5$. When μ is small, Re$\lambda_0 > 0$, which indicates an unstable positive equilibrium. In (a) and (b), β, μ are age-independent, and the cannibalism rate is derived from K_3 in Eq. (17). (c) The first five eigenvalues for $\mu = 0.6, 0.7, 0.8$ (open circle, triangle, square, respectively). When $\mu = 0.6$, λ_0 has a positive real part; when $\mu = 0.7, 0.8$, λ_0 has a negative real part, implying stability of the steady state.

For $L' > L$, we can consider the following ODE model

$$\begin{aligned}\frac{\mathrm{d}n_0}{\mathrm{d}t} &= -\mu_0(t)n_0(t) - n_0(t)\sum_{j=i}^{L} K_{j,0}(t)n_j(t) + \sum_{j=1}^{L}\beta_j(t)n_j(t) - \frac{n_0(t)}{\Delta x},\\ \frac{\mathrm{d}n_i}{\mathrm{d}t} &= -\mu_i(t)n_i(t) - n_i(t)\sum_{j=i}^{L} K_{j,i}(t)n_j(t)\\ &\qquad - \frac{n_i(t)-n_{i-1}(t)}{\Delta x}, \quad L \geq i > 0,\\ \frac{\mathrm{d}n_i}{\mathrm{d}t} &= \frac{n_{i-1}(t)-n_i(t)}{\Delta x}, \quad i > L\end{aligned} \tag{106}$$

which has a positive equilibrium $(n_0^*, \dots, n_L^*, n_{L+1}^*, \dots, n_{L'}^*), n_i^* = n_L^*, i > L$. Denoting the Jacobian matrix of the equilibrium of the ODE Eq. (106) to be $\mathbf{J}_{L'}$, it is obvious that λ is also an eigenvalue of $\mathbf{J}_{L'}$ with the corresponding eigenvector

$$\mathbf{v}_{L'} = \left(v_1, \dots, v_L, \tfrac{1}{1+\Delta x\lambda}v_L, \dots, \left(\tfrac{1}{1+\Delta x\lambda}\right)^{L'-L}v_L\right). \tag{107}$$

Therefore, all reduced ODE systems with $L' > L$ compartments have a positive equilibrium whose Jacobian matrix has a positive eigenvalue and the positive equilibrium can be unstable.

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