

# Enhancing population stability with combined adaptive limiter control and finding the optimal harvesting–restocking balance

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## ARTICLE INFO

### Article history:

Received 7 June 2019

Available online 30 September 2019

### Keywords:

Population size fluctuations

Outbreak risk

Culling

Population augmentation

Discrete-time model

## ABSTRACT

Fluctuations in population size may have negative consequences (e.g., an increased risk of extinction or the occurrence of repeated outbreaks), and many management strategies are aimed at avoiding them by either only restocking or only harvesting the population. Two of these strategies are adaptive limiter control (ALC) and adaptive threshold harvesting (ATH). With ALC the population is controlled by only restocking and with ATH by only harvesting. We propose the strategy of combined adaptive limiter control (CALC) as the combination of ALC and ATH and study the potential advantages of CALC over ALC and ATH. We consider two different population models, namely a stochastic overcompensatory model and a host–pathogen–predator model. For the first model, our results show that the combination of restocking and harvesting under CALC improves the constancy stability of the managed populations when the harvesting and restocking intensities are high enough. Otherwise the effect is marginal or in rare cases negative. For the second model, we show that combining harvesting with restocking reduces the outbreak risk only if the harvesting intensity is low. For medium harvesting intensities the effect is marginal and for high harvesting intensities the risk of outbreaks is increased. In addition, we study the optimal harvesting–restocking balance by considering a proxy of the benefit obtained in terms of the reduction in the outbreak risk and the harvesting and restocking costs.

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## 1. Introduction

In the last decades, the concern about the consequences of population oscillations for ecosystems has grown (Barraquand et al., 2017). These fluctuations are ubiquitous (Elton, 1924; Ranta et al., 1998; Lundberg et al., 2000) and have multiple causes (Royama, 1992; Kendall et al., 1999; Turchin, 2003; Barraquand et al., 2017). Although they may have positive effects, e.g., increased biodiversity (Armstrong and McGehee, 1980; Huisman and Weissing, 1999) or enhanced persistence in metapopulations because of desynchronization (Allen et al., 1993), their consequences can also be negative, e.g., more variable yield of exploited populations (Wilson et al., 1990), the occurrence of pest outbreaks (Dwyer et al., 2004), increased extinction risk (Rosenzweig, 1971) or the loss of genetic variability and increased inbreeding (Bijlsma et al., 2000; Allendorf and Luikart, 2007).

Potential management strategies to deal with population fluctuations have recently come into focus (Barraquand et al., 2017).

They can be aimed at maintaining oscillations because of their positive effects but at avoiding some undesirable aspects (Hilker and Westerhoff, 2007b), or at inducing certain responses at targeted points in time (Hilker and Westerhoff, 2007a). Many management strategies, however, are concerned with reducing fluctuations to avoid some of their negative consequences. Two of these strategies are adaptive limiter control (ALC) and adaptive threshold harvesting (ATH). ALC supplements the population size to a certain proportion of its value in the preceding time step, provided the population size has fallen below this proportion (Sah et al., 2013). By contrast, ATH culls the population size to another proportion of its value in the preceding time step, provided the population size has increased above this proportion (Segura et al., 2016). ALC has been demonstrated to work in experimental populations and metapopulations of *Drosophila melanogaster* (Sah et al., 2013), and both ALC and ATH have been analytically and numerically investigated (Franco and Hilker, 2013; Sah et al., 2013; Franco and Hilker, 2014; Sah and Dey, 2014; Tung et al., 2014; Segura et al., 2016, 2017). Like ATH and ALC, many other strategies are aimed at reducing fluctuations in population size by either exclusively culling or supplementing the population,

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e.g., different harvesting strategies like constant-yield, constant-effort and threshold harvesting (Fryxell et al., 2005; Sinclair et al., 2006) or constant (McCallum, 1992; Stone, 1993) and proportional (Güemez and Matías, 1993) feedback strategies.

The combination of harvesting and restocking has proved useful for the management of many populations, e.g., aqua-cultured fish (Bell et al., 2006, 2008; Lorenzen, 2008), game species of birds and mammals (Champagnon et al., 2012), sea urchins (Couvray et al., 2015) or prawns (Taylor, 2017). Moreover, control strategies that combine the removal and restocking of individuals of a population have been shown in mathematical models to be generally very effective, e.g., both limiter control (BLC) (Tung et al., 2014, 2016a,b) or target-oriented control (TOC) (Dattani et al., 2011; Franco and Liz, 2013; Tung et al., 2016b; Braverman and Franco, 2017). These strategies expand the range of choices for the control and allow the users to achieve management goals that would not be possible by either only restocking or only culling the population (Tung et al., 2016b).

When combined, restocking and harvesting can play a central role in population management. For instance, in the case of coastal fisheries (Bell et al., 2006), when the goal is to restock depleted populations, the release of juveniles should be combined with large reductions in culling. By contrast, when the goal is to overcome recruitment limitation, releases may be combined with relatively high culling efforts. In this paper, we propose a new management strategy that allows for both restocking and harvesting by combining ALC and ATH. If the population size grows beyond a certain proportion, ATH is applied to cull part of the increase, whereas if the population size declines below another proportion, ALC is applied to restock part of the diminished population. We will refer to this strategy as *combined adaptive limiter control* (CALC).

CALC avoids the state variable becoming too low or too high. This is somewhat analogous to certain biological processes at the level of organism homeostasis. One example is the integral rein control (Saunders et al., 1998), in which glucagon inputs prevent blood glucose from becoming too low and insulin inputs prevent blood glucose from becoming too high.

The novelty of CALC with respect to other strategies combining restocking and harvesting is that it is ‘adaptive’ (like the strategies ALC and ATH that it combines), given that the magnitude of the intervention depends on the proportion between the population sizes in the current and previous generations. This adaptiveness can have important advantages. One of them is that it allows to implement the control in cases in which the knowledge of the underlying dynamics is poor. Moreover, Franco and Hilker (2013) showed that the intervention magnitude of ALC was lower than that of lower limiter control (LLC) (Hilker and Westerhoff, 2005) in their simulations. One might expect that there is a similar advantage of CALC over BLC.

How to combine harvesting and restocking will depend on biological, economic and social factors (Lorenzen, 2005, 2008; Taylor, 2017). In particular, the economic side seems to often play a central role. For instance, in the case of aqua-cultured fishes, the cost of hatchery fish can determine the optimal management. At a high cost, no increase in the total yield and stock abundance is expected (Lorenzen, 2005). An example of this is the management of Alaskan pink salmon, which has proved uneconomic under current conditions (Boyce et al., 1993; Hilborn, 1998). By contrast, high efforts of both fishing and restocking can be optimal when the cost is low (Lorenzen, 2005), this being the case for Japanese chum salmon (Arnason, 2001; Morita et al., 2006). Another example of the relevance of the economic aspect is the release of hatchery-reared sea urchins in wild populations. In that case, restocking can recover local productivity (Juinio-Menez et al., 2008a,b), but the high cost of hatchery sea urchins can make the

management uneconomic (Lawrence, 2013; Couvray et al., 2015). In this paper, in addition to studying the stabilizing effect that can be attained by the combination of restocking and harvesting under CALC, we analyze the trade-off between this stabilizing effect and the cost of the management interventions.

The main goal of this paper is to show in which cases CALC may be advantageous over ALC and ATH. Since the aim is to reduce fluctuations in the population size, we will only consider the application of these strategies to unstable populations. Optimal management strategies are commonly determined by optimizing a single objective function, e.g., the maximum sustainable yield (Schaefer, 1954; Chapman et al., 1962; Clark, 1976; Stevenson, 1978) or the maximum economic yield (Anderson, 1975; Kompas, 2005; Dichmont et al., 2010; Guillen et al., 2013; Reid et al., 2013). In our case, such an approach would provide specific values for harvesting and restocking efforts at the optimum but no information for other values. Contrary to this, our aim is to provide a more holistic view by studying the behavior of the managed populations for all possible combinations of harvesting and restocking and for different stability criteria. We are convinced that adopting such a perspective enriches the analysis. In this sense, the reader is cautioned to not expect absolute conclusions about which is the “best” strategy.

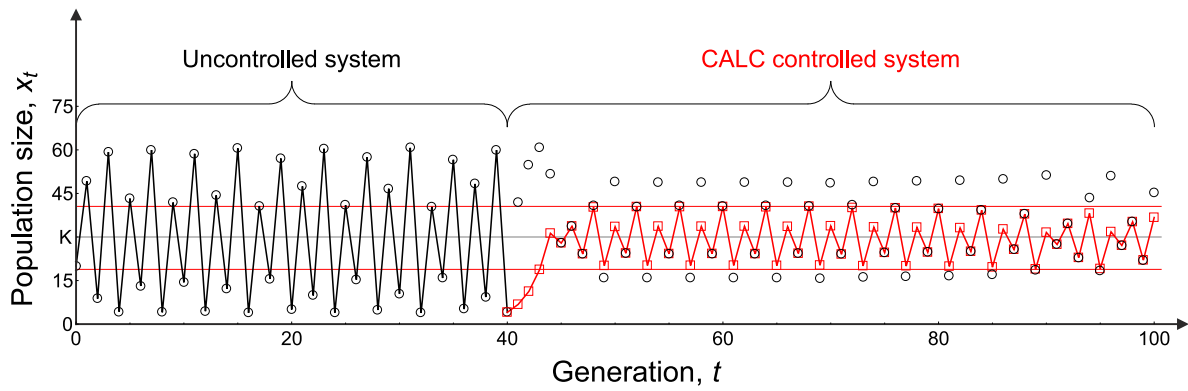
In the next section, we describe CALC in mathematical terms and introduce CALC as a management strategy in different population models. Section 3 studies the effect of CALC on the constancy stability of a stochastic population with overcompensation. Section 4 analyzes the capability of CALC to prevent outbreaks of forest-defoliating insects in a stochastic three-species model. We also consider the economic benefit that would be obtained by reducing outbreaks depending on both the restocking and harvesting costs. Section 5 extends the discussion of our results and draws conclusions.

## 2. Models and methods

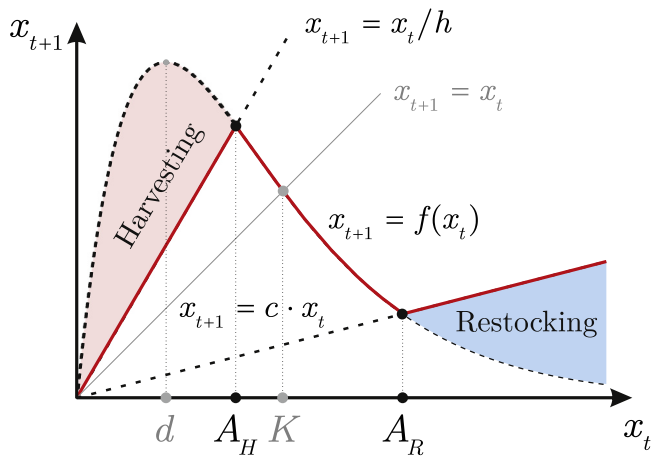
### 2.1. Combined adaptive limiter control

CALC aims at reducing the fluctuations in population size by avoiding crashes and outbreaks. Let  $x_t$  be the population size at time step  $t$ . If  $x_t$  drops below a certain proportion of its value in the previous generation (which we denote by  $c \cdot x_{t-1}$ , with  $c \in (0, 1)$ ), individuals are restocked to that proportion. We will refer to  $c$  as the *restocking intensity*, since higher values of  $c$  correspond to higher restocking efforts. If  $x_t$  exceeds another proportion of  $x_{t-1}$  (which we denote by  $x_{t-1}/h$ , with  $h \in (0, 1)$ ), the population is harvested to that proportion. Notice that we have denoted the proportion of  $x_{t-1}$  that determines when individuals are removed by  $x_{t-1}/h$ , with  $0 < h < 1$ , instead of  $h \cdot x_{t-1}$ , with  $h > 1$ . This allows us to interpret  $h$  as a *harvesting intensity*, since higher values of  $h$  correspond to lower values of  $1/h$ , and thus to higher removal efforts. Moreover, both control intensities ( $c$  and  $h$ ) range in the same interval  $(0, 1)$ .

The control strategy described above can be seen as the combination of ALC and ATH, both of which are able to reduce the fluctuations in the population size (Franco and Hilker, 2013; Sah et al., 2013; Franco and Hilker, 2014; Sah and Dey, 2014; Tung et al., 2014; Segura et al., 2016, 2017). Fig. 1 illustrates that CALC shares this property with them. Moreover, CALC is an adaptive management strategy because the magnitude of the intervention is nonconstant and depends on the proportion between the population sizes in the current and the previous generation. It differs from other strategies for which the magnitude of the intervention is also nonconstant, like proportional feedback, for which a fixed proportion of the population is harvested or restocked every generation (Güemez and Matías, 1993). In the case of CALC, no



**Fig. 1.** During the first 40 generations the population is uncontrolled and its dynamics are described by the Ricker map  $f(x) = x \exp(r(1 - x/K))$  with  $r = 2.7$  and  $K = 30$ . In the next 60 generations, the population is managed by CALC with intensities  $c = 0.5$  and  $h = 0.6$ . Black circles (red squares) correspond to the population size before (after) the control intervention. The horizontal red lines represent the limits of the interval that traps the size of populations managed according to CALC with the given control intensities (see Eqs. (B.2) and (B.3) in Appendix B.2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** CALC function (2) in red solid line, for a given map  $f$  in dashed line describing the underlying dynamics. The red area corresponds to the cases in which the population is harvested, and the blue to those in which it is restocked. Value  $d$  corresponds to the abscissa of the maximum of  $f$ ,  $K$  is the carrying capacity of the uncontrolled population, and  $A_H$  and  $A_R$  are respectively harvesting and restocking activation thresholds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

action is taken if the proportion between population sizes in two consecutive generations is within the stipulated limits  $c$  and  $1/h$ .

To further understand the effect of CALC and its relation with ALC/ATH, assume that the underlying population dynamics, i.e., in the absence of CALC, are given by

$$x_{t+1} = f(x_t), \quad x_0 \in [0, +\infty), \quad t \in \mathbb{N}, \tag{1}$$

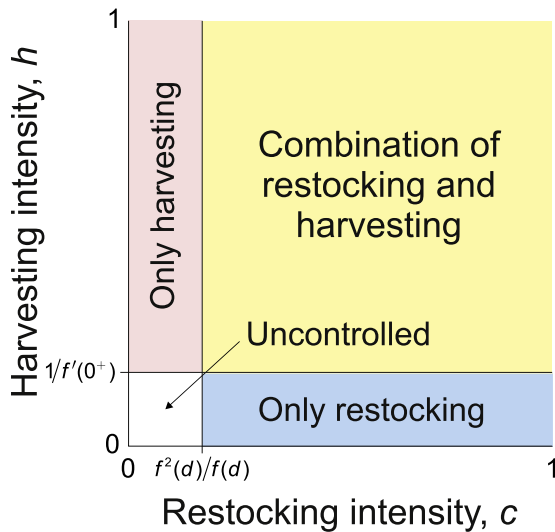
where  $f: [0, +\infty) \rightarrow [0, +\infty)$  is a continuously differentiable hump-shaped production function with two fixed points, namely (i) the extinction state  $x = 0$  and (ii) a positive equilibrium  $x = K$ , which corresponds to the carrying capacity of the population. Many common models with overcompensatory dynamics satisfy these conditions, e.g., the Ricker (1954), Hassell (1975) and generalized Beverton–Holt (Bellows, 1981) model. Assuming that the population is managed by CALC with intensities  $c, h \in (0, 1)$  after reproduction has taken place leads to (see Appendix A)

$$x_{t+1} = \max\{\min\{f(x_t), x_t/h\}, c \cdot x_t\}. \tag{2}$$

We can see CALC as a general framework for adaptive limiters, including both ALC and ATH as particular cases if we allow the control parameters to be null. Given that  $c$  and  $h$  respectively represent the restocking and harvesting intensities,  $c = 0$  corresponds to only harvesting (ATH) and  $h = 0$  to only restocking (ALC). However, the latter is not well defined in Eq. (2). To overcome this, we redefine the equation describing CALC with  $h = 0$  to  $x_{t+1} = \max\{f(x_t), c \cdot x_t\}$ . The CALC map for various production functions is studied in Appendix C.

Fig. 2 shows function (2) with  $c, h \in (0, 1)$  for a certain map  $f$  describing the underlying dynamics (which is compatible, for instance, with the Ricker map). The population is harvested when the population size  $x$  is such that the graph of  $f$  is strictly above the straight line  $y = x/h$ . Similarly, the population is restocked when the graph of  $f$  is strictly below  $y = c \cdot x$  (cf. Fig. 2). Therefore, in case the population is controlled, the type of intervention (harvesting or restocking) depends on the population size in the previous generation, the control intensities  $c$  and  $h$ , and the production function  $f$ . It is important to highlight that restocking and harvesting cannot take place simultaneously at a given time since  $c < 1/h$ . Yet, for certain combinations of control intensities, the population can be restocked at some time steps and harvested at other time steps. For the sake of simplicity, we will refer to this case as the *combination* of restocking and harvesting throughout the rest of this paper. Similarly, for certain values of the control intensities interventions can consist of harvesting only or restocking only. Given a production function  $f$ , we can determine for which control intensities the population will remain uncontrolled and for which control intensities the interventions used in CALC will consist of only harvesting, only restocking or a combination of harvesting and restocking (cf. Fig. 3 and Appendix C).

In Appendix B, we rigorously prove the following two results. These results also exist in similar form for ALC and ATH (Franco and Hilker, 2013; Segura et al., 2016), so we show that they translate to the two-parametric strategy of CALC. First, there are two activation thresholds  $A_H$  and  $A_R$  that respectively allow us to know in advance about the need of harvesting or restocking the population in the following time step. More specifically, harvesting is not necessary if the population size in the preceding generation was above  $A_H$ , while restocking only takes place if the population size in the preceding generation was above  $A_R$  (cf. Fig. 2 and Appendix B.1). Second, the stabilizing effect of CALC is reached by “trapping” the population size in a certain interval around the carrying capacity, the length of which decreases with the control intensities (cf. Fig. 1 and Appendix B.2).



**Fig. 3.** Type of intervention (restocking, harvesting or a combination of both) for the production function  $f$  represented in Fig. 2 in terms of the control intensities. Value  $f(d)$  is the maximum of the population production, achieved by populations with size  $d$ , and  $f^2 = f \circ f$ . The first generation was omitted for the determination of the type of intervention in the only restocking area. See Appendix C for more details.

## 2.2. Simulations

To study the pros and cons of CALC versus ALC and ATH, we perform several numerical experiments with two different population models.

### 2.2.1. CALC of a stochastic overcompensatory population

The first model is based on the Ricker map and includes environmental and demographic stochasticity as well as a lattice effect (Henson et al., 2001). We use the negative-binomial-environmental (NBe) model introduced by Melbourne and Hastings (2008). This model reads  $x_{t+1} \sim \text{NegBinom}(f(x_t), \alpha)$ , where  $\text{NegBinom}$  denotes the negative-binomial distribution,  $f$  is the deterministic production function of the population and  $\alpha$  is a parameter driving the shape of the distribution. Specifically, we consider for numerical simulations the equation

$$x_{t+1} = \begin{cases} \max\{\min\{z_t, x_t/h\}, c \cdot x_t\}, & h > 0, \\ \max\{z_t, c \cdot x_t\}, & h = 0, \end{cases} \quad (3)$$

with  $z_t \sim \text{NegBinom}(x_t \exp(2.7(1 - x_t/30)), 100)$  and  $(c, h) \in [0, 1) \times [0, 1)$ . This describes the dynamics of a population subject to both demographic and environmental stochasticity that is managed by CALC with restocking intensity  $c$  and harvesting intensity  $h$ , and for which the uncontrolled deterministic dynamics are described by the Ricker model with growth parameter  $r = 2.7$  and carrying capacity  $K = 30$ . Moreover, the discrete character of the statistical distribution that is considered implies the integerization of population size. Note that Eq. (3) does not account for measurement error in the population census.

With this equation, we study the effect of CALC on the constancy stability of managed populations, which refers to the propensity of the population size to remain essentially unchanged (Grimm and Wissel, 1997). It has been previously reported that the effect of management strategies can sometimes be stabilizing or destabilizing depending on which constancy measure is used (see, for example, Segura et al., 2016). In this sense, it is important to rely not just on one measure, because this could give results that do not hold for other measures. In view of this, we consider three different measures of the constancy stability,

namely the fluctuation index (FI), the fluctuation range (FR) and the coefficient of variation (CV). The FI is a dimensionless measure of the average one-step variation of the population size scaled by the average population size in a certain period. It was introduced by Dey and Joshi (2006) and employed by Franco and Hilker (2013) and Sah et al. (2013) to study stability properties of ALC and by Segura et al. (2016) to study stability properties of ATH. Mathematically, the FI is given by

$$\text{FI} = \frac{1}{T\bar{x}} \sum_{t=0}^{T-1} |x_{t+1} - x_t|, \quad (4)$$

where  $\bar{x}$  is the mean population size over a period of  $T$  time steps. The FR is the difference between the maximum and minimum population sizes over a period of  $T$  time steps. Finally, the CV is a standardized measure of the dispersion in the population size obtained as the ratio of the standard deviation to the mean of the population size over a period of  $T$  time steps. Constancy stability of a population is inversely related to the magnitude of fluctuation in size it shows across time. Thus, decreases in any of these three measures are associated with enhancements in the constancy stability.

Given a combination of control intensities  $(c, h)$ , we evaluate the above three measures for Eq. (3) averaged over series of  $T = 30$  time steps and over 500 replicates with random initial conditions in  $(0, M]$ , where  $M$  is the maximum population production. To study the statistical significance of the differences in the considered measures, we conduct  $t$ -tests for the comparison of their means for different combinations of control intensities. We focus on the differences between the cases in which the populations are managed by harvesting only ( $c = 0$ ) or restocking only ( $h = 0$ ) and the cases in which they are managed by a certain combination of harvesting and restocking ( $c, h \neq 0$ ). Given a constancy measure  $m \in \{\text{FR}, \text{FI}, \text{CV}\}$  and a fixed harvesting intensity  $h = h_0$ , we denote by  $p_{h=h_0}(c)$  the  $p$ -value of the  $t$ -test for the comparison of means of  $m$  between the case in which the population is managed with control intensities  $(0, h_0)$  and the case in which it is managed with control intensities  $(c, h_0)$ . Similarly, for a fixed restocking intensity  $c = c_0$ , we denote by  $p_{c=c_0}(h)$  the  $p$ -value for the comparison of means of  $m$  between the cases given by control intensities  $(c_0, 0)$  and  $(c_0, h)$ . The significance level is set at 0.05 and all statistical analyses are performed with IBM® SPSS Statistics 23 for Windows®.

### 2.2.2. CALC of a host–pathogen–predator model

The second model to be considered was introduced by Dwyer et al. (2004) and used by Segura et al. (2017) to study the effectiveness of ALC and ATH in the prevention of population outbreaks. This model incorporates the effect of generalist predators (i.e., as a constant parameter) in a classical host–pathogen system and its non-dimensionalized stochastic version reads

$$\begin{aligned} 1 - I(x_t, z_t) &= \left(1 + \frac{1}{k}(x_t I(x_t, z_t) + z_t)\right)^{-k}, \\ x_{t+1} &= \lambda x_t (1 - I(x_t, z_t)) \left(1 - \frac{2ABx_t}{B^2 + x_t^2}\right) \varepsilon_t, \\ z_{t+1} &= \phi x_t I(x_t, z_t), \end{aligned} \quad (5)$$

where the two variables  $x_t$  and  $z_t$  represent the host and pathogen densities in generation  $t$ , respectively. Given these densities,  $I(x_t, z_t)$  is the fraction of infected hosts. The term  $\varepsilon_t$  introduces stochasticity and is a log-normal random variable with median 1. Parameter  $\lambda$  represents the net host fecundity,  $\phi$  is the between-season impact of the pathogen,  $A$  is the maximum fraction of hosts killed by the predator,  $B$  is the ratio of the density at maximum predation to the epidemic threshold and  $k$  is the

inverse squared coefficient of variation of the transmission rates, which follows a gamma distribution. Parameter values have been estimated for populations of the gypsy moth *Lymantria dispar* as the host (defoliator) and a baculovirus as the pathogen, yielding  $\lambda = 74.6$ ,  $\phi = 20$ ,  $A = 0.967$ ,  $B = 0.14$ , and  $k = 1.06$  (Dwyer et al., 2004). For these values, the deterministic model has three equilibria with high, intermediate and low defoliator densities. The high-density equilibrium is unstable and induces an oscillatory attractor, and on this attractor the defoliator is regulated by the pathogen while the predator is relatively unimportant. The intermediate-density equilibrium is also unstable. Finally, the low-density equilibrium is stable and the defoliator is regulated by the predators, with the influence of the pathogen being fairly irrelevant. The inclusion of stochasticity makes the defoliator density move unpredictably among attractors and induces high variability in the time between insect outbreaks.

Here, we consider management actions of the state variable  $x_t$  only. Then, the model including CALC with control intensities  $(c, h) \in [0, 1) \times [0, 1)$  is obtained by modifying the second equation of (5) to

$$x_{t+1} = \begin{cases} \max \{ \min \{ J(\lambda, A, B, x_t, z_t), x_t/h \}, c \cdot x_t \} \varepsilon_t, & h > 0, \\ \max \{ J(\lambda, A, B, x_t, z_t), c \cdot x_t \} \varepsilon_t, & h = 0, \end{cases}$$

where  $J(\lambda, A, B, x, z) := \lambda x(1 - I(x, z)) \left( 1 - \frac{2ABx}{B^2 + x^2} \right)$ .

With this equation, we calculate the probability of defoliator outbreaks as follows. We assume that the system is in the basin of attraction of the low-density attractor of (5), namely  $x_0 = 0.2516$  and  $z_0 = 11.6420$ . The maximum defoliator density for the deterministic attractors of (5) is approximately 44, and we will assume that an outbreak happens in generation  $t$  when the defoliator density  $x_t$  exceeds 35. The probability of these events is calculated for time series of length 50 and averaged over 5000 replicates.

### 3. Constancy stability

In this section, we study if the combination of restocking and harvesting can bring any benefit in terms of the constancy stability of populations managed by CALC compared to the cases of harvesting only and restocking only. We consider stochastic overcompensatory populations that are modeled by (3) in two different scenarios.

#### 3.1. Scenario 1: adding restocking to harvesting

In this subsection, we study if the addition of restocking to harvesting reduces the FI, FR or CV of the managed populations. Let us start by studying the FR. As can be observed in Fig. 4a, for  $h \lesssim 0.45$  the FR decreases as the restocking intensity increases, while for higher values of  $h$  such a reduction is not observed for low restocking intensities ( $c = 0.1$ ). This suggests that for a given harvesting intensity the addition of restocking entails a significant reduction in the FR only if the restocking intensity is above a certain threshold. We will see that the same is true for both the FI and the CV. In view of this and for easy reference, we denote by  $c_m(h)$  the restocking intensity threshold that must be exceeded for a given harvesting intensity  $h$  to obtain a significant reduction in the constancy measure  $m \in \{FR, FI, CV\}$  with respect to the case of only harvesting ( $c = 0$ ). The term “significant” is used here following statistical criteria (for more details, see Section 2). Table 1 shows the statistical analysis of the aforementioned differences in the constancy measures and lists the values of  $c_m(h)$  for different harvesting intensities within the ranges considered throughout this study (for other values in these ranges similar results were obtained, but they are not shown

here). Table 1 confirms that for  $h \lesssim 0.45$  and with respect to the case of only harvesting the reduction in the FR obtained with the inclusion of restocking is statistically significant even if the restocking intensity is very low, so that in this case  $c_{FR}(h) \leq 0.1$ . For higher values of  $h$ , reductions in the FR are only significant for higher restocking intensities since in this case  $c_{FR}(h) \in (0.1, 0.4]$ .

Let us now consider the FI. Fig. 4b shows that for harvesting of low intensity  $h \lesssim 0.15$  the addition of restocking of low intensity ( $c = 0.1$ ) increases the FI. For harvesting intensities  $0.15 \lesssim h \lesssim 0.3$ , the inclusion of restocking significantly reduces the FI even for very low restocking intensities ( $c_{FI}(h) \leq 0.1$ ; see Fig. 4b and Table 1). For  $0.3 \lesssim h \lesssim 0.9$ , significant reductions in the FI are only reached at higher restocking intensities ( $c_{FI}(h) \in (0.1, 0.4]$ ; see Fig. 4b and Table 1). For very high harvesting intensities  $h \gtrsim 0.9$ , significant reductions in the FI are again observed from very low restocking intensities onward ( $c_{FI}(h) \leq 0.1$ ; see Fig. 4b and Table 1).

Finally, let us study the CV. For  $h \lesssim 0.85$ , the behavior of this measure is similar to the one observed for the FR (see Fig. 4c and Table 1). Above this range, increasing the harvesting intensity increases the CV for populations managed by only harvesting. Interestingly, the inclusion of restocking nullifies this effect from low restocking intensities onward.

#### 3.2. Scenario 2: adding harvesting to restocking

Now we study the same measures of constancy stability in the case in which harvesting is added to restocking. As in the previous scenario, significant reductions in the FR, FI or CV are reached only when the harvesting intensity is above a certain threshold  $h_m(c)$ , which depends on the constancy measure  $m \in \{FR, FI, CV\}$  and the restocking intensity  $c$  (see Fig. 4d–f and Table 1). Yet, the behavior of the three constancy measures is in this case similar—cutbacks in any of them due to the inclusion of harvesting require higher harvesting intensities for higher restocking intensities.

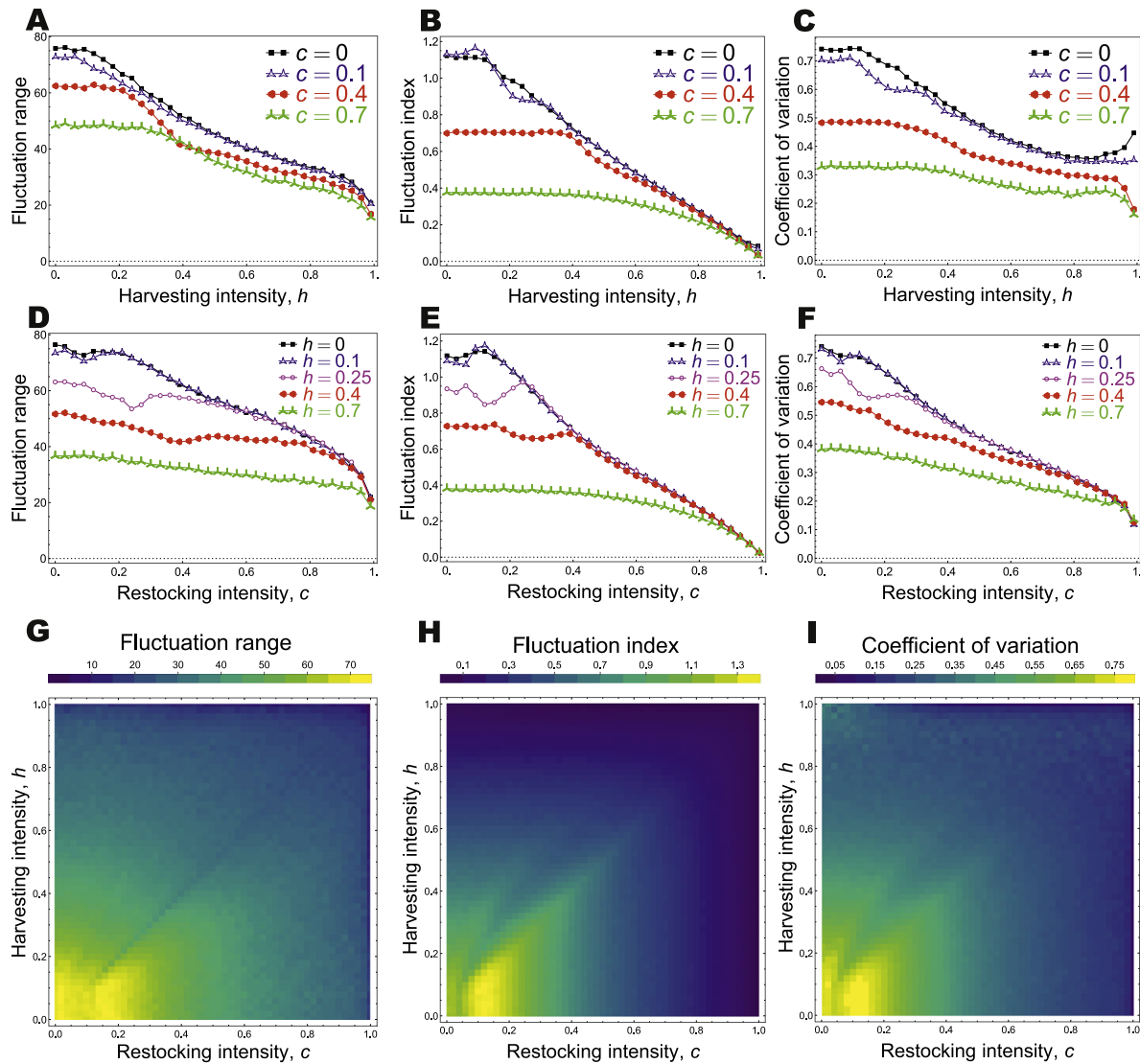
In summary, the combination of harvesting and restocking enhances the constancy stability of the managed populations in comparison to the cases of restocking only or harvesting only whenever the control intensities are high enough. This is further supported by the two-parameter diagrams in Fig. 4g–i, where we vary both restocking and harvesting intensities. Here we can observe that if  $c$  (respectively  $h$ ) is large enough, all three constancy stability measures are enhanced in comparison to the absence of restocking (respectively harvesting) for all  $h$  (respectively  $c$ ).

## 4. Population outbreaks

In this section we study the capability of CALC to prevent outbreaks in the population size. Moreover, we analyze the trade-off between the reduction in the risk of population outbreaks and the cost of the intervention. We consider the host–pathogen–predator model (5).

### 4.1. Outbreak risk

Population outbreaks are inherent to forest-defoliating insects, for which the population size may rest in a low-density state for several generations until some perturbation makes it burst to a higher-density attractor. Usually, management strategies aimed at avoiding pest outbreaks are based on only harvesting the population. In this section, we study if in the case of CALC the combination of such strategies with restocking may enhance the capability of the control to contain the population size. Specifically, we study the effect of CALC on the probability of outbreak for model (5). The results are shown in Fig. 5a–b. For low harvesting intensities ( $h \lesssim 0.3$ ) restocking defoliators reduces the



**Fig. 4.** Constancy stability measures for the stochastic overcompensatory population model (3) for varying harvesting and restocking intensities ( $h$  and  $c$ , respectively). All values were obtained for time series of length 30 and averaged over 500 replicates (a–f) or 200 replicates (g–i) for which the population persisted. The initial population sizes were chosen as pseudo-random real numbers in  $(0, M]$ , where  $M$  is the maximum population production.

probability of outbreaks whenever the restocking intensity is not too high ( $c \lesssim 0.8$ ). Therefore, in that case harvesting and restocking defoliators is more effective for the prevention of outbreaks than the strategy based only on their removal. Yet, this is not always the case. For medium and high harvesting intensities ( $h \gtrsim 0.3$ ), restocking defoliators is never beneficial for the prevention of outbreaks in their population density. Interestingly, which is also somehow counter-intuitive, for high removal intensities restocking even a small proportion of the density of defoliators in the previous generation promotes outbreaks in their population. A potential explanation for this behavior lies in the fact that new uninfected defoliators would be added and a large number of infected defoliators would be removed from the defoliator population at high harvesting intensities, which could be highly destabilizing.

In summary, if we can manage the defoliator with only a low harvesting intensity, then it is beneficial to combine harvesting with restocking. On the contrary, if we are able to implement harvesting with a high intensity, then it seems better to not restock the defoliator.

#### 4.2. Intervention cost

The previous analysis does not take into account that interventions always have a cost. In this sense, from a management perspective, the control strategies that are the most effective at reaching a specific goal may not be the best option if they come at a higher cost. Thus, a trade-off between the goals that are reached and the cost of the intervention must be considered. Here, we study the benefit that is obtained with CALC in terms of the reduction of the risk of outbreaks. Undoubtedly, this is an extremely ambiguous concept that requires the monetarization of both the goal that is reached and the cost of the intervention, which could be done in many different ways. We consider a proxy in which the cost is measured in terms of the restocking and harvesting frequencies. In the following analysis we consider that management has a fixed “budget” for control interventions, which can be partitioned into harvesting and restocking. The sum of harvesting and restocking intensities is thus constant—here we assume  $c + h = 1$ . With  $c = \lambda$  and  $h = 1 - \lambda$ , where  $\lambda \in [0, 1]$ , we see that  $\lambda = 0$  means only harvesting,  $\lambda = 1$  only restocking and intermediate values some combination. We therefore refer to  $\lambda$  as the *harvesting–restocking balance*. Note

**Table 1**

Statistical analysis of the differences in the fluctuation index (FI), fluctuation range (FR) and coefficient of variation (CV) of the stochastic overcompensatory population model (3) in the two different scenarios and for various combinations of control intensities. See Section 2 for more details.

Scenario 1: adding restocking to harvesting			
<i>h</i>		<i>p</i> -values	Restocking intensity threshold
<i>h</i> = 0.21	FR	$p_{h=0.21}(0.1) \approx 0^*$	$c_{FR}(0.21) \leq 0.1$
	FI	$p_{h=0.21}(0.1) \approx 0^*$	$c_{FI}(0.21) \leq 0.1$
	CV	$p_{h=0.21}(0.1) \approx 0^*$	$c_{CV}(0.21) \leq 0.1$
<i>h</i> = 0.51	FR	$p_{h=0.51}(0.1) = 0.572, p_{h=0.51}(0.4) \approx 0^*$	$c_{FR}(0.51) \in (0.1, 0.4]$
	FI	$p_{h=0.51}(0.1) = 0.881, p_{h=0.51}(0.4) \approx 0^*$	$c_{FI}(0.51) \in (0.1, 0.4]$
	CV	$p_{h=0.51}(0.1) = 0.018^*$	$c_{CV}(0.51) \leq 0.1$
<i>h</i> = 0.75	FR	$p_{h=0.75}(0.1) = 0.676, p_{h=0.75}(0.4) \approx 0^*$	$c_{FR}(0.75) \in (0.1, 0.4]$
	FI	$p_{h=0.75}(0.1) = 0.426, p_{h=0.75}(0.4) \approx 0^*$	$c_{FI}(0.75) \in (0.1, 0.4]$
	CV	$p_{h=0.75}(0.1) = 0.143, p_{h=0.75}(0.4) \approx 0^*$	$c_{CV}(0.75) \in (0.1, 0.4]$
<i>h</i> = 0.84	FR	$p_{h=0.84}(0.1) = 0.668, p_{h=0.84}(0.4) \approx 0^*$	$c_{FR}(0.84) \in (0.1, 0.4]$
	FI	$p_{h=0.84}(0.1) = 0.939, p_{h=0.84}(0.4) \approx 0^*$	$c_{FI}(0.84) \in (0.1, 0.4]$
	CV	$p_{h=0.84}(0.1) = 0.215, p_{h=0.84}(0.4) \approx 0^*$	$c_{CV}(0.84) \in (0.1, 0.4]$
<i>h</i> = 0.93	FR	$p_{h=0.93}(0.1) = 0.201, p_{h=0.93}(0.4) \approx 0^*$	$c_{FR}(0.93) \in (0.1, 0.4]$
	FI	$p_{h=0.93}(0.1) = 0.024^*$	$c_{FI}(0.93) \leq 0.1$
	CV	$p_{h=0.93}(0.1) = 0.014^*$	$c_{CV}(0.93) \leq 0.1$
Scenario 2: adding harvesting to restocking			
<i>c</i>		<i>p</i> -values	Harvesting intensity threshold
<i>c</i> = 0.21	FR	$p_{c=0.21}(0.1) = 0.550, p_{c=0.21}(0.25) \approx 0^*$	$h_{FR}(0.21) \in (0.1, 0.25]$
	FI	$p_{c=0.21}(0.1) = 0.787, p_{c=0.21}(0.25) \approx 0^*$	$h_{FI}(0.21) \in (0.1, 0.25]$
	CV	$p_{c=0.21}(0.1) = 0.543, p_{c=0.21}(0.25) \approx 0^*$	$h_{CV}(0.21) \in (0.1, 0.25]$
<i>c</i> = 0.51	FR	$p_{c=0.51}(0.1) = 0.839, p_{c=0.51}(0.25) = 0.005^*$	$h_{FR}(0.51) \in (0.1, 0.25]$
	FI	$p_{c=0.51}(0.25) = 0.497, p_{c=0.51}(0.4) \approx 0^*$	$h_{FI}(0.51) \in (0.25, 0.4]$
	CV	$p_{c=0.51}(0.25) = 0.403, p_{c=0.51}(0.4) \approx 0^*$	$h_{CV}(0.51) \in (0.25, 0.4]$
<i>c</i> = 0.75	FR	$p_{c=0.75}(0.25) = 0.550, p_{c=0.75}(0.4) \approx 0^*$	$h_{FR}(0.75) \in (0.25, 0.4]$
	FI	$p_{c=0.75}(0.25) = 0.195, p_{c=0.75}(0.4) \approx 0^*$	$h_{FI}(0.75) \in (0.25, 0.4]$
	CV	$p_{c=0.75}(0.25) = 0.972, p_{c=0.75}(0.4) \approx 0^*$	$h_{CV}(0.75) \in (0.25, 0.4]$
<i>c</i> = 0.84	FR	$p_{c=0.84}(0.25) = 0.874, p_{c=0.84}(0.4) \approx 0^*$	$h_{FR}(0.84) \in (0.25, 0.4]$
	FI	$p_{c=0.84}(0.4) = 0.092, p_{c=0.84}(0.7) \approx 0^*$	$h_{FI}(0.84) \in (0.4, 0.7]$
	CV	$p_{c=0.84}(0.25) = 0.306, p_{c=0.84}(0.4) = 0.032^*$	$h_{CV}(0.84) \in (0.25, 0.4]$
<i>c</i> = 0.93	FR	$p_{c=0.93}(0.4) = 0.145, p_{c=0.93}(0.7) \approx 0^*$	$h_{FR}(0.93) \in (0.4, 0.7]$
	FI	$p_{c=0.93}(0.4) = 0.681, p_{c=0.93}(0.7) \approx 0^*$	$h_{FI}(0.93) \in (0.4, 0.7]$
	CV	$p_{c=0.93}(0.4) = 0.729, p_{c=0.93}(0.7) = 0.019^*$	$h_{CV}(0.93) \in (0.4, 0.7]$

\*Statistically significant at level 0.05.

that due to this assumption we have reduced the number of free control parameters from two to one, which simplifies the analysis.

Under the above assumption, we consider the function

$$B(\lambda, v_1, v_2, v_3) = \underbrace{v_1(P_u - P_c(\lambda))}_{\text{revenue}} - \underbrace{(v_2 \cdot F_R(\lambda) + v_3 \cdot F_H(\lambda))}_{\text{cost}}, \quad (6)$$

where *B* is the benefit function and  $P_u, P_c(\lambda), F_R(\lambda)$  and  $F_H(\lambda)$  respectively represent the probability of outbreak for the uncontrolled and controlled populations and the restocking and harvesting intervention frequencies of CALC for control intensities  $c = \lambda$  and  $h = 1 - \lambda$ , with  $\lambda \in [0, 1]$ . Parameter  $v_1$  represents the unitary revenue that corresponds to the monetarization of the reduction in the probability of outbreak, while  $v_2$  and  $v_3$  represent the unitary cost of harvesting and restocking interventions, respectively.

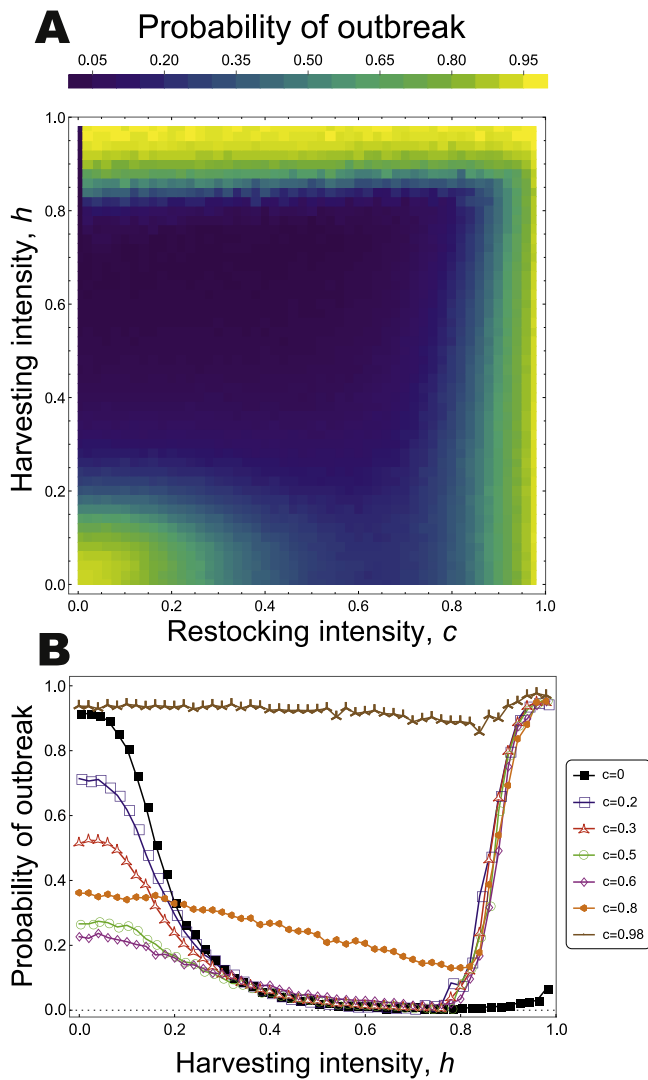
We rescale (6) by setting  $v_1 = 1$ . Our goal is to study which combination of parameters yields the maximum benefit, which naturally depends on which type of intervention (restocking or harvesting) is more costly. In this sense, we can set  $v_2$  at a fixed value (for instance,  $v_2 = 1$ ) and study the benefit for  $v_3 > 1$  (harvesting more costly than restocking),  $v_3 = 1$  (harvesting and restocking equally costly) and  $v_3 < 1$  (restocking more costly than harvesting). For these values, Fig. 6 shows the graphical representation of (6) in terms of  $\lambda$  for different values of  $v_3$ . When harvesting is less costly than restocking ( $v_3 = 1/4$ ), the maximum benefit is reached when the harvesting intensity is higher than the restocking intensity ( $\lambda < 0.5$ ). As the cost of harvesting

increases, the peak of the benefit curve moves to the right, which means increasing the restocking intensity and decreasing the harvesting intensity. When restocking and harvesting are equally costly ( $v_3 = 1$ ), the maximum benefit is reached when the two control intensities are approximately equal, i.e.,  $\lambda \approx 0.5$ . Finally, when harvesting is more costly than restocking the maximum benefit is reached for a restocking intensity higher than the harvesting intensity ( $v_3 = 4$ ). The same behavior is observed when  $v_2$  is set at other values different from 1 (not shown here).

As already mentioned, similar analyses could be performed by considering different criteria for the definition of the benefit of the intervention. A similar analysis could also be performed for model (3) by considering the trade-off between the reduction in either the FI, FR or CV and the intervention costs. The example considered here does not pretend to be representative of all of them, but shows that choosing the values of the control intensities depends on the formulation of the cost function, and in the cases considered here the intervention costs play a role.

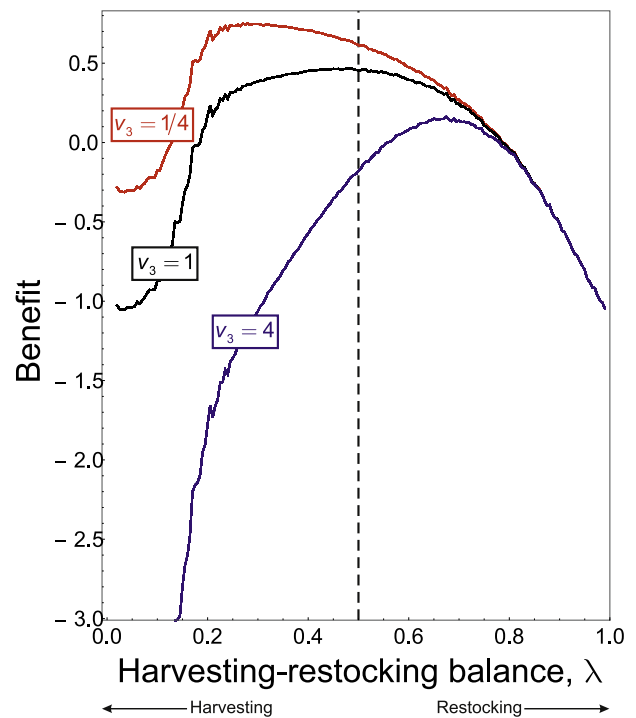
### 5. Discussion and conclusions

We have introduced CALC as a strategy for the management of biological populations that combines restocking and harvesting according to two already known techniques, namely ALC and ATH. This new strategy has not been previously considered in the literature and constitutes a general framework for adaptive limiters, since it includes the existing methods ALC and ATH as particular cases.



**Fig. 5.** Probability of insect outbreak for the host–pathogen–predator model (5). The initial conditions for defoliator and pathogen are  $x_0 = 0.2516$  and  $z_0 = 11.6420$ , respectively. Outbreaks are assumed to occur when the defoliator density exceeds 35, and their probability is calculated by estimating the frequency of their occurrence in time series of length 50 over 5000 replicates.

The main goal of this paper has been to study the advantages that combining restocking and harvesting may have over restocking only and harvesting only. To that end, we have considered two different population models. The first is a stochastic overcompensatory model, for which we have analyzed the constancy stability of the managed populations by considering three different measures of this property, namely the fluctuation index, the fluctuation range and the coefficient of variation. In our case, all these measures showed the same trend: the constancy stability of the managed populations is improved when harvesting and restocking are combined, provided the harvesting and restocking intensities are high enough. More specifically, complementing restocking (respectively harvesting) with harvesting (respectively restocking) enhances the constancy stability of the managed populations if the harvesting (respectively restocking) intensity is above a certain critical value, which depends on the constancy measure and the restocking (respectively harvesting) intensity that are considered. Below this critical value, the impact of combining restocking and harvesting on the constancy stability is in most cases negligible and in rare cases negative. The latter is the



**Fig. 6.** Graphical representation of the benefit of managing the host–pathogen–predator system by CALC, as given by (6), in terms of the restocking–harvesting balance  $\lambda$ , with  $c = \lambda$ ,  $h = 1 - \lambda$  and  $\lambda \in [0, 1]$ . For all curves,  $v_1$  and  $v_2$  are set at 1. Parameter  $v_3$  represents the proportion of the cost of harvesting to the cost of restocking. The vertical dashed line corresponds to  $\lambda = 0.5$ .

case of the FI, whose value can be increased by the combination of harvesting and restocking when the intensities of each are low. Such a behavior in the FI for low intensities was previously reported for both ALC (Franco and Hilker, 2013) and ATH (Segura et al., 2016). Interestingly, contrary to other methods that combine harvesting and restocking like BLC or TOC (Tung et al., 2016b), the improvement in the constancy stability obtained by that combination is in the case of CALC observed for relatively low control intensities (cf. Fig. 4 and Table 1). This case is especially interesting because achieving high control intensities may be unfeasible due to the cost of the intervention, to logistical issues or to the unavailability of a high number of individuals to be restocked.

When the goal is to prevent outbreaks in the population size, we have shown that combining harvesting with restocking under CALC can also be beneficial. Yet, again, this depends on the control intensities. If outbreaks are to be controlled by harvesting of low intensity ( $h \lesssim 0.3$ ), combining this strategy with restocking of not very high intensity ( $c \lesssim 0.8$ ) helps to contain the population size. On the contrary, if outbreaks are to be controlled by harvesting of intermediate or high intensity ( $h \gtrsim 0.3$ ), restocking individuals with any intensity is either ineffective or counterproductive. Special care must be taken in the case of harvesting of high intensity ( $h \gtrsim 0.8$ ), for which the combination with restocking, even of very low intensity, clearly promotes population outbreaks. We wish to stress that we are not aware of an example where pest species have been actually restocked in the field and that we would expect resistance to this approach in real applications. We only know of the laboratory experiments in Tung et al. (2016b).

As a method that combines ATH and ALC, the stabilizing properties of CALC could be expected to be similar to those already observed separately for ATH and ALC. In fact, we have extended the stability results for ATH and ALC to CALC (Appendix B.2).



We have shown that for unimodal maps the stabilizing effect of CALC is attained by asymptotically trapping the population size in an interval around the carrying capacity of the population. We have provided analytical expressions for the endpoints of this interval in terms of the harvesting and restocking intensities. Moreover, we have shown that when CALC combines restocking and harvesting with high enough intensities there exist activation thresholds that inform us in advance of the need of intervention in the following time step.

Several papers put forward the idea that the advantage of combining restocking and harvesting depends on multiple factors, especially on the economic side (Bell et al., 2006, 2008; Lorenzen, 2005, 2008). With a particular example, we have studied the trade-off between the stabilizing goals that are reached with the application of CALC and the cost of the intervention. This allows us to conclude that the decision about appropriate control intensities for CALC cannot be exclusively based on stability criteria. In this sense, we draw attention to the fact that we should not only focus on theoretical or numerical results predicting a certain stabilizing effect, but on the benefit that is expected to be obtained with the intervention. While allowing us to conclude that the decision about the “best” combination of control intensities is not trivial, our approach is very simplistic. For instance, in coastal fisheries, there is great controversy about the appropriateness of combining fishing and restocking. It is known that few restocking or stock enhancement programmes have succeeded because many other aspects different from stability issues have not been taken into account, as can be the necessity of the intervention or the integration of technology with the participation and understanding of the stakeholders by means of an appropriate management scheme (Bell et al., 2006).

**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.

**Acknowledgments**

D. Franco was supported by grant 2019-MAT11 (UNED-ETSI Industriales, Spain). D. Franco and J. Segura were supported by grant MTM2017-85054-C2-2-P (AEI, Spain/FEDER, Spain, UE). J. Segura acknowledges funding from Osnabrück University to visit the Institute of Environmental Systems Research for a period of two months, during which parts of the research were conducted.

**Appendix A. Modeling CALC**

Assume that  $b_t$  denotes the population size at time step  $t$  before the control intervention and  $a_t$  the population size after intervention. The dynamics of populations subject to CALC are given by the equations

$$\begin{aligned}
 b_{t+1} &= f(a_t), \\
 a_{t+1} &= \begin{cases} c \cdot a_t, & b_{t+1} < c \cdot a_t, \\ b_{t+1}, & c \cdot a_t \leq b_{t+1} \leq a_t/h, \\ a_t/h, & b_{t+1} > a_t/h, \end{cases} \tag{A.1}
 \end{aligned}$$

where  $f$  is the production function or stock–recruitment curve of the uncontrolled population, and  $c, h \in (0, 1)$  are the restocking and harvesting intensities, respectively. Substituting the value of  $b_{t+1}$  into the second equation of (A.1), the dynamics

of populations subject to CALC are described by the piecewise one-dimensional difference equation

$$a_{t+1} = \begin{cases} c \cdot a_t, & f(a_t) < c \cdot a_t, \\ f(a_t), & c \cdot a_t \leq f(a_t) \leq a_t/h, \\ a_t/h, & f(a_t) > a_t/h, \end{cases}$$

which can be rewritten in a single line as

$$a_{t+1} = \max\{\min\{f(a_t), a_t/h\}, c \cdot a_t\}. \tag{A.2}$$

**Appendix B. CALC of unimodal maps**

Both ALC and ATH were originally stated and investigated for unimodal maps. In this section, we extend the theoretical results about their effect on the population stability to the case of CALC.

The unimodal maps that we consider are described by the following conditions:

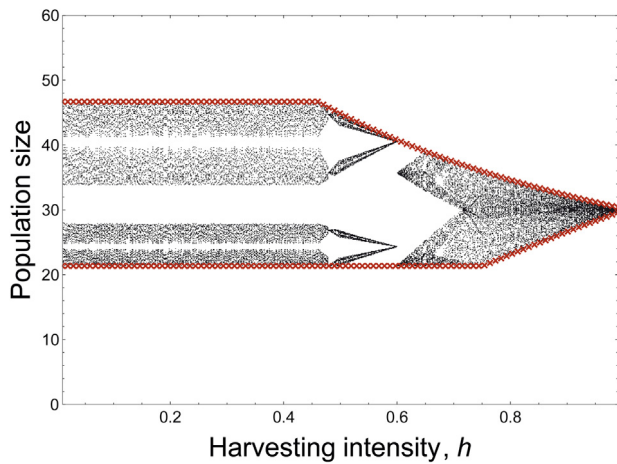
- (C1)  $f : [0, b] \rightarrow [0, b]$  ( $b = \infty$  is allowed) is continuously differentiable and such that  $f(x) > 0$  for all  $x \in (0, b)$  and  $f'(0^+), f'(b^-) \in \mathbb{R}$ .
- (C2)  $f$  has two non-negative fixed points  $x = 0$  and  $x = K > 0$ , with  $f(x) > x$  for  $0 < x < K$  and  $f(x) < x$  for  $x > K$ .
- (C3)  $f$  has a unique critical point  $d \in (0, K)$  in such a way that  $M = f(d) \leq b, f'(x) > 0$  for all  $x \in (0, d)$  and  $f'(x) < 0$  for all  $x \in (d, b)$ .

**Remark 1.** The above conditions are standard in the literature to describe unimodal maps and were also used in the study of the stabilizing properties of both ALC (Franco and Hilker, 2013) and ATH (Segura et al., 2016). We want to stress that imposing differentiability facilitates the description of these maps, but it is not a necessary condition in most of the results about ALC, ATH or in those that follow for CALC whenever the unimodal character of the map is not altered.

**B.1. Activation thresholds**

Given the adaptive character of CALC, managers implementing this control method are supposed to wait until measurements of the population size have been taken to conclude about the need of the intervention. However, depending on the shape of the map that describes the underlying dynamics the control may induce activation thresholds in the controlled population that allow one to predict the need of intervention in the following generation. This is the case for maps satisfying (C1)–(C3). For these maps, the activation threshold of harvesting (which we denote by  $A_H$ ) exists for  $h > \inf_{x \in (0, b)} x/f(x)$  and corresponds to the abscissa of the leftmost nonzero intersection of the curve  $y = f(x)$  and  $y = x/h$ . No harvesting will be necessary in generation  $t$  if the population size in the preceding generation is above  $A_H$  (Segura et al., 2016). Moreover, if  $f$  is concave downward in  $(0, d)$  (which is true for many unimodal maps, e.g., Ricker) the population is culled in generation  $t$  if its size in the previous generation was below  $A_H$  (cf. Fig. 2). Similarly, the activation threshold for restocking (which we denote by  $A_R$ ) exists for  $c > f(b)/b$  and corresponds to the abscissa of the unique nonzero intersection of the curve  $y = f(x)$  and  $y = c \cdot x$ . Restocking only takes place if  $A_R$  was exceeded in the preceding generation (Franco and Hilker, 2013). Given that  $c < 1 < 1/h$ , when both  $A_H$  and  $A_R$  exist they are always different and satisfy  $A_H < K < A_R$  (cf. Fig. 2).

The determination of  $A_R$  and  $A_H$  for a given combination of control parameters requires knowing the production function of the uncontrolled population, which can be obtained from fitting to time series data. It should be noticed that in the case of lack of information about the system or in presence of very



**Fig. B.1.** Bifurcation diagram of (2) with  $c = 0.6$  and varying  $h$ . The underlying population dynamics are given by the Ricker map  $f(x) = x \exp(r(1 - x/K))$  with  $r = 2.7$  and  $K = 30$ . Initial population sizes were obtained as pseudo-random real numbers in the interval  $(0, M]$ . For each initial condition, black dots represent 30 generations of the population subject to CALC after a transient of 10,000 time steps. Red crosses correspond to the limits of the trapping region given by Proposition 2.

strong noise this determination can be difficult. However, for deterministic systems, the knowledge of these thresholds helps managers to know early on if an intervention is necessary in the next generation.

**B.2. Trapping interval**

The following results summarize the stabilizing properties of CALC. We start by proving that the effect of the control does not stabilize any equilibrium point.

**Proposition 1.** Assume that (C1)–(C3) hold and that the carrying capacity  $K$  is an unstable equilibrium of the uncontrolled system. Then, independent of the magnitude of CALC,  $(c, h) \in [0, 1) \times [0, 1)$ , the controlled system has no asymptotically stable equilibria.

**Proof.** Denote  $h_0 = \inf_{x \in (0, b)} x/f(x)$ . For  $(c, h) \in [0, f(b)/b] \times (h_0, 1)$ , restocking is never activated and the control corresponds to ATH, which has no asymptotically stable equilibria (Segura et al., 2016, Proposition 2). The same is true for  $(c, h) \in (f(b)/b, 1) \times [0, h_0]$ , in which case harvesting is never activated and the control corresponds to ALC (Franco and Hilker, 2013, Proposition 2). For the remaining control intensities,  $(c, h) \in (f(b)/b, 1) \times (h_0, 1)$ , CALC combines both restocking and harvesting. Clearly,  $(x, y) \in [0, b] \times [0, b]$  is an equilibrium of the controlled system (A.1) if and only if

$$\begin{cases} x = f(y), \\ y = \max\{\min\{x, y/h\}, c \cdot y\}. \end{cases} \tag{B.1}$$

Since  $c, h < 1$ , the second equation of (B.1) yields  $y = x$ , and thus  $y = f(y)$ . Therefore, the controlled system (A.1) only has  $(0, 0)$  and  $(K, K)$  as equilibrium points. According to Segura et al. (2016, Proposition 1), for  $h > h_0$  the activation threshold  $A_H$  exists. Consider the neighborhood of  $(0, 0)$  given by  $U = (0, A_H) \times (0, A_H)$  and assume that  $(a_t, b_t) \in U$  for all  $t \geq 0$ . Given that  $f(x) > x/h$  for  $x \in (0, A_H)$ ,  $a_{t+1} = \max\{a_t/h, c \cdot a_t\} = a_t/h$  for all  $t \geq 0$ , and thus  $a_t = (1/h)^t \cdot x_0$ . Consequently,  $a_t \rightarrow +\infty$ , which contradicts the hypothesis and proves that  $(0, 0)$  is unstable.

Let us now prove that  $(K, K)$  is also unstable. Since  $f$  is continuous and  $c \cdot K < K = f(K) < K/h$ , there exists a neighborhood

$V$  of  $K$  such that  $c \cdot x < f(x) < x/h$  for all  $x \in V$ . Assume that  $(a_t, b_t) \in V \times V$  for all  $t \geq 0$ . Then,  $a_{t+1} = f(a_t)$  for all  $t \geq 0$ , and thus  $a_t = f^t(x_0)$ . Since  $K$  is an unstable equilibrium for the uncontrolled system, this last equality contradicts the hypothesis and proves that  $(K, K)$  is unstable.  $\square$

The following result shows that the stabilizing effect of CALC is attained by asymptotically trapping the population size within an interval around the carrying capacity. Moreover, it provides analytical expressions in terms of the control parameters for the endpoints of this interval, which are shown in Fig. B.1 together with a bifurcation diagram.

**Proposition 2.** Assume that (C1)–(C3) hold and  $(c, h) \in (0, 1) \times (0, 1)$  are such that the activation thresholds  $A_R$  and  $A_H$  exist. Then, applying CALC with intensities  $(c, h)$  asymptotically confines the population sizes  $a_t$  for any  $a_0 \in (0, b)$  within an interval  $I_a = [l(c, h), u(c, h)]$  around the positive equilibrium  $K$ , with endpoints given by the expressions

$$l(c, h) = \begin{cases} \max\{c \cdot A_R, f(A_H/h)\}, & d \leq A_H, \\ \max\{f^2(d), c \cdot A_R\}, & d > A_H, \end{cases} \tag{B.2}$$

$$u(c, h) = \begin{cases} \min\{f(c \cdot A_R), A_H/h\}, & d \leq c \cdot A_R, d \leq A_H, \\ A_H/h, & d > c \cdot A_R, d \leq A_H, \\ f(c \cdot A_R), & d \leq c \cdot A_R, d > A_H, \\ f(d), & d > c \cdot A_R, d > A_H. \end{cases} \tag{B.3}$$

**Proof.** Eq. (2) can be expressed as  $a_{t+1} = \max\{F_H(a_t), c \cdot a_t\}$ , where  $F_H: [0, b] \rightarrow [0, b]$  is given by  $F_H(x) = \max\{f(x), x/h\}$ . Thus, (2) can be considered as a system describing the dynamics of a population with production function  $F_H$  that is controlled by only restocking (ALC). One can check that  $F_H$  satisfies conditions (C1)–(C3) except for the existence of a point where this map is not differentiable. This does not affect our conclusion since the existence of such a point does not alter the unimodal character of the map. Moreover, one can check that there exists  $T_0 > 0$  such that  $F_H^2(d_H) \leq a_t \leq F_H(d_H)$  for all  $t \geq T_0$ , where  $d_H$  denotes the abscissa of the maximum of  $F_H$ . This, together with Franco and Hilker (2013, Theorem 1), leads to conclude that there exists  $T \geq T_0$  such that for  $t \geq T$  the population size  $a_t$  for any  $a_0 \in (0, b)$  is asymptotically trapped within an interval  $I_a = [l(c, h), u(c, h)]$  with endpoints given by the expressions

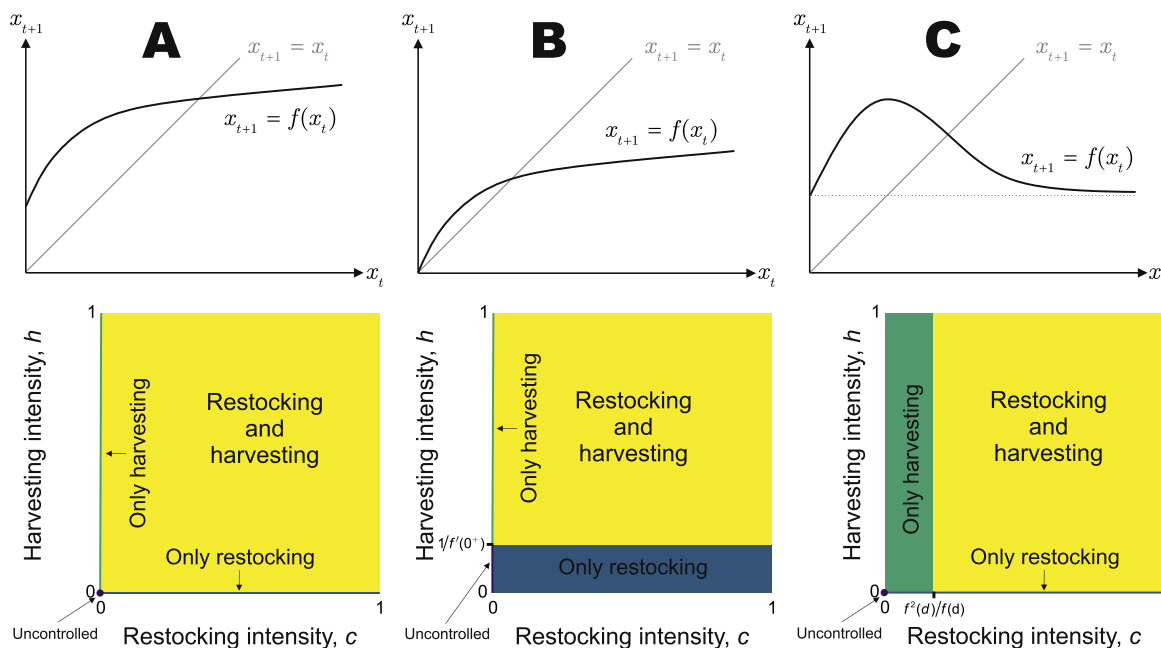
$$l(c, h) = \max\{F_H^2(d_H), c \cdot A_R\}, \tag{B.4}$$

$$u(c, h) = \begin{cases} F_H(c \cdot A_R), & d_H \leq c \cdot A_R, \\ F_H(d_H), & d_H > c \cdot A_R. \end{cases} \tag{B.5}$$

Assume that  $d > A_H$ . Then,  $d_H = d$  and  $F_H(d_H) = f(d)$ . Since  $f(d) > d > A_H$ , it follows that  $F_H^2(d_H) = F_H(f(d)) = f^2(d)$ . On the other hand, if  $A_H < d = d_H \leq c \cdot A_R$  then  $F_H(c \cdot A_R) = f(c \cdot A_R)$ . With this, all the results given in the statement for  $d > A_H$  follow.

Suppose now  $d \leq A_H$ . Then,  $d_H = A_H$  and  $F_H(d_H) = A_H/h$ . Since  $A_H/h > A_H$ , we conclude  $F_H^2(d_H) = F_H(A_H/h) = f(A_H/h)$ . This completes all the cases for  $l(c, h)$ . To derive the expression for  $u(c, h)$ , we consider two cases. If  $d > c \cdot A_R$ , then  $A_H > c \cdot A_R$  and  $u(c, h) = F_H(A_H) = A_H/h$ . If  $d \leq c \cdot A_R$ , then  $f$  is strictly decreasing in the interval defined by  $c \cdot A_R$  and  $A_H$ , being  $\min\{f(c \cdot A_R), f(A_H)\} = A_H/h = f(\max\{c \cdot A_R, A_H\})$ . For  $A_H > c \cdot A_R$ , we have  $u(c, h) = F_H(A_H) = f(A_H) = \min\{f(c \cdot A_R), A_H\}$ , and for  $A_H \leq c \cdot A_R$  it follows that  $u(c, h) = F_H(c \cdot A_R) = f(c \cdot A_R) = \min\{f(c \cdot A_R), A_H\}$ . This completes the proof.  $\square$

The analysis of the expressions for the endpoints of the trapping interval given in Proposition 2 reveals that harvesting does not affect the fluctuation range of the population when  $d \geq A_H$ . The reason for this is that in such a case the stock–recruitment



**Fig. C.1.** Type of intervention (restocking, harvesting or their combination) that corresponds to the effect of CALC on different production functions. For each column, the first row shows a production function  $f$  and the second row the corresponding distribution of the type of intervention in terms of the control intensities. Value  $f(d)$  is the maximum of the population production, achieved by populations with size  $d$ , and  $f^2 = f \circ f$ . In (c), the first generation was omitted in the only harvesting area.

curves of both controlled and uncontrolled populations have a common maximum  $f(d)$ . Consequently, if we want harvesting to reduce the fluctuation range with respect to the uncontrolled population, the harvesting intensity must be higher than  $d/f(d)$ .

### Appendix C. CALC for different production functions

In this section, we study the type of intervention (restocking, harvesting or their combination) that corresponds to CALC depending on the control parameters for different production functions of the uncontrolled population. We consider four cases.

First, we consider unimodal maps (e.g., Ricker), for which the CALC function is shown in Fig. 2. If  $d$  denotes the abscissa of the maximum production, after the first generation the population size is always below  $f(d)$ . Thus, for low enough values of  $c$  (namely,  $c \leq f^2(d)/f(d)$ , where  $f^2 = f \circ f$ ) and after the first generation, all possible interventions consist of harvesting only. Similarly, for low enough values of  $h$  (namely,  $h \leq 1/f'(0^+)$ ), the graph of  $f$  is below the straight line  $y = x/h$  for all values of  $x$ . Thus, in that case all possible interventions consist of restocking only. For  $c > f^2(d)/f(d)$  and  $h > 1/f'(0^+)$  the population can be either harvested or restocked depending on its size. Finally, for  $c \leq f^2(d)/f(d)$  and  $h \leq 1/f'(0^+)$ , the population remains uncontrolled. The distribution of the type of intervention (uncontrolled, restocking only, harvesting only or a mixture of harvesting and restocking) is represented in Fig. 3.

Second, we consider maps like the one represented in Fig. C.1a, which is compatible with the Beverton–Holt model with constant immigration. In this case, CALC leads to restocking for any  $c > 0$  and to harvesting for any  $h > 0$ . Consequently, restocking and harvesting are combined for  $(c, h) \in (0, 1) \times (0, 1)$ , only restocking is implemented for  $(c, h) \in (0, 1) \times \{0\}$ , only harvesting for  $(c, h) \in \{0\} \times (0, 1)$ , and the population remains uncontrolled for  $(c, h) = (0, 0)$ .

Third, for the production function shown in Fig. C.1b, which is compatible with the Beverton–Holt model, there is a threshold for harvesting given by  $h_0 = 1/f'(0^+)$ , while there is no threshold for restocking. Therefore, CALC leads to a combination of restocking

and harvesting for  $(c, h) \in (0, 1) \times (h_0, 1)$ , only restocking for  $(c, h) \in (0, 1) \times [0, h_0]$ , only harvesting for  $(c, h) \in \{0\} \times (h_0, 1)$ , and the population remains uncontrolled for  $(c, h) \in \{0\} \times [0, h_0]$ .

Finally, for the map shown in Fig. C.1c, which is compatible with the Ricker model (or any other unimodal map) with constant immigration, there is a restocking threshold  $c_0 = f^2(d)/f(d)$  and no harvesting threshold. In this case, restocking can act in the first generation for any restocking intensity, but the population is never supplemented in subsequent generations if  $c < c_0$ . Consequently, after the first generation harvesting and restocking are combined for  $(c, h) \in (c_0, 1) \times (0, 1)$ , only restocking for  $(c, h) \in (c_0, 1) \times \{0\}$ , only harvesting for  $(c, h) \in [0, c_0] \times (0, 1)$ , and the population remains uncontrolled for  $(c, h) \in [0, c_0] \times \{0\}$ .

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