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Assessing critical population thresholds under periodic disturbances

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Abstract

Population responses to repeated environmental or anthropogenic disturbances depend on complicated interactions between the disturbance regime, population structure, and differential stage susceptibility. Using a matrix modeling approach, we develop a methodological framework to explore how the interplay of these factors impacts critical population thresholds. To illustrate the wide applicability of this approach, we present two case studies pertaining to agroecosystems and conservation science. We apply sensitivity analysis to the two case studies to examine how population and disturbance properties affect these thresholds. Contrasting outcomes between these two applications, including differences in how factors such as disturbance intensity and pre-disturbance population distributions impact population responses, highlight the importance of accounting for demographic features when performing ecological risk assessments.

KEYWORDS
agroecosystem models, conservation science, critical population thresholds, integrated pest management, matrix population models, periodic disturbances, sustainable harvesting

INTRODUCTION

A central theme of ecology is understanding how populations react to disturbance (Battisti et al., 2016; Moloney & Levin, 1996; Winfree et al., 2009). Key to this understanding is elucidating the details of species' population dynamics; experiments and models exploring population drivers have revealed important nuances influencing both birth and death processes in myriad ecological settings (Holmes et al., 1994; Molofsky, 1994; Neverova et al., 2016; Rogers & Munch, 2020). Efforts focused on issues ranging from the conservation of biological diversity and vulnerable species (Battisti et al., 2016) to pest control in agroecosystems (Valpine & Rosenheim, 2008) and a combination of both (Tooker et al., 2020) have explored how disturbance affects species persistence with an eye toward underlying mechanisms. While there have been recent calls to consider the effects of larger scale, "chronic" anthropogenic disturbance on entire ecosystems (Albuquerque et al., 2018), little is known about the effects of continuous, periodic disturbances on species-specific population dynamics (see Liao et al., 2015; Meng & Zhang, 2016). Theoretical and empirical work in this area has important implications for both conservation science and pest management.

The influence of stage structure and stage distribution on population outcomes is another area that has been well developed in the recent decades in ecology (Ackleh et al., 2019; Caswell, 2000; Forbes et al., 2008, 2016; Stark et al., 2004; Stark & Banken, 1999). The intersection of stage-structured population perspectives with biotic or abiotic disturbance is especially important in understanding population regulation (Ackleh et al., 2019;

Banks et al., 2014, 2016; Banks, Dick, et al., 2008; Stark & Banken, 1999). For instance, arthropod life stages often vary in their susceptibility to pesticides, so general assumptions about populations being in stable age distributions may yield overestimates/underestimates of population persistence and extinction (Hilton et al., 1998; Stark et al., 2020; Stark & Banken, 1999). This is a critically important consideration when prescribing optimal control strategies in applied settings; insect populations in annual cropping systems, for instance—with their short growing seasons—often fail to attain stable age distributions during the crucial management period. This has consequences for calculating population thresholds that inform management decisions; critical thresholds in both pest management and conservation of biological diversity may vary with stage structure, level/intensity of disturbance, and predator–prey behavior (Boulanger et al., 2019; Miksanek & Heimpel, 2019).

Matrix models offer a powerful but simple means of describing population dynamics; infused with parameters from laboratory or field studies, these models can provide population projections that are useful as a comparative measure for management decisions (Ackleh et al., 2017, 2019; Banks, Bommarco, et al., 2008; Banks, Dick, et al., 2008; Crouse et al., 1987; Morris & Doak, 2002). Matrix model formulations describing repeated disturbances typically assume periodically or stochastically occurring disturbances that reduce either vital rates or species abundance (Beissinger, 1995; Canales et al., 1994; Giho & Seno, 1997; Hoffmann, 1999; Lirman, 2003; Seno & Nakajima, 1999; Silva et al., 1991; Sletvold & Rydgren, 2007). However, previous studies have primarily focused on long-term persistence metrics that may not always be realized within the relevant time frame of a given application (except see Lirman, 2003). Here, we develop a methodological framework for exploring the interplay of population stage structure and periodic disturbance on transient population dynamics. Using a model parasitoid–host agroecosystem model, we parameterize a simple matrix model with lab-derived data and explore the effects of varying stage structure and periodic disturbance on critical population thresholds. Furthermore, we extend our model formulation to salmonid conservation to illustrate the wide applicability of this approach.

METHODS

Model formulation for a population under periodic disturbances

We model a population using a discrete-time, stage-structured matrix model that allows for the differentiation of developmental stages. We divide a population into m stages, letting the column vector $\mathbf{n}(t) := [n_1(t), n_2(t), \ldots, n_m(t)]^\top$, where $\top$ denotes the transpose of a vector, give the densities of the different stages. Then, in the absence of a disturbance, changes in the population from time t to time $t+1$ are determined by the projection matrix $\mathbf{A}$ according to

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \tag{1}$$

where the matrix $\mathbf{A}$ contains life history information, such as survival and transition probabilities and fecundity. Here, we consider a linear model, which means that $\mathbf{A}$ is constant and does not depend on density-dependent factors. Iterating Equation (1) from an initial population $\mathbf{n}(0)$, we obtain $\mathbf{n}(t) = \mathbf{A}^t\mathbf{n}(0)$. To simplify the presentation, we assume that the life cycle graph derived from the projection matrix is strongly connected and the dominant eigenvalue λ_1 of $\mathbf{A}$ is both strictly dominant and greater than one. These assumptions ensure that the population is able to survive in the absence of a disturbance, and for sufficiently large t, the population grows according to $N(t) \sim cv\lambda_1^t$. Here, v is the strictly positive normalized eigenvector corresponding to λ_1 which is called the stable stage distribution as it gives the long-term proportion of individuals in each stage. See Caswell (2000) for more details.

Disturbances are assumed to occur periodically with magnitude of effect ϵ and frequency $k \geq 1$. When a disturbance occurs, it results in immediate mortality with additional mortality lasting for up to $n-1 \geq 0$ time units so that, in total, the impact of disturbance lasts for n time units. Here, we make the assumption that the effects of the disturbance are greatest when first applied and then decrease over time. For simplicity, we also assume that $n < k$, which means that the effects of a disturbance disappear before the subsequent disturbance occurs. Altogether, this means that population projections every tk time units may be described by the equation:

$$\mathbf{n}(tk) = \left(\prod_{j=0}^{k-1} \mathbf{A}\mathbf{S}_j(\epsilon)\right)\mathbf{n}(t(k-1)), \tag{2}$$

where $\mathbf{S}_j(\epsilon)$ is a diagonal matrix containing the proportional reductions (i.e., death) in stage i, $0 \leq m_{ji} < 1$, following a disturbance event j time units ago. Specifically, $\mathbf{S}_j$ is defined as

$$\mathbf{S}_j(\epsilon) = \begin{cases} \operatorname{diag}(1 - m_{ji}(\epsilon)) & \text{if} \quad 0 \leq j < n, \\ \mathbf{I} & \text{if} \quad j \geq n, \end{cases} \tag{3}$$

where if no disturbance effects are present, then $\mathbf{S}_j$ is the identity matrix $\mathbf{I}$, meaning that no additional mortality occurs. Notice that, under periodic disturbances as described in Equation (2), population survival or extinction is determined by the dominant eigenvalue of the matrix $\prod_{j=0}^{k-1}\mathbf{AS}_j(\epsilon)$.

Model formulations (2) and (3) are similar to those used in Giho and Seno (1997) and Seno and Nakajima (1999), which considered the impact of periodic disturbances on monocarpic plant populations described by two- and three-dimensional projection matrices, respectively. Here, we differ from this formulation in that Equations (2) and (3) assume vital rates are constant but allow for the disturbance to impact a population over multiple time units, whereas in previous studies (Giho & Seno, 1997; Seno & Nakajima, 1999), it is assumed that a disturbance impacts the population for one time unit while restoring vital rates that are decreasing due to environmental degradation.

It is also possible to consider the case where the effects of a previous disturbance event are still present when the next disturbance occurs; that is, $n \geq k$. However, in such a case, it is necessary to make an assumption about how the effects of these different disturbances interact (e.g., additively, synergistically, or antagonistically); we do not consider this complication here.

Matrix formulation for case studies

Model equations (1)–(3) are general enough to be applied to a wide range of species and disturbance regimes. Here, we explore two such scenarios: one related to the control of agricultural pests and another to conservation biology and sustainable harvesting. Each of these scenarios has its own specific projection matrix **A**, describing population dynamics, and disturbance regime, as described by k and $\mathbf{S}_j(\epsilon)$. In what follows, we define these terms for each application.

Application to the biological control agent *Diaeretiella rapae*

In the first application, we consider the parasitoid *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae), a common parasitoid of the economically important cabbage aphid, *Brevicoryne brassicae* (L.), and an important biological control agent for many other aphid species. Because biological control is often coupled with pesticide use in integrated pest management (IPM) schemes, understanding how pesticide spraying may affect biological control agents is critical to IPM success (Hill et al., 2017; Roubos et al., 2014; Stark et al., 2007, 2020).

We model the population dynamics of *D. rapae* using four developmental stages: eggs n_1, larvae n_2, pupae n_3, and adults n_4. Population model (1) is given by

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} s_1(1-\gamma_1) & 0 & 0 & f_4 \\ s_1\gamma_1 & s_2(1-\gamma_2) & 0 & 0 \\ 0 & s_2\gamma_2 & s_3(1-\gamma_3) & 0 \\ 0 & 0 & s_3\gamma_3 & s_4 \end{pmatrix} \times \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}, \tag{4}$$

where s_i denotes the (per unit time) survival probability of stage i, γ_i denotes the probability of a stage i individual maturing to the next developmental stage, and f_4 denotes adult fecundity. Here, we take the unit of time to be one day.

To estimate the life history parameters contained in matrix **A**, we apply laboratory data collected from Acheampong and Stark (2004). Based on these data, we estimate the average stage length as 3 days for eggs, 5 days for larvae, 4 days for pupae, and 10 days for adults. We convert the vital rate estimates collected from Acheampong and Stark (2004) to daily survival probabilities and fecundity. Following Caswell (2000), we estimate the probability of leaving stage n_i by $\gamma_i = 1/T_i$, where T_i is the average time spent in stage n_i. Meanwhile, the per unit time survival probabilities may be determined from the following stage-to-stage survival probabilities found in Acheampong and Stark (2004):

$$\widetilde{s}_1 = 1,\ \widetilde{s}_2 = 1,\ \widetilde{s}_3 = 1,\ \widetilde{s}_4 = 0.1.$$

Specifically, if stage n_i lasts on average T_i time units, then the probability of surviving T_i time units must equal $\widetilde{s}_i$, $s_i^{T_i} = \widetilde{s}_i$. Thus, we have $s_i = (\widetilde{s}_i)^{1/T_i}$. To estimate daily fecundity, we divide the total reproductive output by the number of adults to get the average reproductive output per adult and then divide this by the average length of time spent in the adult stage. Parameter estimates used in model (4) to describe *D. rapae* are provided in Table 1. We note that the data collected from Acheampong and Stark (2004) were obtained under ideal laboratory conditions and we would not, in general, expect 100% survival of the immature stages in field conditions.

In this application, we assume that life history parameters are constant in time. The eggs of *D. rapae* are laid within hosts; in particular, this means that hosts (i.e., aphids) must already be established in the field. As a result, the assumption that constant fecundity is appropriate for short-term (transient) dynamics is considered here.

To describe the effect of toxicant spraying on *D. rapae*, we apply the data obtained from Stark et al. (2020), which assessed the toxicity of imidacloprid to the pupa and adult stages of *D. rapae* for field spray concentrations $\epsilon = \{0, 1/8, 1/4, 1/2, 1\}$; see Figure 1a. In Stark et al. (2020), spray concentration was defined as the proportion of aphids that the toxicant would kill. For example, a field spray concentration of $\epsilon = 1/2$ is assumed to result in the death of $1/2$ of the aphids. Since the egg and larva stages occur within live hosts, we

TABLE 1 Daily life history parameter estimates for *D. rapae*.

Unit of time	s_1	s_2	s_3	s_4	γ_1	γ_2	γ_3	f_4
Day	1	1	1	0.7943	1/3	1/5	1/4	2.545

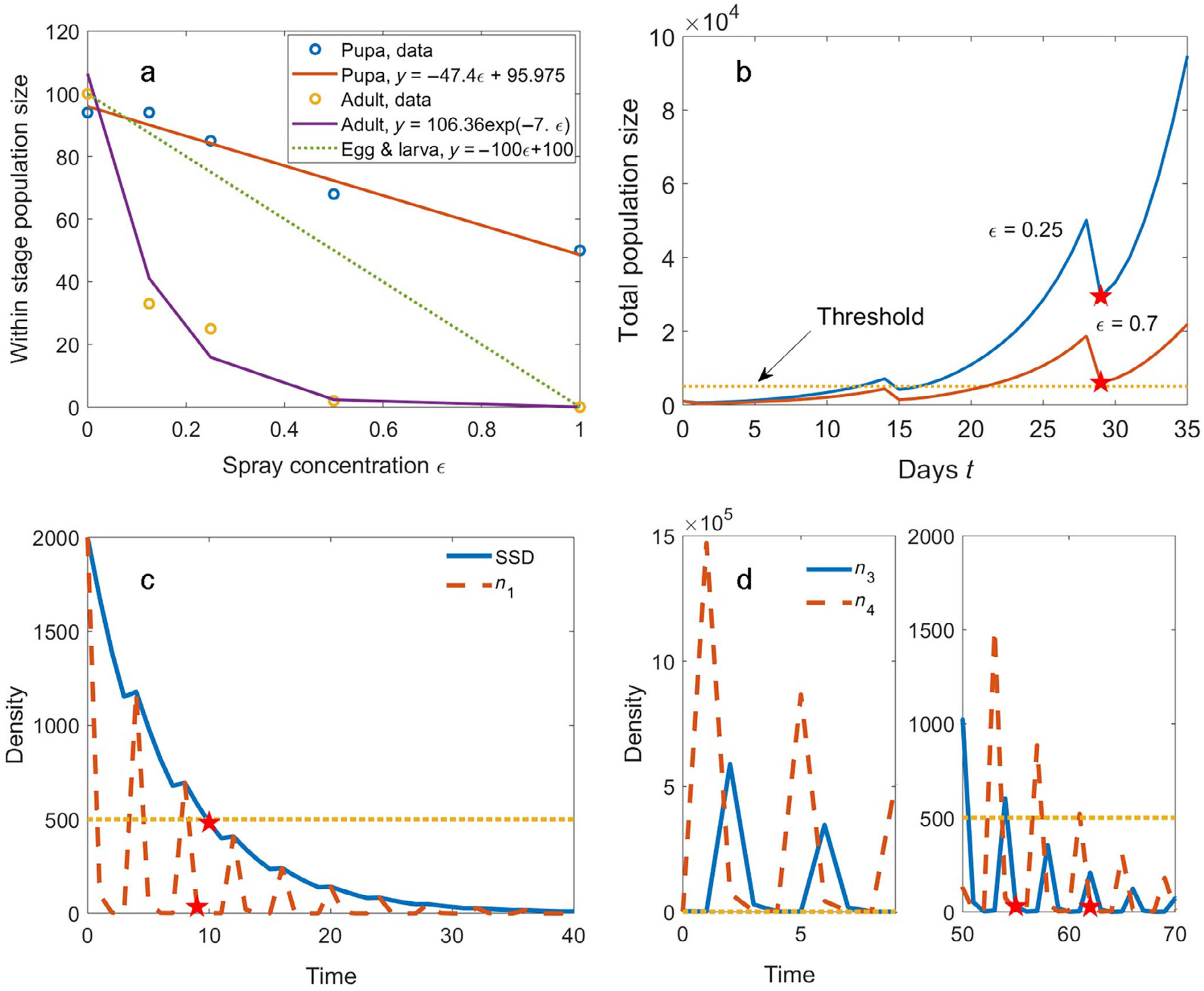

FIGURE 1 (a) Pupa and adult mortality as a function of the spray concentration ϵ (Stark et al., 2020). (b) Total population size of *D. rapae* over time assuming an initial population of 1000 pupae, a spray frequency of $k = 14$ days, and a spray concentration of $\epsilon = 0.25$ and $\epsilon = 0.7$. (c, d) Total population size of salmonids over time assuming an initial population size of 2000, yearly harvesting, and a 20% harvesting strategy. We consider four different initial distributions: (c) the stable stage distribution (solid blue line) and all neonates (dashed red line); (d) all young reproductives (solid blue line) and all mature reproductives (dashed red line). For graphing purposes, we omit the case where the initial distribution is all juveniles, which results in a threshold time of 32 years. In graphs (b–d), the population threshold is indicated by a yellow dotted line and the time to reach the threshold is indicated by a red star.

assume that spray concentration also gives the proportion of eggs and larvae of *D. rapae* that are killed by the toxicant. Meanwhile, in order to define mortality effects for any spray concentration, $0 < \epsilon < 1$, for the pupa and adult stages, the data from Stark et al. (2020) were fit to a linear function for the pupa stage and an exponential function for the adult stage, as shown in Figure 1a.

The data provided in Stark et al. (2020) describe immediate mortality effects, but no long-term effects on the vital rates. In the model formulation described above, this corresponds to the case where $n = 1$. Thus, Equation (2) simplifies to

$$\mathbf{n}(tk) = \mathbf{A}^k \mathbf{S}(\epsilon)\mathbf{n}(t(k-1)), \tag{5}$$

where $\mathbf{S}(\epsilon) = \mathrm{diag}(1 - m_i(\epsilon))$. In Figure 1b, we provide an illustration of how periodic spraying of imidacloprid would affect the population dynamics of *D. rapae* when the frequency is two weeks ($k = 14$) and the spray concentration is either $\epsilon = 0.25$ or $\epsilon = 0.7$. Notice that in the long term (i.e., as t approaches infinity), the total population size of *D. rapae*, as shown in Figure 1b, would grow unbounded. However, here we are interested in a single growing season, such as the summer growing season in the northern hemisphere, which lasts approximately 105 days (Stark et al., 2020).

Application to harvested salmonids

Our second application concerns conservation science and sustainable harvesting. Specifically, we consider the Chinook and Coho salmon (*O. tshawytscha* and *O. kisutch*) using the life history parameter estimates provided in Banks et al. (2010). The matrix equation for these salmonids is given by

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & s_4 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}, \tag{6}$$

where the stages represent neonates n_1, juveniles n_2, young reproductives n_3, and mature reproductives n_4, and the unit of time is taken to be one year. Parameters s_i and f_i represent survival and fecundity of stage n_i, respectively, and are provided in Table 2.

For this application, we consider the impact of harvesting on species growth. In what follows, we assume that harvesting occurs annually ($k = 1$), all stages but the neonate stage are harvested, and harvest amounts for each stage are proportional to abundance of that given stage. Thus, population dynamics under harvesting are described by Equation (5) with $k = 1$. Figure 1c,d demonstrates the impact of harvesting on the salmonid population for four different initial distributions.

TABLE 2 Yearly life history parameter estimates for salmonids, Banks et al. (2010).

Unit of time	s_1	s_2	s_3	s_4	f_3	f_4
Years	0.05	0.05	0.5	0	0.3	920

Assessment of periodic disturbances: Thresholds and sensitivity

The long-term impact of periodic disturbances, specifically species persistence or extinction, may be assessed through asymptotic analysis, as determined by the dominant eigenvalue λ_1. However, since this analysis applies only after a long period of time, the results may not be realized in a relevant time scale, such as a growing season. An alternative approach, which we take here, is to consider the short-term, or transient, effects of disturbances.

To evaluate the transient effects of disturbances, we make use of the concept of a *population threshold*. Specifically, we assume that the population under consideration has some threshold density $\overline{N}$ for which we either want to maintain the population above or below. We also assume that we do not have continuous population data. That is, rather than knowing the population size at every time point, we assume that the population is periodically censused either just before or just after a disturbance is imposed. Since population size over time will be oscillatory due to the periodicity of disturbances, as shown in Figure 1b, we define the time it takes to reach the population threshold to be the first time either the local maximum (obtained just before a disturbance) or local minimum (obtained immediately after a disturbance) population size is above or below the desired threshold. This conservative perspective ensures that the population will remain above or below the threshold value for all subsequent time. Note that these thresholds do not account for cases in which there is a hormetic effect of pesticide disturbance on predators or prey (Cutler et al., 2022).

If the population under consideration starts below the threshold $\overline{N}$, then to determine how long it takes the population to be above this value (and then remain above), we need to solve for the first time the local minimum is above the threshold. That is, we need to find the smallest integer t such that

$$\mathbf{1}_m^\top \mathbf{A}\mathbf{S}_0(\epsilon)\left[\prod_{j=0}^{k-1}\mathbf{A}\mathbf{S}_j(\epsilon)\right]^t \mathbf{n}(0) \geq \overline{N}, \tag{7}$$

where $\mathbf{1}_m$ denotes an $m \times 1$ column vector of ones. The solution t_{crit} tells us that the threshold is achieved at time $T = t_{\text{crit}}k + 1$. In what follows, we apply this criterion to study *D. rapae*, as may be appropriate if the parasitoid wasp is introduced into an agricultural field and a certain density is desired to ensure control of a pest species. In the example provided in Figure 1b, the time at which the threshold is reached is indicated by a red star. Notice here that both spray concentrations result in the same threshold time.

Alternatively, if the population under consideration starts above the threshold $\overline{N}$, then to determine how long it takes for the population to be below this value (and then remain below), we need to solve for the first time the local maximum is below the threshold. That is, we need to find smallest integer t such that

$$\mathbf{1}_m^\top \left[\prod_{j=0}^{k-1}\mathbf{A}\mathbf{S}_j(\epsilon)\right]^t \mathbf{n}(0) \leq \overline{N}, \tag{8}$$

where the solution t_{crit} tells us that the threshold is achieved at time $T = kt_{\text{crit}}$. We use this second equation in the fisheries application. In this case, we wish to know how long a certain harvesting strategy can be maintained before the population gets below the threshold value (see Figure 1c,d).

For a given application, the threshold time is impacted by both the initial population distribution and the nondominant eigenvalues of the projection matrix. In particular, though a population eventually approaches its stable stage distribution, it may initially exhibit oscillatory dynamics. Therefore, the above inequalities are formulated under the assumption that oscillations due to transient dynamics are negligible compared with the oscillations created by the periodic disturbance. If this assumption is not satisfied in a particular application, then the formulas derived may still be applied after first shifting the initial condition to be beyond the period of significant transient oscillations. Here, we observe that the threshold time may vary significantly depending on the initial distribution and that initial trajectories may exhibit significant oscillations due to stage structure (Figure 1c,d).

The maximum possible duration of transient oscillations is determined by the damping ratio defined as $\rho = \lambda_1/|\lambda_2|$, where λ_2 is the subdominant eigenvalue. Specifically, a solution converges to the stable stage distribution exponentially with a rate at least as fast as $\log\rho$. In Figure 2, we provide damping ratios for each application under a range of disturbance regimes. It is noticeable that in the application to *D. rapae* the damping ratio is significantly larger, particularly when disturbance events are not frequent. Intuitively, we should expect that, for less frequent disturbances (large k), the solution to (2) stabilizes faster (i.e., the damping ratio is larger). For example, suppose that $\mathbf{S}_j(\epsilon) = s_j(\epsilon)\mathbf{I}$; that is, each stage in the population is impacted by the same amount. In this case, the eigenvalues of the matrix $\prod_{j=0}^{k-1}\mathbf{A}\mathbf{S}_j(\epsilon)$ are given by $\lambda_i^k \prod_{j=0}^{k-1} s_j(\epsilon)$ where λ_i is an eigenvalue of $\mathbf{A}$. Since the ratio $\lambda_1/|\lambda_2| > 1$, the damping ratio increases as k increases.

In addition to obtaining the solution triplet (ϵ, k, T), we also calculate how sensitive this solution is to model parameters. The sensitivity of an output variable y with respect to additive changes in an input variable x is defined as the derivative $\frac{dy}{dx}$. A related measurement, elasticity, describes the effect of proportional changes and is defined as $\frac{x}{y}\frac{dy}{dx}$. Elasticity is often preferred over sensitivity

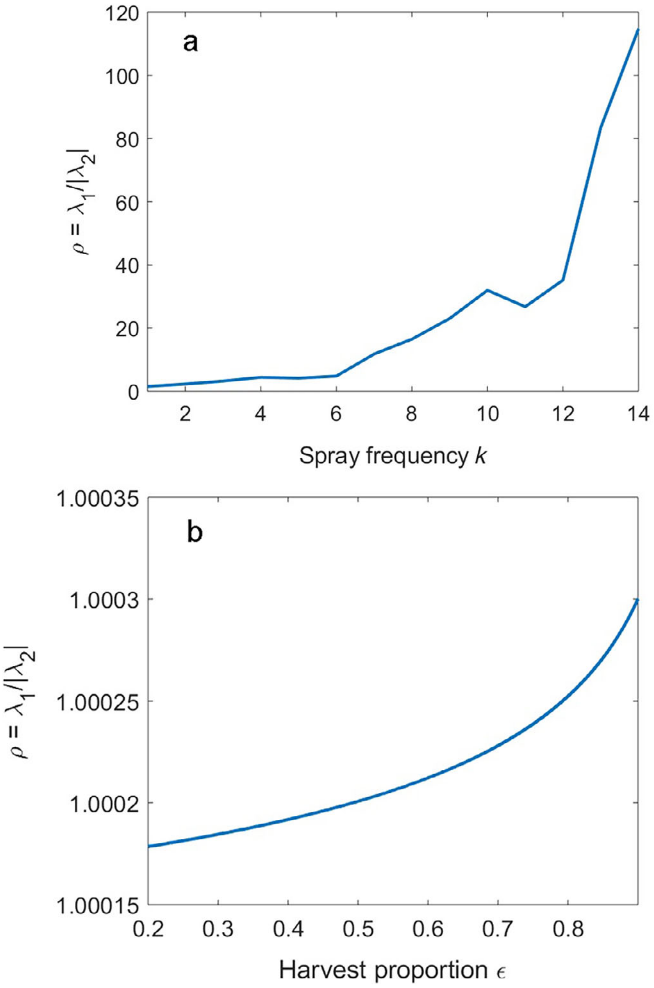

FIGURE 2 Damping ratios for the matrix $\mathbf{A}^k\mathbf{S}(\epsilon)$ for each application. (a) The damping ratio when applied to *D. rapae* for a spray concentration fixed at $\epsilon = 0.5$ and (b) to salmon when the harvest frequency is annual; that is, $k = 1$.

as it allows for the comparison of variables that may be on different scales (Caswell, 2000; Morris & Doak, 2002). Therefore, we mainly focus on this second metric.

Here, we take the approach of considering the sensitivity of threshold time T to properties of the population or disturbance regime. There are two options for calculating these sensitivities from the implicit inequalities (Equations 7 and 8). The first is to numerically calculate the derivative of T using a numerical scheme such as a forward difference equation. Alternatively, under certain technical assumptions on the projection matrix, we may derive explicit expressions for this derivative by implicitly differentiating the threshold inequalities. See Appendix S1 for more details. Similar approaches, which combine implicit differentiation with properties of matrix calculus, have previously been applied to study the sensitivity of other metrics for transient dynamics (Ackleh et al., 2019; Caswell, 2007, 2013, 2019).

RESULTS

We apply the developed methodology to the two case studies: the parasitoid wasp and the salmonid species. Though the threshold time is technically integer-valued, in all graphs we instead report the real-valued solutions since, even though two different scenarios may produce the same integer-valued time to threshold, there may still be significant variation in the population size over time which may result in significantly different economic or environmental impacts (Figure 1b). Therefore, differences in the real solution for the threshold time indicate differences in the population's responses to the tested scenarios.

Application to *D. rapae*

For simulation purposes, we take an initial population size of $N_0 = 1000$ and a threshold size of $\overline{N} = 5000$. For this application, all figures were generated numerically using the standard forward difference approximation. However, the sensitivity formulas provided in Appendix S1 may also be applied here. We also note, as shown in Appendix S1, that the threshold times and their sensitivities are dependent on the ratio $\overline{N}/N_0$ but not on the specific values of $\overline{N}$ and N_0.

Effects of initial stage distribution

We found that the initial stage distribution has a marked influence on the threshold time. To explore this interplay, we compared the extreme cases in which all individuals are in exactly one developmental stage with the case in which individuals are distributed according to the stable stage distribution given by $\mathbf{n}(0) = N_0(0.4199, 0.3418, 0.1488, 0.0896)^\top$ (Figure 3a). We found that the threshold was reached soonest (28.83 days) if all individuals began as pupae, while it took almost four times longer (110.90 days) if all individuals began as adults. In practice, the former scenario may often be the case since *D. rapae* are typically introduced into the field as mummies (pupae). However, if the parasitoid is already established in the field before spraying begins,

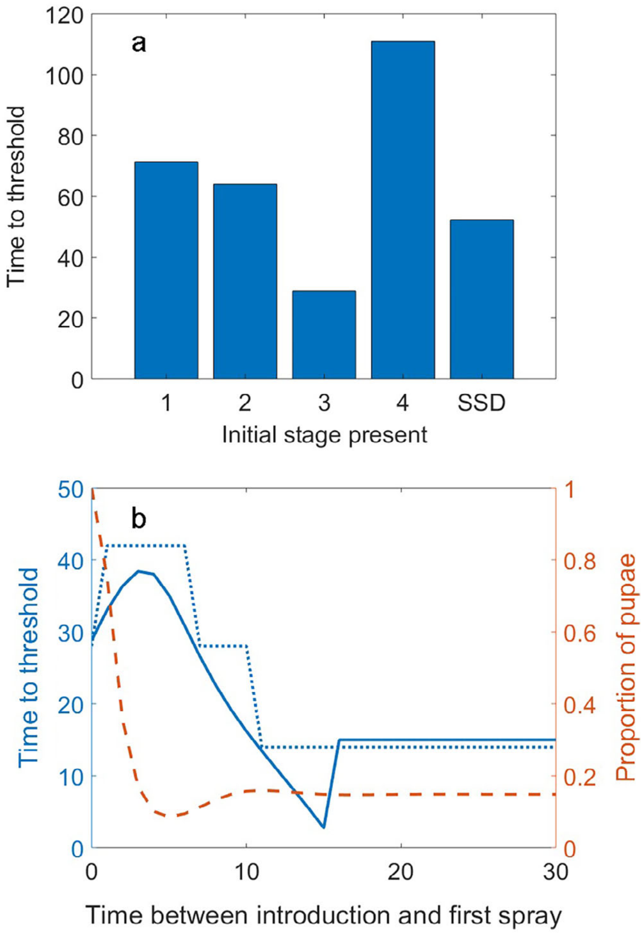

FIGURE 3 (a) The threshold time given an initial distribution in which all individuals are in exactly one developmental stage or the stable stage distribution (SSD). (b) The left axis is the time to reach the population threshold given the number of days between the introduction of parasitoid mummies and the next pesticide spay. Here, the solid blue line gives the real solution to the threshold inequality while the dotted blue line gives the integer solution. The right axis indicates how the proportion of the population that are pupae changes following introduction (in the absence of spraying). For both simulations, the spray concentration is $\epsilon = 0.9$ and the frequency is $k = 14$ days.

then it may be at its stable stage distribution in which case the threshold is reached in 52.28 days. If parasitoids are introduced as pupae, in the absence of spraying, the stable stage distribution is reached in approximately two weeks, which corresponds to when the proportion of pupae becomes constant (Figure 3b). Furthermore, a delay between the introduction of parasitoid pupae and the first spray event in which parasitoids are present greatly modifies threshold times. In particular, spraying one to six days after the pupae are introduced results in a longer threshold time than if pupae introduction and spraying occur concurrently (Figure 3b). This is because the threshold is exceeded before any spraying occurs, and spraying cannot lower the population back below the threshold. Meanwhile, the shortest threshold time is achieved if spraying occurs 15 days after the introduction of pupae. We also note that the threshold time becomes constant after 16 days.

Threshold elasticities with respect to stage distribution

Next, we consider the elasticity of the threshold time with respect to the initial population distribution. In order to calculate threshold elasticities, we assume that the parasitoid population is at its stable stage distribution, which means that spraying occurs after the parasitoid population is established in the field. Because a population distribution vector must add up to one, an increase in one stage must be compensated by a decrease in at least one of the other stages. We compared two different compensation strategies, which we refer to as "proportional" and "one-for-one" (Figure 5). In the proportional compensation scheme, we assume that an increase in one stage results in decreases in the other three stages with this decrease being proportional to the relative abundance of each of the three stages. For example, if the initial distribution is given by $(x_1,x_2,x_3,x_4)^\top$, and stage one is increased by δ, then stage i, $i=2,3,4$, is decreased by $\delta x_i/(x_2+x_3+x_4)$ (Figure 4a). Because the elasticity of the threshold time with respect to the proportion of pupae is negative, this indicates that the population reaches the threshold sooner if the proportion of pupae is increased, as is to be expected based on Figure 3a. Meanwhile, an increase in the proportion of individuals in any of the other stages results in an increase in the time to the threshold. For example, a small proportional increase in the number of pupae reduces the threshold time by 19.51% while an equal proportional increase in the number of eggs increases the threshold time by 17.95%. In addition, we may conclude that, when the population is at its stable stage distribution, proportional perturbations in the pupae stage have the greatest overall effect on the threshold time.

The second compensation scheme, "one-for-one," simply describes a strategy in which a perturbation in one stage is compensated by an equal but opposite perturbation in another stage. This results in a pattern similar to the first compensation strategy in which changes in the proportion of pupae, particularly decreases in this proportion, have a greater effect overall (Figure 4b).

We compared these perturbation results (Figure 4c) with the effects on threshold hold time stemming from perturbations from a uniform distribution; that is, $\mathbf{n}(0)=N_0(1/4,1/4,1/4,1/4)^\top$. In this case, both the sensitivity and the elasticity of the threshold time with respect to the adult stage are larger compared with the first two immature stages (Figure 4c). Thus, increasing the adult proportion will have a greater effect on increasing the threshold time than increasing either of the first two stages.

Threshold elasticities with respect to spray regime

Sensitivity analysis revealed a complex interaction between spray regimes and threshold times. For the relationship between threshold time and both elasticity with respect to spray concentration (Figure 5a) and sensitivity with respect to decreases in spray frequency (Figure 5b), we see that moving from left to right corresponds to a more intense spray regime. In both cases (Figure 5a,b), we see that the harsher the spray regime, the more pronounced effect changes in the regime have on the threshold time (i.e., for more frequent spraying or higher pesticide concentrations). In contrast, as the time between sprays increases, the sensitivity of the threshold approaches zero. Hence, when spraying is infrequent, the effect of small changes in the frequency becomes negligible. For example, if the spray frequency is every two weeks and the concentration is 50%, then the time to the threshold is 18.91 days. Making the spray regime stronger by decreasing k or increasing ϵ by 50% increases the threshold time by 17.16 and 11.85 days, respectively. Alternatively, increasing k or decreasing ϵ by 50% decreases the threshold time by 2.45 and 5.62 days, respectively.

Threshold elasticities with respect to vital rates

Finally, we calculated the threshold time and its elasticity with respect to decreases in the survival and transition probabilities for *D. rapae* (Figure 5c,d). This analysis considers decreases rather than increases in survivorship since

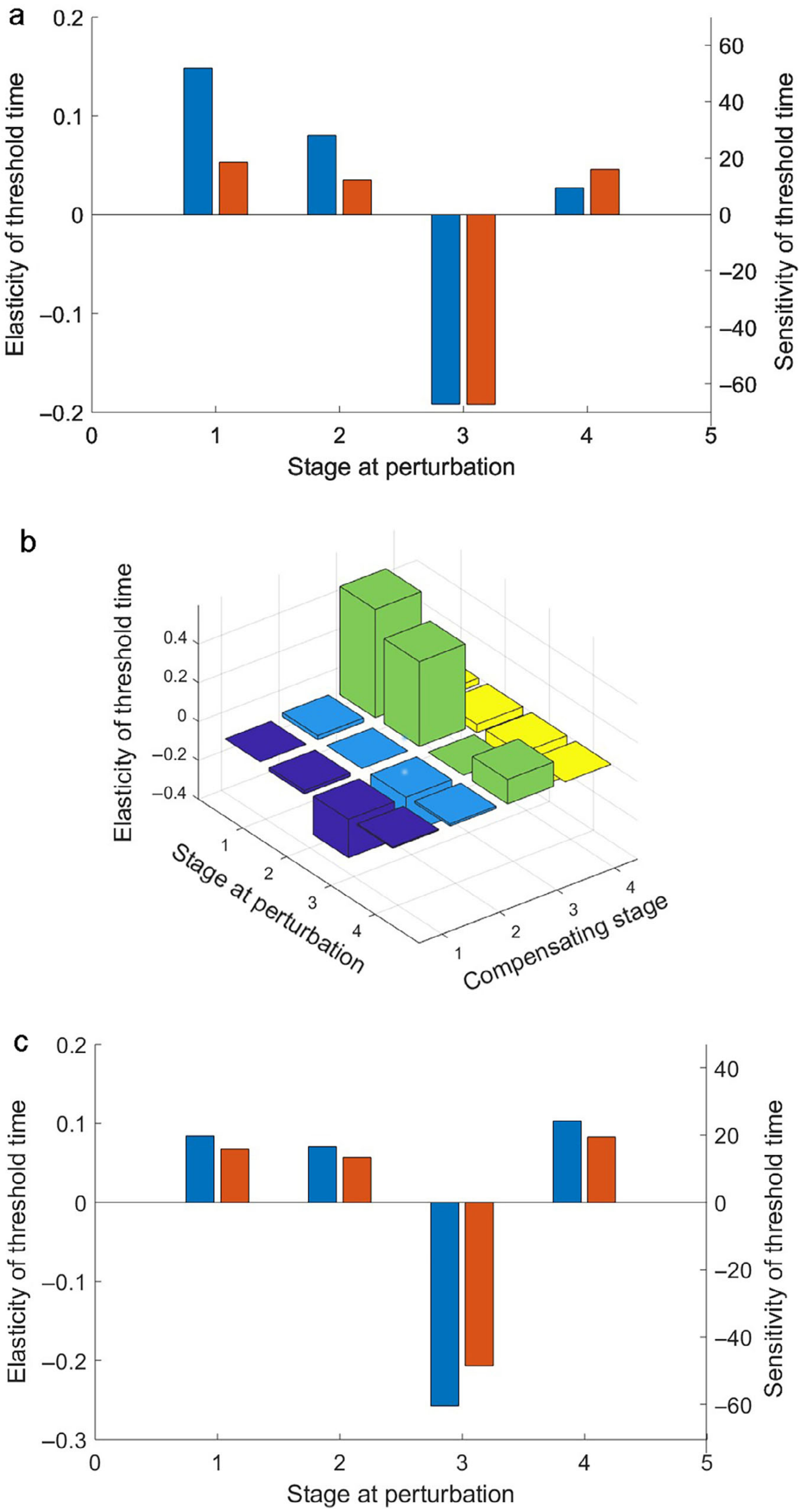

FIGURE 4 (a, b) Elasticity of the threshold time with respect to two compensating strategies when the initial distribution is given by the stable stage distribution and spraying occurs every 14 days with spray concentration $\varepsilon = 0.9$. For this scenario, the threshold time is 52.27 days. (a) An increase in one stage is compensated by a proportional decrease in the other three stages. Here the left blue bars represent elasticity and the right red bars represent sensitivity. (b) An increase in one stage is compensated by an equal decrease in another stage. Graph (c) is the same as (a) except with a uniform initial distribution.

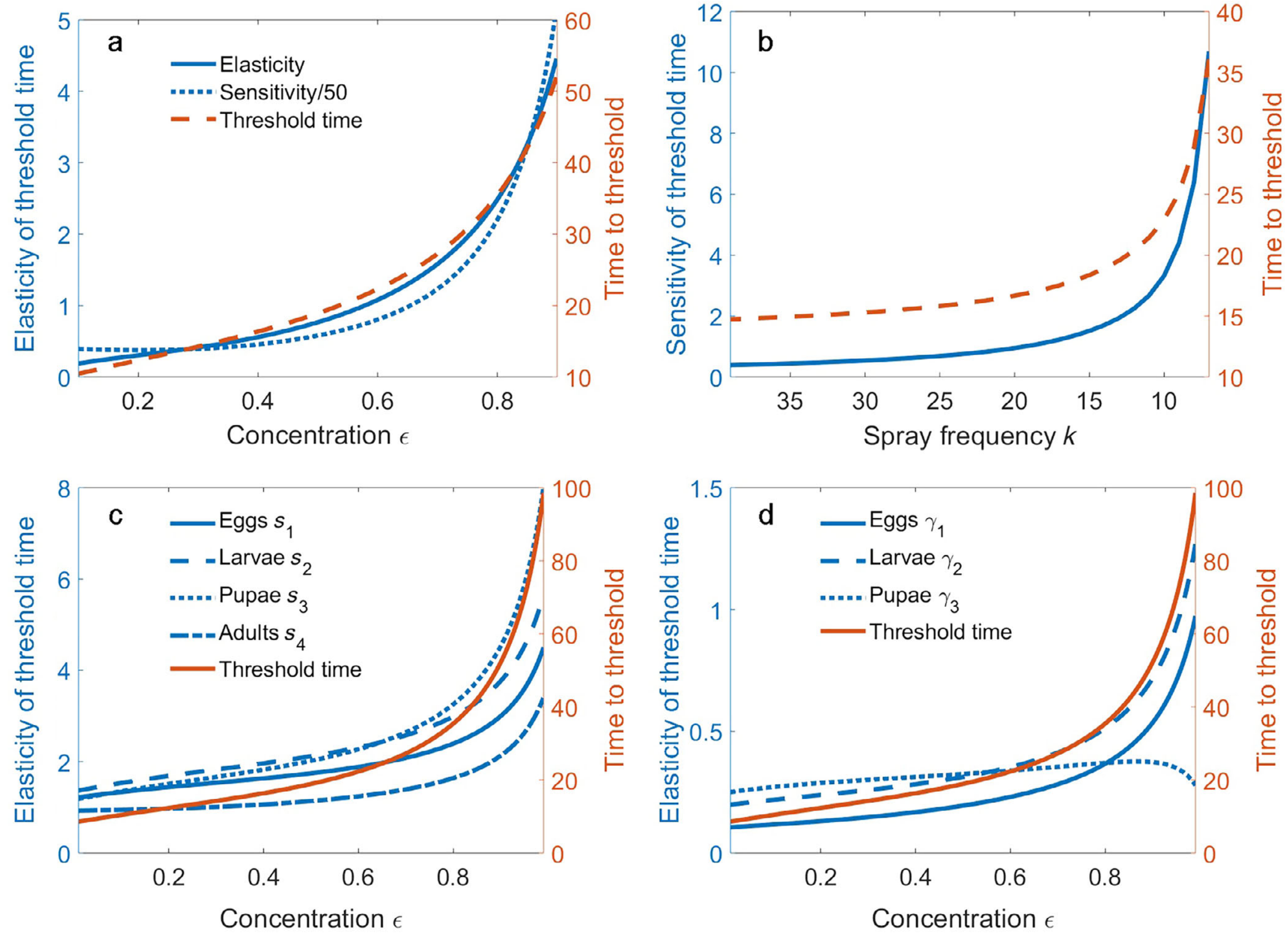

FIGURE 5 (a) Threshold time (in days) and elasticity with respect to the spray concentration ε when the spray frequency is 14 days. For graphing purposes, sensitivity has been scaled by dividing by 50. (b) Threshold time (in days) and sensitivity with respect to decreases in the spray frequency k when the spray concentration is $\epsilon = 0.5$. (c, d) Threshold time (in days) and elasticity with respect to decreases in (c) the survival probabilities and (d) the maturation probabilities when the spray frequency is 14 days.

our parameter estimates have 100% survival for the immature stages. As is expected, decreasing survival or maturation probabilities increases the time to reaching the threshold. For the survival probabilities, changes in the pupa and larva stages have the greatest effect. Meanwhile, for the maturation probabilities, changes in the larva stage have the greatest effect while changes in the pupa stage have almost a constant effect for all ϵ values.

Application to salmonids

For simulation purposes, we take an initial population size of $N_0 = 2000$ with individuals initially distributed according to the stable stage distribution of $\mathbf{A}$. Specifically, we take $\mathbf{n}(0) = N_0(0.9508, 0.02459, 0.0022, 0.0011)^\top$. We assume a population threshold of $\overline{N} = 500$ and consider annual harvesting; that is, $k = 1$. We also assume that all stages but the neonates are harvested with an equal harvest proportion ϵ which we vary. Since the sensitivity formulas provided in Appendix S1 are not applicable to this application, here the sensitivities used to generate all graphs were calculated numerically using the standard forward difference approximation.

Threshold elasticities with respect to stage distribution

We compared the effect of a proportional compensation scheme when the initial distribution is either the stable stage distribution (Figure 6a) or a uniform distribution (Figure 6b). When the initial population is given by the stable stage distribution, an increase in the number of individuals in one of the two reproductive stages increases the threshold time, meaning that the more

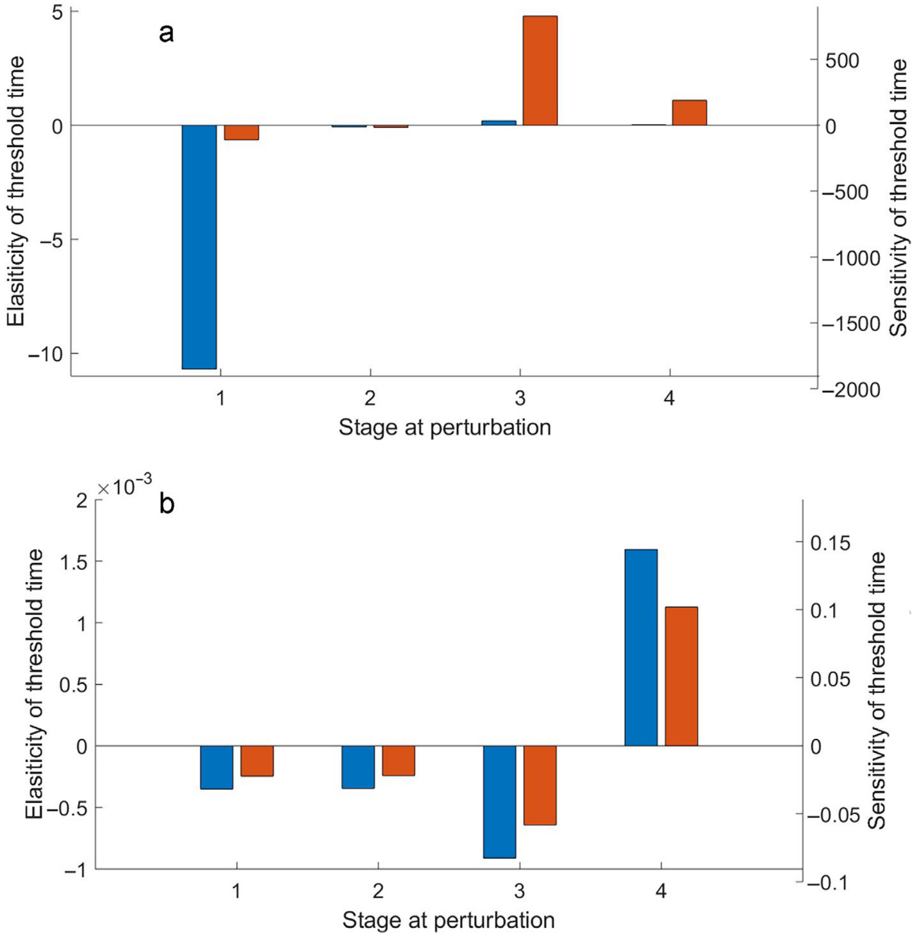

FIGURE 6 The elasticity (left blue bars) and sensitivity (right red bars) of the threshold time with respect to a proportional compensation strategy when the harvest proportion is 20%, harvesting occurs annually, and the initial distribution is given by (a) the stable stage distribution or (b) a uniform distribution. With this harvesting strategy, the threshold time is 10 years for (a) and 50 years for (b).

reproductive individuals in a population, the slower the population will reach the threshold time (Figure 6a). In contrast, only increases in the mature reproductive stage increase the threshold time when the initial distribution is uniform (Figure 6b). As in the previous application, when the initial distribution is given by the stable stage distribution, elasticity and sensitivity calculations produce different results with elasticity being most sensitive to proportional changes in the neonate stage, while sensitivity is most sensitive to additive changes in the young reproductive stage (Figure 6a). However, when the number of individuals is the same for all stages, changes in the two reproductive stages have the greatest effect on the threshold time (Figure 6b).

Threshold elasticities with respect to harvest regime

Increases in the harvest proportion when that proportion is small cause a greater decrease in the threshold time than equal increases at larger harvest proportions (Figure 7). Due to the small dampening ratio, the threshold time as a function of ϵ is not a smooth curve (Figure 7a). This results in oscillations in both elasticity and sensitivity.

Threshold elasticities with respect to vital rates

The threshold time is most sensitive to changes in the vital rates of the first two immature stages, while it is significantly less sensitive to changes in the survival of the mature reproductives (Figure 7b). Moreover, though the elasticities exhibit a general downward trend as the harvesting rate increases, they do so in an oscillatory manner.

DISCUSSION

The threshold inequalities provided in (7) and (8) and the corresponding elasticities of the threshold time provide a

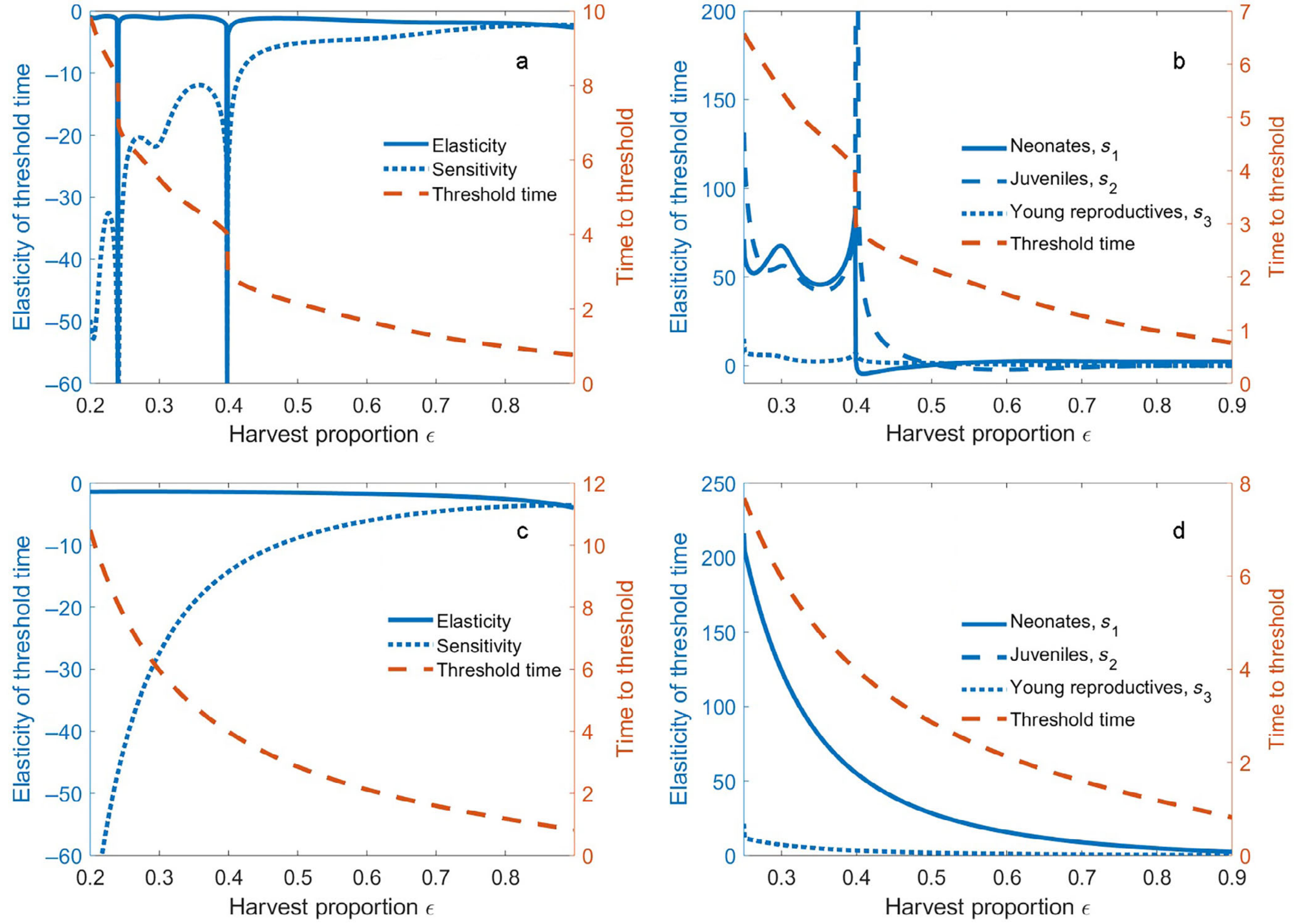

FIGURE 7 (a) Threshold time (in years) and elasticity with respect to the harvest proportion ϵ when harvesting occurs annually. (b) Elasticity of the threshold time with respect to survival probabilities when harvesting occurs annually. Vertical asymptotes in elasticities occur at $\epsilon = 0.24$ and $\epsilon = 0.398$ in (a) and at $\epsilon = 0.401$ in (b) as a result of the derivative of the threshold time being undefined at these points. Graphs (c, d) are the same as (a, b) except with the initial distribution given by the stable stage distribution of $\mathbf{AS}(\epsilon)$ rather than $\mathbf{A}$.

method for assessing the impact of reoccurring periodic disturbances, as are common when a population is impacted by anthropogenic disturbance. The two applications presented here highlight the importance of accounting for demographic properties of the population, such as initial stage structure and differential susceptibility, as these properties can heavily impact predictions.

When *D. rapae* are exposed to a pesticide, changes under harsher pesticide regimes have a greater effect on the threshold time. Specifically, increases in the pesticide concentration at high concentrations increase the threshold time more than equal increases at low concentrations (Figure 5a). Similarly, changes in the spray frequency at higher frequencies have a greater impact on the threshold time than equal changes at lower frequencies (Figure 5b). This suggests that managers need to be more cautious when making changes to a control strategy with heavy pesticide use. In contrast, when a salmonid population is harvested, changes in small harvesting proportions have a greater impact on the recovery time than changes in larger harvest proportions (Figure 7a).

Since the threshold time is a transient property of the population dynamics, it is impacted by the initial population distribution. In general, we should expect a population with a larger proportion of mature reproductives to grow faster since these individuals are able to more quickly contribute to the creation of new individuals. This occurs for salmonids where increasing the number of individuals in the mature reproductive stage increases the threshold time, allowing for a given harvesting strategy to be sustainable for a longer period of time (Figure 6). However, when we account for life stage differential susceptibility to a disturbance, this may no longer be the case. Since imidacloprid results in high mortality in adult parasitoids but relatively low mortality in pupae (Figure 1a), the threshold time is reached sooner if we increase the number of individuals in the pupa stage. Moreover, the threshold time is reached sooner when there are more immature individuals (eggs or larvae) than when there are more adults (Figure 4c). Thus, this application emphasizes the importance of quantifying disturbance effects at the developmental stage, not just at the population level.

The initial population distribution also influences how elasticity and sensitivity calculations are interpreted. For example, suppose a manager wants to know whether the threshold time will be reached sooner if the number of parasitoid eggs is increased or the number of adults is increased. When the parasitoid population is at its stable stage distribution, for equal proportional increases (elasticity), it is better to increase the number of adults, but for equal additive increases (sensitivity), it is better to increase the number of eggs (Figure 4a). This seemingly contradictory result, which is even more noticeable in the salmonid application (Figure 6a), is due to the fact that, in the stable stage distribution, the proportions of individuals in each of these two stages differ in magnitude. Specifically, though these proportions are on the same scale (i.e., between zero and one), the proportion of adults is an order of magnitude smaller than the proportion of the first two immature stages. Therefore, an equal additive increase results in a more significant increase in the adult stage, while an equal proportional increase has the opposite effect. As a result, this question can better be addressed by examining perturbations from the uniform distribution (Figures 4c and 6b).

In addition to the initial population distribution, underlying properties of the population structure can also affect the threshold time and its sensitivities. Since the damping ratio for *D. rapae* is much larger than that for salmonids (Figure 2), the transient dynamics for *D. rapae* are short relative to the threshold time. This resulted in the threshold time and its elasticities being smooth, monotonic curves (Figure 5) that produce straightforward predictions. In contrast, the elasticity of the threshold time with respect to the harvest proportion and survival probabilities for salmonids changes in an oscillatory manner as the harvest proportion is increased (Figure 7a,b). That these oscillations are a result of the transient dynamics of this system may be verified by starting the initial distribution to be the stable stage distribution of the projection matrix $\mathbf{AS}(\epsilon)$ of the disturbed population rather than the projection matrix $\mathbf{A}$ of the undisturbed population (Figure 7c,d).

Though the oscillations observed in the salmonid application are an interesting mathematical phenomenon, from a management perspective, they may be disregarded. Specifically, since the amplitude of the oscillations is of the same order of magnitude as the elasticities, these oscillations result in only minor concavity changes in the threshold time curve that do not change its overall decreasing pattern as the harvest proportion increases. However, it remains an open question as to whether more extreme oscillations may occur in other applications such that these result in oscillations in the threshold time itself.

Stage-structured models have been effectively used in the management of myriad taxa, especially in agricultural systems where predictions of pest and natural enemy population dynamics outcomes can critically inform management strategy decisions (Banks, Bommarco, et al., 2008; Bommarco, 2001; Westerberg & Wennergren, 2003). Applications to conservation also abound, ranging from plants (Menges, 2000) to bighorn sheep (Conner et al., 2018) to seabirds (Koehn et al., 2021) to Monarch butterflies (Grant et al., 2020) to sea turtles (Crouse et al., 1987). The latter example famously resulted in legislation being enacted aimed at bolstering conservation of an endangered species as a result of model predictions (Crowder et al., 1994). Although translating science into policy is a complex undertaking (Murray & Sandercock, 2020), stage-structured matrix models provide a powerful means of evaluating resource management strategies and informing action and policies.

We present here a general framework for a threshold model, based on stage-structured matrix models, that may be applied to a wide range of applications amenable to being modeled with stage-structured matrix models. This approach is tailored to posing management what-if scenarios, enabling resource managers to define acceptable outbreaks of/declines in population levels and then to explore different management strategies and their resulting population consequences. We suggest that this framework may be easily combined with more specific/complex models to tackle specific management decisions. For instance, the framework could be used in conjunction with recent advances to better estimate the ratio of natural enemy to pests for optimal augmentative biological control releases (Gontijo & Carvalho, 2020). We anticipate that this approach may be further expanded and modified to fit a wide range of applications.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript were obtained from the following published manuscripts: Acheampong and Stark

(2004); Banks et al. (2010); Stark et al. (2020). Specifically, the following data were used from each manuscript: Data collected from Acheampong and Stark (2004) were used to estimate life history parameters for *D. rapae*. These data have been reproduced in Ackleh et al. (2023) with the authors' permission. The life history parameters provided in tab. I of Banks et al. (2010) were used to parameterize the projection matrix for the salmonid application. These parameters have been provided in Table 2 of this manuscript. The data provided in tabs. 3 and 4 of Stark et al. (2020) were used to parameterize the matrix $\mathbf{S}(\epsilon)$ for the *D. rapae* application. These data have also been reproduced in Figure 1a of this manuscript. Code used to generate the results (Ackleh et al. 2023) is available from Figshare: https://doi.org/10.6084/m9.figshare.21728246.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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